LOYOLA UNIVERSITY CHICAGO

COMBINED EFFECTS OF INVASIVE *TYPHA* × *GLAUCA* AND *HYDROCHARIS MORSUS-RANAE* ON AQUATIC MACROINVERTEBRATES IN A LAKE HURON COASTAL MARSH

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ABSTRACT

Invasive wetland plants alter habitat structure and biogeochemical cycles as well as reduce plant biodiversity in the ecosystems they invade. Invasive hybrid cattail (*Typha* × *glauca*) is a widespread invader in Great Lakes coastal wetlands that produces large quantities of litter which reduce plant diversity and submerged vegetation cover. European Frogbit (*Hydrocharis morsus-ranae*; EFB) is a recent Great Lakes invasive macrophyte that forms dense floating mats with dangling roots. Invasive *Typha* reduces wind and wave energy which facilitates the invasion of EFB, which thrives in the *Typha* understory. The effects of EFB on macroinvertebrate communities are not well studied and have not been observed in the Great Lakes. To determine the effects of EFB invasion on macroinvertebrates, I surveyed vegetation and macroinvertebrates in meadow, submerged, *Typha*-dominant, and *Typha* and EFB codominant plant communities in Munuscong Bay, Michigan and compared macroinvertebrate biomass, diversity, and community composition using ANOVA and multivariate methods. EFB invasion increased total vegetation cover by nearly 50% compared to the *Typha* community and altered plant species composition. Despite vegetation differences, there were no significant differences in macroinvertebrate metrics between the *Typha* and *Typha* + EFB communities. However, EFB and other floating vegetation reduced the abundance of scraper macroinvertebrates, most likely due to decreased algae cover. EFB also reduced submerged vegetation cover compared to the *Typha* community and averaged 0.92 ± 0.16 mg/L dissolved oxygen in September. This indicates that EFB likely affects specific macroinvertebrate taxa rather than the entire macroinvertebrate community.

INTRODUCTION

Great Lakes Coastal Wetlands and Invasive Plants

Great Lakes coastal wetlands (GLCWs) are valuable ecosystems that provide critical wildlife habitat for bird and fish populations and ecosystem services such as nutrient retention, sediment retention, and carbon sequestration (Jude and Pappas 1992, Howe et al. 2007, Sierzen et al. 2012). However, wetland ecosystems are particularly vulnerable to non-native plant invasions due to their position as landscape “sinks” where they accumulate water, nutrients, and debris that facilitate plant invasions (Zedler and Kercher 2004). Over 50 invasive wetland plants are now established within GLCWs due to a history of commerce, industry, anthropogenic disturbances, and international shipping (Ricciardi and MacIsaac 2000, Ricciardi 2006). Invasive wetland plants tend to share traits such as high phenotypic plasticity, high growth rate, or novel weapons that help them establish populations and alter wetland communities through changing habitat structure, biodiversity, and soil chemistry (Tulbure et al. 2007, Tuchman et al. 2009, Lavergne and Molofsky 2010, Schultz and Dibble 2012).

Multiple invasive wetland plants in GLCWs pose a threat to the ecosystem services and the unique habitats of GLCWs and may result in an invasional meltdown in the Laurentian Great Lakes, where established invasive species alter habitat and facilitate subsequent invasions by other non-native species (Simberloff and Von Holle 1999). Invasive plants alter hydrology, sedimentation rates, and nitrogen (N) and phosphorus (P) cycling in wetlands, supporting the conditions that help to facilitate further plant invasions (Zedler and Kercher 2004). New species interactions and ecosystem dynamics resulting from an invasional meltdown can shift GLCWs into an alternative stable state with new community assemblages, reduced biodiversity, and modified food webs (Hobbs and Norton 1996, Ricciardi 2001, Stewart et al. 1998). Understanding how other communities (e.g., bird, fish, macroinvertebrate) respond to the new ecosystem dynamics created by co-occurring invasive plants can determine how the functional structure of the plant community has been altered from the native community.

Invasive *Typha*

Narrow leaf and hybrid cattail (*Typha angustafolia* L., *T.* × *glauca* Godr.; hereafter *Typha*) are common invasive emergent macrophytes in GLCWs which began spreading in the early 1900s (Tulbure et al. 2007, Shih and Finkelstein 2008). *Typha* possesses numerous qualities which make it an aggressive invader: high phenotypic plasticity with a wide range of environmental tolerances, the ability to form clonal monotypic stands, high seed and litter production, and greater biomass production and average height (>2m) than the native plants it replaces (Woo and Zedler 2002, Tuchman et al. 2009, Larkin et al. 2012, Bansal et al. 2019). *Typha* uses these traits to capitalize on both natural and anthropogenic ecological disturbances in wetlands, such as changes in hydrology or nutrient cycling, and quickly establish populations. Stabilized hydrological regimes help to facilitate *Typha* invasion at both low and high water when native plant communities are under stress and there is less wave energy at low water to disrupt *Typha* growth (Boers et al. 2007, Boers and Zedler 2008, Lishawa et al. 2010). Research shows that *Typha* can also absorb excess N and P rapidly and increase above ground biomass growth to reach heights of >3 meters, making eutrophication from agricultural and urban runoff containing high nutrient concentrations from common fertilizers a driver of *Typha* expansion

(Woo and Zedler 2002). *Typha* produces large quantities of litter each season which has been found to increase soil N and P and create a positive feedback loop where *Typha* litter from previous growing seasons contributes to the rapid growth and spread of new above ground biomass (Farrer and Goldberg 2009, Tuchman et al. 2009). Rapid growth, litter production, and efficient nutrient use allow *Typha* to grow quickly in a wide variety of aquatic ecosystems while outcompeting native vegetation, and it is the dominant vegetation type across 13% of GLCW total area as of 2013 (Carson et al. 2018).

Typha invasion is associated with biogeochemical and abiotic changes in wetlands. Greater quantities of N, P, and soil organic matter are found in *Typha*-invaded soils (Angeloni et al. 2006, Tuchman et al. 2009) as a result of accumulating nutrient rich leaf litter decomposing over time (Farrer and Goldberg 2009). *Typha* invasion increases denitrification potential as well as methane emission in wetland soils, most likely due to increased N and carbon substrates in the soil that provide ample resources for anaerobic processes (Lishawa et al. 2014, Lawrence et al. 2017). *Typha* outcompetes existing plants through more efficient use of nutrients and greater productivity that allows them to outgrow most native plants (Woo and Zedler 2002). Accumulating leaf litter from *Typha* has been found to significantly reduce soil temperature and the amount of light that penetrates the plant canopy, nearly entirely preventing light from reaching the soil surface (Larkin et al. 2012, Lishawa et al. 2015). With less light available and lower soil temperatures, *Typha* litter reduces the germination rate of native plant seeds making it difficult for native plants to reestablish themselves in *Typha*-dominated wetlands (Vaccaro et al. 2009). Plant species richness, diversity, and biomass are all reduced in the presence of *Typha*, and the impacts of *Typha* on native plant communities have been shown to increase over time as more litter accumulates and new rhizomes and stems are grown (Farrer and Goldberg 2009, Larkin 2012, Lishawa 2010, Lishawa et al. 2014, Tuchman et al. 2009).

The loss of native plants resulting from *Typha* invasion changes plant community composition and physical habitat structure as complex, heterogeneous vegetation is homogenized and replaced with simple stems (Lishawa 2010, Schultz and Dibble 2012). Dense *Typha* stems lower fish abundance and species richness even in recently invaded wetlands (~10 years) when they reduce the amount of physical space for fish to swim and forage in (Schrank and Lishawa 2019). Hypoxia is also associated with *Typha* stands as leaf litter decomposition rapidly consumes oxygen and litter physically blocks water movement, restricting fish and macroinvertebrate community composition to species that are hypoxia-tolerant (Christensen and Crumpton 2010, Schrank and Lishawa 2019). Reduced submerged and floating vegetation cover decreases macroinvertebrate abundance and biomass as *Typha* replaces native species such as *Utricularia* spp. and reduces habitat complexity (Grabas et al. 2012, Lawrence et al. 2016).

Hydrocharis morsus-ranae

European frogbit (*Hydrocharis morsus-ranae* L., EFB) is a recent invader to the Upper Great Lakes. EFB is a small, perennial free-floating aquatic plant with heart-shaped floating leaves that connect to well-developed roots. EFB spreads and reproduces quickly through small, asexual vegetative propagules known as turions. A single EFB plant can produce 100-150 turions per season (Zhu et al. 2018). Flowing waters, boats, and migratory birds easily disperse turions to new locations where they can remain dormant for at least two years (Catling et al. 2003). EFB is native to Europe and was first introduced to North America when it was intentionally brought to the Ottawa botanic garden in 1932 where it escaped into the Rideau Canal (Zhu et al. 2018).

From the canal, EFB spread into and up the St. Lawrence River through Lakes Ontario, Erie, and Huron, to its current northernmost extent in the St. Marys River between Lakes Huron and Superior (Zhu et al. 2018, Monks et al. 2019). Due to its rapid spread and potential for further invasion throughout the Great Lakes region, state and provincial governments identified EFB as a high-risk species (Nault and Mikulyuk 2009, Weibert 2015).

Few studies exist on EFB's ecological impacts or its ability to alter wetlands in its non-native range. The floating leaves and roots of EFB occur in intertwining bundles and form dense mats on the surface of the water that prevent light penetration and shade out or displace native submerged plants (Catling et al. 2003, Bain and Mills 2004, Zhu et al. 2014). Dissolved oxygen concentrations as low as 1.9 mg/L have been reported under EFB mats resulting from a lack of atmospheric gas exchange, and anoxic conditions also occur from seasonal die-offs and decomposition of EFB mats (Zhu et al. 2008, Zhu et al. 2018). The loss of native submerged plants as well as reduced DO decreases abundance and richness in Cyprinid and Centrarchid fish populations (Bunch et al. 2015, Shrank and Lishawa 2019) and reduces macroinvertebrate abundance (Stiers et al. 2011). EFB's impacts on macroinvertebrates are more complex, however. In Oneida Lake, New York, sites with EFB present had greater macroinvertebrate diversity at the surface of the water compared to sites with no plants present (Zhu et al. 2015). Benthic macroinvertebrate communities under EFB mats in Oneida Lake shifted in community composition from plant absent sites, having reduced oligochaete, leech, and flatworm abundance and greater chironomid abundance. Despite shifts in benthic community composition, macroinvertebrate communities may benefit from the presence of EFB, and the removal of EFB may have unintended negative consequences as EFB provides food, refuge, and invertebrate nursery habitat (Zhu et al. 2015, Zhu et al. 2018).

Typha dominated wetlands have relatively low native plant diversity and lack submerged and floating vegetation structure (Tuchman et al. 2009, Lishawa et al. 2010, Lawrence et al. 2016, Schrank and Lishawa 2019), but EFB co-occurs and is positively associated with invasive *Typha* across the Great Lakes (Monks et al. 2019, Leimen et al. 2017, Bain and Mills 2004). In nine of thirteen GLCWs surveyed within the Detroit River International Wildlife Refuge, EFB was found in the understory of *Typha* and *Phragmites australis* populations (Bonnello and Judd 2020). Fetch, a proxy measurement for exposure to wind and waves, is negatively associated with EFB at the plot level scale, indicating that wind and wave action in GLCWs are limiting the establishment and persistence of EFB (Monks et al. 2019). *Typha* likely facilitates the spread of EFB by reducing incoming wind and wave energy, creating habitats with reduced physical stress.

While many ecological impacts of *Typha* are well documented (Bansal et al 2019) and the ecology and impacts of EFB are currently under investigation (Zhu et al. 2018, Monks et al. 2019), there are no present studies on the combined effects of both EFB and *Typha* on GLCW ecosystems despite the high rate of spread and co-occurrence by both invasive plants. The primary invasion of *Typha* reduces native submerged vegetation, creating opportunities for the secondary invasion of EFB. This secondary invasion has the potential to provide critical submerged vegetation structure (Grabas et al. 2012) and increase habitat complexity, which is scarce in *Typha* dominated wetlands (Fig. 1). Because of the important ecosystem services and wildlife habitat GLCWs provide (Sierzen et al. 2012), developing an understanding of how the increasing co-occurrence of EFB and *Typha* affects ecosystem structure and GLCW communities is essential.

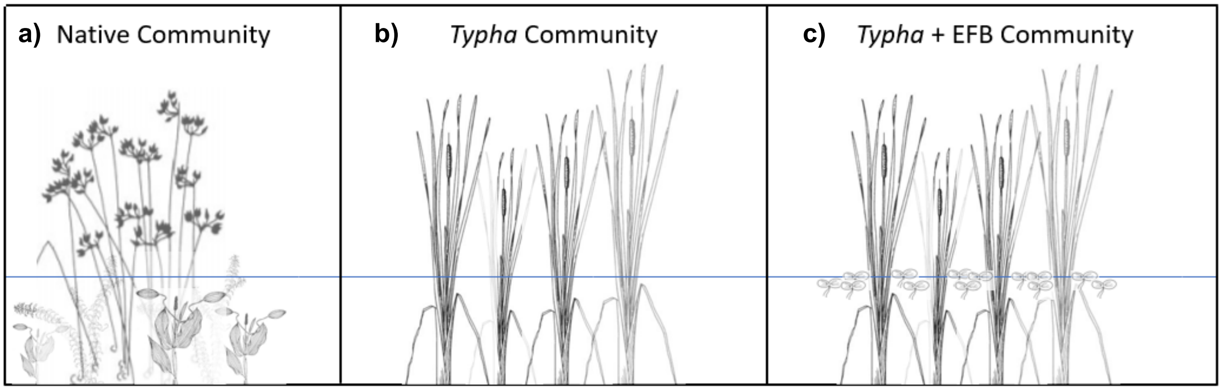


Fig. 1. Illustration of the changes in habitat structure from a a) native community to a b) *Typha* community with the primary invasion of *Typha*, and then to a c) *Typha* + EFB community with the subsequent secondary invasion of *Hydrocharis morsus*-ranae (EFB). Plant illustrations from Houghton, M.K. and Bacon, E. (2020) Common Aquatic Plants of Michigan, Michigan Department of Environment, Great Lakes, and Energy.

Wetland Macroinvertebrates

Macroinvertebrate communities contribute to wetland ecosystem services through bioturbation, decomposition of leaf litter, and water filtration (Prather et al. 2012). As a major food source for migratory birds, fish, and other wetland species, macroinvertebrates link primary producers and secondary consumers and facilitate the transfer of energy from aquatic to terrestrial ecosystems (Wallace and Webster 1996, Kostecke et al. 2005, Merritt et al. 2019). Ecological disturbances that affect macroinvertebrate abundance may cause a trophic cascade effect, wherein predator food resources, such as small fish, are reduced as a direct result of macroinvertebrate scarcity (Young et al. 2018).

Macroinvertebrates are appropriate organisms for studying wetland ecosystem dynamics as they are important in wetlands with standing water and act as indicators of ecosystem health and water quality (Burton et al. 1999, Weigal et al. 2002, Foote and Hornung 2005). Macroinvertebrates are also useful in studying plant communities as they use vegetation for habitat and food, show preferences for specific plant communities, and directly respond to any changes in water quality conditions that may accompany plants (Voigts 1976, Burton et al. 2002, Christensen and Crumpton 2010, Gathman and Burton 2011, Walker et al. 2013, Lawrence et al. 2016). Macroinvertebrates occur in areas suitable for their survival and have a wide range of environmental tolerances and sensitivities among taxa, providing a gradient of water quality and ecosystem health conditions based on their relative abundances (Lencioni et al. 2012).

Macroinvertebrate responses to plant invasions may be positive or negative depending on the invader and its traits, such as biomass production and leaf dissection (Schultz and Dibble 2012). Studies found that invaders such as *Myriophyllum* spp. or *Trapa natans* increase vegetation surface area as well as biomass to increase habitat complexity and provide better refuge for macroinvertebrates from predators, increasing macroinvertebrate abundance and diversity (Strayer et al. 2003, Valinoti et al. 2011). However, when invaders displace native plants and subsequently reduce both vegetation surface area and biomass, research has shown that a lack of suitable habitat reduces macroinvertebrate biomass and abundance (Houston and Duivenvoorden 2003, Lawrence et al. 2016). Invasive plants that form floating mats or produce large quantities of litter have been shown to reduce dissolved oxygen concentrations and limit macroinvertebrate communities to the most resilient taxa, negatively impacting diversity and community composition (Christensen and Crumpton 2010, Rose and Crumpton 1996, Stiers et al. 2011). Large litter inputs from highly productive invaders also shift the community composition of macroinvertebrates from grazer-based to detritivore-based functional feeding groups as food resources shift (Zedler and Kercher 2004). Even if the quantity of litter does not change after invasion, plants with lower quality litter (i.e., high lignin and tannin concentrations) are difficult for aquatic shredders to consume and alter macroinvertebrate community composition or reduce litter decomposition rates (Youngquist et al. 2020).

Despite the rapid spread of EFB throughout the Great Lakes, there is only one study that has examined the relationship between EFB and macroinvertebrates. Zhu et al. (2015) compared areas invaded by EFB to unvegetated areas to determine the effects of EFB management, however, *Typha* often accompanies EFB and management methods should take this codominance into account. The presence of EFB in *Typha* dominated GLCWs may provide food, refuge, and nursery habitat for macroinvertebrate communities as invasive macrophytes increase macroinvertebrate abundance when they increase vegetation biomass and surface area (Cyr and Downing 1988b, Schultz and Dibble 2012). This contrasts with the invasional meltdown hypothesis (Simberloff and Von Holle 1999) which suggests that co-occurring invasive species will continue to facilitate further invasions and reduce native species diversity additively with each invasion. Macroinvertebrate community responses to invasive plants are complex and appear to be driven by plant traits and structural complexity more so than whether a species is native or not (Balci and Kennedy 2003, Strayer et al. 2003, Stiers et al. 2011, Vallinoti et al. 2011, Lawrence et al. 2016). Thus, the structure provided by EFB in *Typha* stands should be functionally equivalent to native submergent species and macroinvertebrate communities should reflect the greater resource complexity.

Study Objective and Hypotheses

My objective for this study was to determine how the secondary invasion of EFB in a *Typha* dominated community affects macroinvertebrate community composition in a northern Lake Huron GLCW. I hypothesized that plant communities containing EFB and *Typha* would have increased vegetation cover and habitat complexity compared to *Typha* dominated communities without EFB, which would result in greater macroinvertebrate diversity, abundance, and biomass in the EFB and *Typha* dominated community because macroinvertebrates are associated with more structurally complex plant communities with greater vegetation cover. I also hypothesized that native plant communities would have greater macroinvertebrate diversity, abundance, and biomass than EFB and *Typha* communities because native plant communities have greater submerged vegetation complexity and structural heterogeneity compared to EFB and *Typha* co-dominant communities (Fig. 1). To investigate this question, I surveyed and compared plant and macroinvertebrate communities present in *Typha* communities, EFB + *Typha* communities, and two native plant communities in a northern Lake Huron coastal marsh.

METHODS

Field Site Description

I conducted all surveys in 2020 at Munuscong Bay in Chippewa County, Michigan (46.20 N, 84.25 W). Munuscong Bay is a river delta marsh (Albert et al. 2005) at the outlet of the Munuscong River along the St. Marys River, the connecting channel between Lake Superior and Lake Huron. Munuscong Bay has been dominated by invasive *Typha* for over 30 years (Albert et al. 1987). European frogbit (*Hydrocharis morsus-ranae*; EFB) was first discovered in Munuscong Bay in 2010 where it has continued to spread throughout the wetland and become a dominant species in the *Typha* understory (Monks et al. 2019). At this site, I identified four distinct plant communities to assess how EFB impacts macroinvertebrate habitat structure: meadow, submerged, *Typha*, and *Typha* + EFB.

Plant communities in Munuscong Bay were delineated using Geographic Information Systems (GIS), aerial photography, and ground truthing during peak growing season in July 2020. I created polygons of each plant community and then used the *Generate Random Points* tool in ET Geo Wizards Toolbox to establish eight 1 × 1 m plots at random points within the delineated zones using ArcMap (Environmental Systems Research Institute, Redlands, CA, USA) for a total of 32 plots (Fig. 2). Up to a three percent areal cover of EFB was allowed in plots which were not in the *Typha* + EFB community due to the widespread distribution of EFB throughout Munuscong Bay. Three percent was chosen as the cutoff to ensure that EFB was not a dominant species within the plot compared to other submerged and floating species, which averaged to approximately three percent.

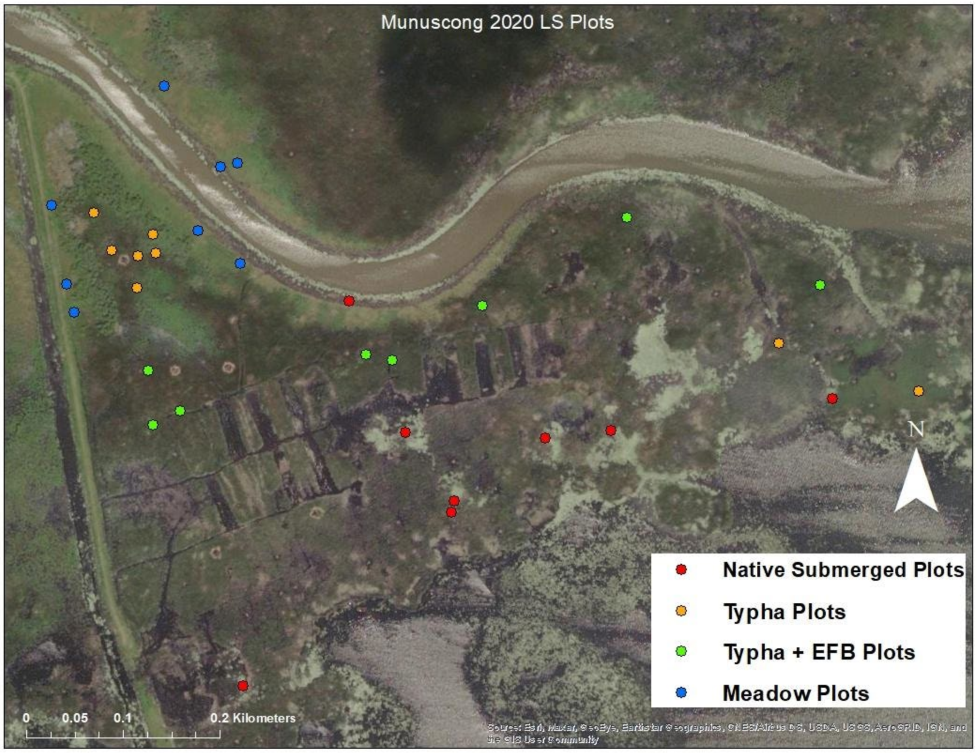


Fig. 2. Satellite imagery of Munuscong Bay in July 2020 showing the locations of the 32 study plots. Image source: Esri, Maker, GeoEye, Earthstar Geographics, CNESAirbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, 2020.

Vegetation Surveys

Methods for vegetation and environmental sampling at each plot followed a modified version of the sampling protocol of the Great Lakes Coastal Wetland Monitoring Program (GLCWMP) (Uzarski et al. 2017). The GLCWMP samples Great Lakes coastal wetlands using a standardized methodology where three transects bisect a wetland perpendicular to its depth contours and cross through wet meadow, emergent, and submergent vegetation zones. Along each transect, five evenly spaced 1-m^2 plots are located within each vegetation zone for a total of 45 plots per wetland. Percent cover for each plant species, total vegetation cover, water depth, organic soil layer thickness, and estimated relative turbidity are recorded for each plot (Uzarski et al. 2017).

In addition to the standard GLCWMP metrics recorded at each 1-m^2 plot I also collected areal percent cover for above water detritus and below water detritus. A graduated pole was used to measure water depth from the water surface to the top of the organic soil layer. The organic soil layer depth was measured by forcing the graduated pole through the organic layer until mineral soil was reached, and the meter stick could no longer move easily. Areal percent cover for total vegetation, above water detritus, below water detritus, and vascular plant cover within a 1-m^2 quadrat were determined through visual inspection from two field trained, calibrated observers standing above the plot. In addition to individual species cover, plant cover was categorized by plant functional groups which included floating, submerged, emergent, and sedge/grass. For plots with any *Typha* cover, the height of each *Typha* stem was measured from the base of the stem to the tallest leaf to calculate the total biomass of *Typha* within the plot. *Typha* heights were converted to biomass using an allometric equation ($g = 0.5265^{1.751 \times \text{height (m)}}$; $r^2 = 0.81$) developed from sampling multiple coastal sites across Northern Michigan (Lishawa et al. 2015).

Water chemistry data was collected using a multi-meter probe which collected data on water temperature, dissolved oxygen (DO), pH, and oxidation-reduction potential (ORP) (Yellow Springs Instruments Yellow Springs, OH, model Professional Plus 2019). The calibration protocols for each meter on the probe were followed before starting sampling to ensure measurement consistency. The probe was held approximately 5-10 cm below the water surface outside the quadrat when collecting water chemistry data. Vegetation sampling occurred from July 27 through July 29, 2020, during peak *Typha* and EFB biomass, and then a second time from September 8 through September 11, 2020, when *Typha* and EFB are undergoing senescence. Sampling protocols were identical between both sampling events, except depth of the organic soil layer and *Typha* stem heights were not measured in September 2020 because little to no change in these variables would occur between sampling events.

Macroinvertebrate Collection

I used two methods to collect macroinvertebrates: dipnet sampling and Hester-Dendy samplers. Dipnet macroinvertebrate samples were collected during July 30 through July 31 and September 8 through September 11 in 2020. Dipnet sampling followed a modified version of the macroinvertebrate sampling and laboratory processing standard operating procedure from the GLCWMP (Uzarski et al. 2017). The GLCWMP collect macroinvertebrates from three haphazardly selected sampling points within each vegetation zones in a wetland (wet meadow, emergent, submergent). At each sampling point, 0.5 mm-mesh D-shaped dipnets sweep the entire water column, substrate, and plant stems. Each sweep is approximately 1 m, and the number of sweeps at each sampling point are recorded. Dipnet contents are spread into gridded white trays and a representative sample of macroinvertebrates are picked and stored in ethanol. They are later identified to the lowest operational taxonomic unit.

All dipnet sweeps were performed after vegetation surveys at each plot. I used a standard 0.5 mm-mesh D-shaped dipnet to sweep aquatic vegetation and benthic sediment through the entire water column for macroinvertebrates in an approximately 1-m^2 area. I performed three approximately 1 m sweeps within each plot to cover the entire plot area. All macroinvertebrate samples and vegetation were transferred from the net into 1 L jars in the field and brought back to the laboratory and processed within 24 hours. I transferred the field collection jar contents into a white enamel pan and picked out all visible macroinvertebrates. Any vegetation present in the collection jar was thoroughly picked through to collect macroinvertebrates in the vegetation. Macroinvertebrates were stored in small collection bottles filled with 80% EtOH.

Hester-Dendy samplers are artificial substrate samplers consisting of multiple Masonite plates that are deployed in water and given time to allow macroinvertebrates to colonize the plates. I constructed Hester-Dendy samplers consisting of eight 7.5 × 7.5 cm Masonite plates spaced approximately 0.95 cm apart (Fig. 3a, Zhu et al. 2015). Hester-Dendy samplers were soaked in water prior to deployment to allow any residual oils or toxins present in the Masonite from production that would discourage colonization by sensitive taxa to leach out (Valenty and Fisher 2012). One Hester-Dendy sampler was deployed at each plot on July 30 and 31, 2020 after vegetation and dipnet surveys were completed. The Hester-Dendy samplers were anchored to a PVC post with an arm projecting over the plot and suspended just below the surface of the water in the center of the plot using a small buoyant cube of foam (Fig. 3c). This was meant to allow the Hester-Dendy samplers to rise and fall with changing water depths during their deployment, however the weight of the Hester-Dendy samplers after soaking caused them to sink below the surface of the water.

Fig. 3. Hester-Dendy samplers are artificial substrate samplers that are deployed in water and given time to allow macroinvertebrates to colonize the plates: a) Hester-Dendy samplers prior to deployment, b) Hester-Dendy sampler after being deployed one month in submergent plant community with colonized macroinvertebrates, c) sampling apparatus used to anchor and suspend Hester-Dendy samplers in the meadow at Munuscong Bay in 2020.

Hester-Dendy samplers were obtained after macroinvertebrate colonization six weeks later from September 8 through September 11, 2020. Hester-Dendy samplers were collected by placing the sampler in a 1.89 L plastic bag while still in the water to avoid macroinvertebrates leaving the samplers before being contained. The samplers and surrounding water were lifted out of the water with the bag and sealed, then sealed again in a second 1.89 L bag. Hester-Dendy samples were processed in the lab within 24 hours by dismantling the samplers in a white enamel pan with water and gently scrubbing debris and macroinvertebrates from each individual plate with fingertips and forceps. Dislodged macroinvertebrates were then collected from the water and preserved in 80% EtOH. I identified all macroinvertebrates to the lowest taxonomic unit possible using Merritt et al. (2019) and Thorp and Covich (2009). Most taxa were identified to genus, except for Aranae, Chironomidae, Hirudinea, Hydrachnidia, and Lumbriculidae. Macroinvertebrates were subsequently classified by functional feeding group using Merritt et al. (2019). Functional feeding groups included collector, shredder, piercer, scraper, and predator.

I used length-mass regressions to calculate biomass of macroinvertebrates because they are faster than direct weighing of biomass, and macroinvertebrates lose biomass during preservation which make dry weights inaccurate (Benke et al. 1999, Mährlein et al. 2016). Length-mass regressions predict mass using the power function $M = aL^b$ where M is organism mass (mg), L is body length (mm), and a and b are taxa specific constants. I measured the body length of each macroinvertebrate from the anterior tip of the head to the posterior tip of the abdomen. I converted body lengths into biomass using established length-mass regressions at the lowest available taxonomic unit (Benke et al. 1999, Johnston and Cunjak 1999, Miserendino 2001, Baumgärtner and Rothhaupt 2003, Grunner 2003, Edwards et al. 2009, Rosati et al. 2012, Mährlein et al. 2016). For taxa that did not have published length-mass regressions (*Cordulia* sp., *Eloeophila* sp., *Neocloeon* sp., *Neoplea* sp., *Neoscuropterus* sp., and *Ranantra* sp.), I used a regression from a species with comparable morphology (Reese and Batzer 2007, Lawrence et al. 2016).

Statistical Analysis

I used analysis of variance (ANOVA) to analyze the effects of plant community type on environmental, plant, and macroinvertebrate data. The data collected in July and September were analyzed separately and not combined or statistically compared. I utilized Shapiro-Wilk tests for normality and Bartlett's test for homoscedasticity to statistically test if the ANOVA models met the assumptions of the test ($p > 0.05$) and I visually assessed the normality of residuals with QQ plots. When response variables did not meet the model assumptions, data were log transformed (except for scraper, predator, and collector abundance, which were square root transformed) to meet assumptions of normality and homogeneity of residuals. Transformed variables included above water litter, water temperature, water depth, macroinvertebrate abundance and biomass, *Typha* biomass, Chironomid abundance, *Caecidotea* abundance, *Crangonyx* abundance, floating vegetation cover, dissolved oxygen, and pH. When a model was significant ($p < 0.05$), Tukey's HSD multiple comparison test was used to assess pairwise differences between treatments. For variables with non-parametric data distribution (plant richness, above water litter, below water litter, total vegetation cover, Chironomid abundance, *Caecidotea* abundance, *Crangonyx* abundance, floating vegetation cover, submerged vegetation cover, emergent vegetation cover, sedge/grass cover, and piercer abundance), a Kruskal-Wallis test was performed to check for significant differences and Wilcox test was used to make pairwise comparisons between treatments. All statistical tests were conducted using R (Version 4.0.3, R Core Development Team, 2020).

The effects of plant community on species assemblage of macroinvertebrates were analyzed using permutational multivariate analysis of variance (PERMANOVA) with the 'adonis' function in R. The data collected in July and September were analyzed separately and not combined or statistically compared. I also used PERMANOVA to conduct pairwise comparisons of macroinvertebrate species assemblages by plant communities. Macroinvertebrate and plant communities were then visualized in a 2-dimensional space using nonparametric multi-dimensional scaling (NMDS) of species abundance (macroinvertebrates) or percent cover (plants) at the plot level, with dissimilarity based on Bray-Curtis distances (McCune and Grace 2002). Fitted vectors of environmental variables were displayed over NMDS plots at a significance level of $p \leq 0.05$ as determined by permutation procedure. The length of fitted vectors is proportional to their explanatory strength. I performed all multivariate analyses using the 'vegan' package (Oksanen et al. 2018) in R. To identify macroinvertebrate taxa that corresponded with the different plant communities, I used indicator species analysis with the 'indicspecies' package (Dufrene and Legendre 1997) in R. Indicator species analysis calculates indicator values that range from 0 (no indication) to 100 (perfect indication) for each species in a plant community.

I used linear regression analysis to determine if environmental and plant variables affected macroinvertebrate metrics. The data collected in July and September were analyzed separately and not combined or statistically compared. Environmental variables included DO, water depth, and water temperature. Plant variables included total vegetation cover, richness, diversity, and functional group cover. The normality of residuals for each regression was assessed with a Shapiro-Wilk test ($p > 0.05$), and variance was assessed using a non-constant variance score test ($p > 0.05$). Normality of residuals and variance were also assessed visually using QQ plots. Outliers were checked for using a Bonferroni test and removed when a result was significant ($p < 0.05$). Response variables were log or square root transformed when the model assumptions were not met (macroinvertebrate diversity and dissolved oxygen, scraper abundance and floating vegetation cover, and collector abundance and plant diversity).

RESULTS

Environmental Variables

Examining environmental data, water depth was significantly higher in the submerged community compared to all other communities while *Typha* and *Typha* + EFB had significantly higher water depth than meadow plots (p = <0.001, Fig. 4, Table 1). Water temperature (p = 0.087) and dissolved oxygen (DO) (p = 0.118, Fig. 4a) did not differ between plant communities in July (Table 1). September water temperature was significantly higher in the submerged community compared to the *Typha* and *Typha* + EFB communities while the meadow did not significantly differ from any other plant community (p = 0.001, Table 1). DO in September was significantly higher in the meadow community compared to the *Typha* and *Typha* + EFB communities, and the *Typha* + EFB community had significantly lower DO compared to the submerged community (p = <0.001, Fig. 4b, Table 1). pH did not significantly differ between any plant communities in July (p = 0.523) or September (p = 0.114, Table 1). Oxidation-reduction potential (ORP) was significantly higher in the submerged community compared to all other plant communities across both time periods (p = <0.001, Table 1).

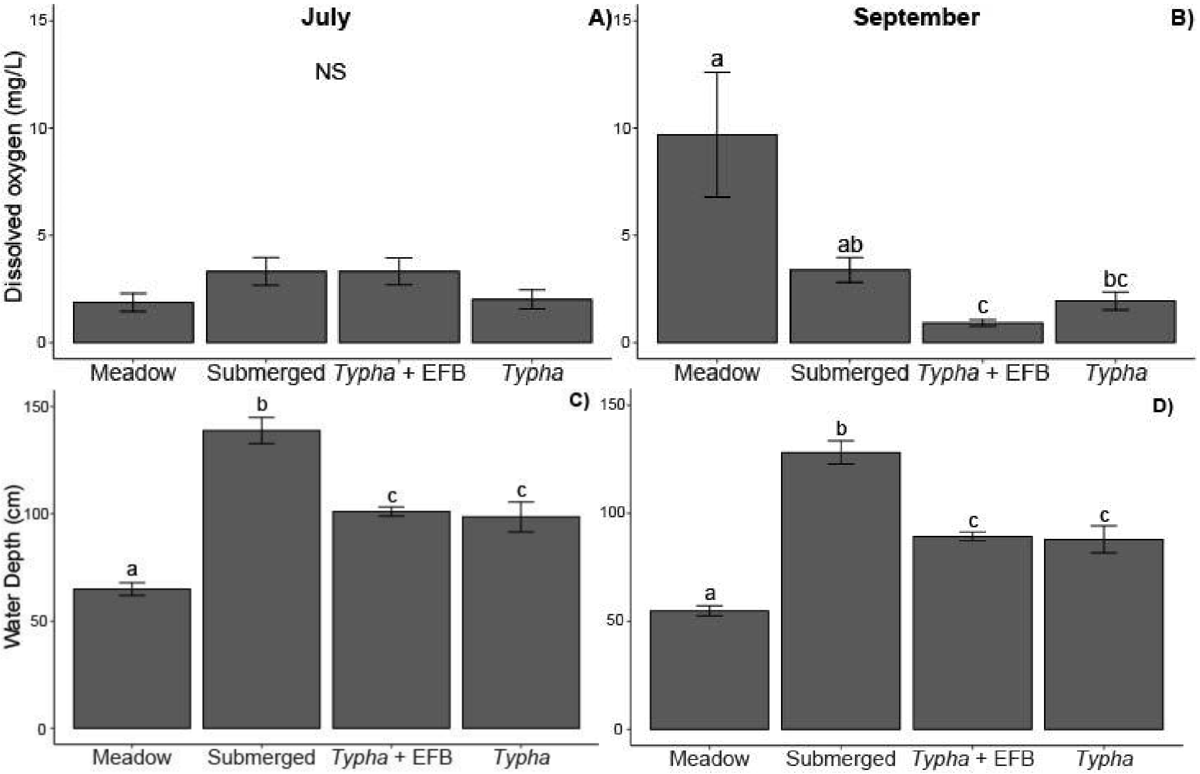


Figure 4. Mean dissolved oxygen concentrations (a, b) and water depth (c, d) from Munuscong Bay, Michigan in July (a, c) and September (b, d) 2020 by plant community (n = 8). Error bars represent ± 1 SE. Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities, NS = no significant differences.

Table 1. Environmental variables (mean ± SE) collected from Munuscong Bay, Michigan in July and September 2020 separated by plant community (n = 8). Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities as determined by ANOVA and Tukey's HSD. Data were log transformed when necessary to meet model assumptions. Differences in non-parametric data were determined using a Kruskal-Wallis and Wilcox test.

Variable	Meadow	Submerged	*Typha* + EFB	*Typha*	*p*
July					
Water depth (cm)	64.88 ± 3.01^{a}	138.75 ± 6.09^{b}	101.00 ± 2.09^{c}	98.50 ± 7.00^{c}	<0.001
Water temperature (°C)	22.95 ± 0.21	23.14 ± 0.34	24.16 ± 0.52	23.23 ± 0.21	0.087
Dissolved oxygen (mg/L)	1.87 ± 0.42	3.32 ± 0.64	3.32 ± 0.62	2.02 ± 0.45	0.118
pH	7.43 ± 0.08	7.52 ± 0.11	7.56 ± 0.11	7.39 ± 0.04	0.523
Oxidation-reduction potential (mV)	-42.85 ± 20.02^{a}	51.44 ± 7.02^{b}	-15.36 ± 11.13^{a}	-11.04 ± 16.21^{a}	<0.001
Organic depth (cm)	12.38 ± 1.60^{a}	15.63 ± 2.46^{ab}	23.00 ± 2.27^{b}	18.75 ± 1.52^{ab}	0.006
September					
Water depth (cm)	54.88 ± 2.30^{a}	128.13 ± 5.41^{b}	89.25 ± 2.02^{c}	87.88 ± 6.20^{c}	<0.001
Water temperature (°C)	14.59 ± 0.33^{ab}	15.55 ± 0.25^{a}	13.61 ± 0.27^{b}	14.16 ± 0.35^{b}	0.001
Dissolved oxygen (mg/L)	9.70 ± 2.91^{a}	3.39 ± 0.58^{ab}	0.92 ± 0.16^{c}	1.94 ± 0.42^{bc}	<0.001
pH	7.74 ± 0.20	7.59 ± 0.07	7.38 ± 0.07	7.39 ± 0.06	0.114

Oxidation-reduction potential (mV)	25.21 ± 9.26^{a}	97.39 ± 12.79^{b}	38.15 ± 7.56^{a}	40.66 ± 7.98^{a}	<0.001

Plant Community

I found differences between plant communities for multiple metrics through analysis of plant community data. Plant Shannon-Wiener diversity was significantly higher in the meadow than the *Typha* community while the submerged and *Typha* + EFB community diversity was not significantly different from any other plant community ($p = 0.004$, Fig. 5a, Table 2) except in September where diversity was significantly higher in the submerged community compared to the *Typha* community ($p = <0.001$, Fig. 5b, Table 2). While not significant, diversity in September was trending higher in *Typha* + EFB compared to *Typha* ($p = 0.077$). There was no effect of plant community on plant richness in July ($p = 0.187$), although plant richness was trending higher in the meadow community in September ($p = 0.057$, Table 2). In both July and September, the submerged community had significantly higher total vegetation cover than all other plant communities, while total vegetation cover in the *Typha* + EFB community was significantly higher than the *Typha* community and the meadow did not differ from the *Typha* + EFB or *Typha* communities ($p = <0.001$, Fig. 5c, Table 2) except for in September where total vegetation cover in the *Typha* + EFB community was also significantly higher than the *Typha* community ($p = <0.001$, Fig 5d, Table 2). *Typha* biomass did not differ between *Typha* and *Typha* + EFB communities ($p = 0.998$, Table 2).

Above water litter cover was significantly greater in the *Typha* + EFB community compared to the meadow and submerged communities in both July ($p = 0.017$) and September ($p = <0.001$, Table 2), while the *Typha* community did not differ from any other plant community in July but was significantly greater than the meadow and submerged communities in September ($p = 0.030$, Table 2). Below water litter cover was significantly higher in the *Typha* and *Typha* +

EFB communities compared to meadow and submerged communities, while meadow communities were significantly higher than submerged communities in July (*p* = <0.001) and September (*p* = <0.001, Table 2).

Plant functional cover results varied by plant community and followed the same patterns of significance in July and September. Floating plant cover was significantly higher in the submerged and *Typha* + EFB communities compared to the meadow and *Typha* communities (*p* = <0.001, Table 2, Fig. 5e, Fig. 5f). Submerged plant cover was significantly higher in the submerged community compared to all other communities, while the meadow and *Typha* communities had significantly higher submerged plant cover compared to the *Typha* + EFB community which had the lowest submerged plant cover (*p* = <0.001, Table 2, Fig. 5g, Fig. 5h). The *Typha* and *Typha* + EFB communities had significantly higher emergent plant cover than the meadow and submerged communities which had nearly no emergent plant cover (*p* = <0.001, Table 2). Lastly, sedge/grass cover was only found in the meadow community, except for one plot within the *Typha* community (*p* = <0.001, Table 2).

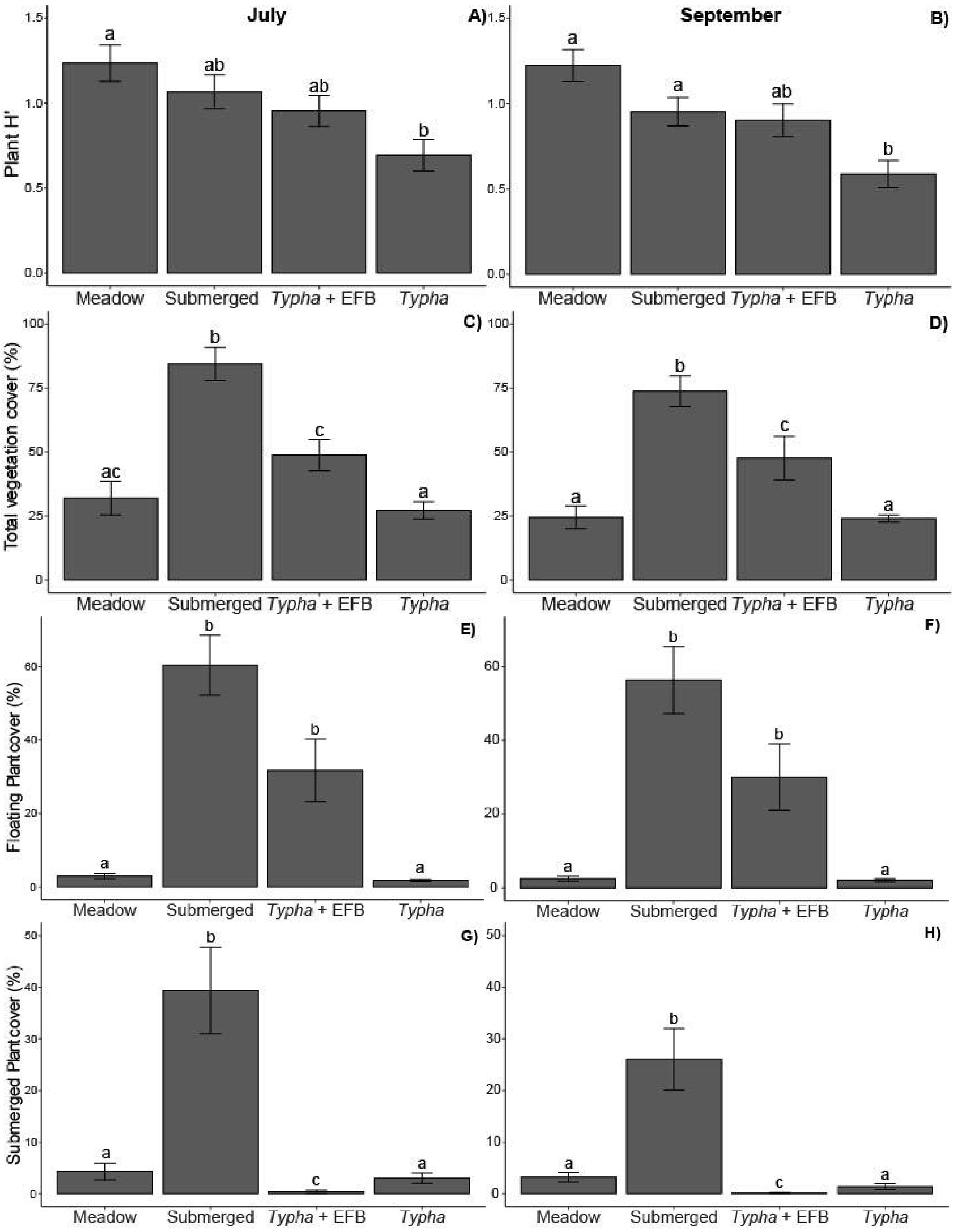


Figure 5. Mean total plant Shannon-Wiener diversity (a, b), total vegetation cover (c, d), floating plant cover (e, f), and submerged plant cover (g, h) from Munuscong Bay, Michigan in July (a, c, e, g) and September (b, d, f, h) 2020 by plant community (n = 8). Error bars represent ± 1 SE. Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities.

Table 2. Plant variables (mean ± SE) collected from Munuscong Bay, Michigan in July and September 2020 separated by plant community (meadow, submerged, *Typha* + EFB, *Typha*; n = 8). Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities as determined by ANOVA and Tukey's HSD. Data were log transformed when necessary to meet model assumptions. Differences in non-parametric data were determined using a Kruskal-Wallis and Wilcox test.

Variable	Meadow	Submerged	*Typha* + EFB	*Typha*	*p*
July					
H'	1.24 ± 0.11^{a}	1.07 ± 0.10^{ab}	0.95 ± 0.09^{ab}	0.69 ± 0.09^{b}	0.004
Richness	6.88 ± 0.55	6.50 ± 0.57	5.13 ± 0.58	6.38 ± 0.75	0.187
Total vegetation cover (%)	32.00 ± 6.61^{ac}	84.38 ± 6.44^{b}	48.75 ± 6.11^{c}	27.25 ± 3.38^{a}	<0.001
Above water litter (% cover)	2.75 ± 1.16^{a}	3.56 ± 1.20^{a}	10.63 ± 4.32^{b}	3.88 ± 0.58^{ab}	0.017
Below water litter (% cover)	74.88 ± 5.90^{a}	28.75 ± 2.27^{b}	99.00 ± 0.00^{c}	97.88 ± 1.125^{c}	<0.001
Typha biomass (g/m^2)	0.00	0.00	4866.4 ± 747.7	5780.9 ± 1568.4	0.998
Floating plant cover (%)	2.94 ± 0.72^{a}	60.38 ± 8.16^{b}	31.69 ± 8.54^{b}	1.81 ± 0.33^{a}	<0.001
Submerged plant cover (%)	4.31 ± 1.60^{a}	39.38 ± 8.38^{b}	0.38 ± 0.38^{c}	3.00 ± 1.02^{a}	<0.001
Emergent plant cover (%)	0.06 ± 0.06^{a}	0.06 ± 0.06^{a}	24.63 ± 1.80^{b}	25.38 ± 3.26^{b}	<0.001
Sedge and grass cover (%)	27.0 ± 6.33^{a}	0.00^{b}	0.00^{b}	0.19 ± 0.13^{b}	<0.001
September					
H'	1.22 ± 0.09^{a}	0.95 ± 0.08^{a}	0.90 ± 0.10^{ab}	0.59 ± 0.08^{b}	<0.001
Richness	6.13 ± 0.55	6.88 ± 0.30	4.75 ± 0.70	5.63 ± 0.50	0.057
Total vegetation cover (%)	24.50 ± 4.49^{a}	73.75 ± 6.11^{b}	47.63 ± 8.51^{c}	24.00 ± 1.36^{a}	<0.001
Above water litter (% cover)	2.31 ± 0.86^{a}	1.13 ± 0.56^{a}	8.25 ± 1.28^{b}	6.13 ± 0.77^{b}	<0.001
Below water litter (% cover)	73.13 ± 1.61^{a}	57.50 ± 6.48^{b}	99.00 ± 0.00^{c}	95.63 ± 1.65^{c}	<0.001
Floating plant cover (%)	2.50 ± 0.65^{a}	56.38 ± 9.06^{b}	30.06 ± 8.95^{b}	2.06 ± 0.42^{a}	<0.001
Submerged plant cover (%)	3.19 ± 0.93^{a}	26.06 ± 5.98^{b}	0.13 ± 0.13^{c}	1.38 ± 0.56^{a}	<0.001
Emergent plant cover (%)	0.00^{a}	0.00^{a}	22.31 ± 1.50^{b}	22.75 ± 1.32^{b}	<0.001
Sedge and grass cover (%)	21.19 ± 4.60^{a}	0.00^{b}	0.00^{b}	0.06 ± 0.06^{b}	<0.001

Macroinvertebrate Community

In July and September 2020, I collected a total of 5009 macroinvertebrates (2116 in July dipnet sampling, 2178 in September dipnet sampling, 715 from Hester-Dendy samplers) representing 43 taxa from 34 families and 14 orders (Appendix A). *Caecidotea* spp., Chironomids, and *Crangonyx* spp. were the most abundant taxa across all plant communities and time periods for dipnet sampling (Appendix A). *Caecidotea* abundance was trending higher in the *Typha* and *Typha* + EFB communities compared to the meadow and submerged communities in July ($p = 0.129$) and September ($p = 0.209$, Table 3). Chironomids were significantly more abundant in the meadow community compared to all other plant communities in July ($p = <0.001$) and were trending higher in September ($p = 0.079$, Table 3). *Crangonyx* abundance was significantly higher in the meadow and submerged communities compared to the *Typha* and *Typha* + EFB communities ($p = <0.001$), except for in September where *Crangonyx* abundance was trending higher ($p = 0.069$, Table 3).

Table 3. Abundance data (mean ± SE) of the three most abundant macroinvertebrate taxa collected by dipnet sampling in July and September 2020 from Munuscong Bay, Michigan separated by plant community (meadow, submerged, *Typha* + EFB, *Typha*; n = 8). Abundance units are individuals/m^2. Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities as determined by ANOVA and Tukey's HSD. Data were log transformed when necessary to meet model assumptions. Differences in non-parametric data were determined using a Kruskal-Wallis and Wilcox test.

Taxa	Meadow	Submerged	*Typha* + EFB	*Typha*	*p*
July					
Caecidotea	9.71 ± 3.15	7.00 ± 3.22	30.0 ± 10.40	47.13 ± 14.71	0.129
Chironomidae	67.63 ± 26.72^a	5.33 ± 2.18^b	5.80 ± 1.57^b	5.00 ± 1.99^b	<0.001
Crangonyx	14.50 ± 3.25^a	18.29 ± 2.81^a	3.60 ± 0.73^b	2.75 ± 0.78^b	<0.001
September					
Caecidotea	13.86 ± 5.51	28.00 ± 13.99	41.88 ± 16.08	58.71 ± 12.67	0.209
Chironomidae	34.80 ± 11.08	3.83 ± 0.69	2.43 ± 0.28	18.50 ± 7.86	0.079
Crangonyx	22.25 ± 13.39	18.63 ± 5.51	10.00 ± 2.83	1.00 ± 0.00	0.069

Dipnet samples of macroinvertebrates did not differ significantly in diversity (July, p = 0.263; September, p = 0.071), richness (July, p = 0.204; September, p = 0.151), or biomass (July, p = 0.631; September, p = 0.782) between plant communities in July and September (Table 4, Fig. 6). Diversity was trending higher in September in the meadow community compared to the *Typha* community (p = 0.071). Macroinvertebrate abundance was significantly greater in the meadow community compared to the submerged community while the *Typha* and *Typha* + EFB communities were not significantly different from other plant communities in July (p = 0.049, Table 4, Fig. 6c), although there were no significant differences in abundance in September (p = 0.939, Table 4, Fig. 6g).

Hester-Dendy samplers collected less than half the number of taxa and individual macroinvertebrates than dip net sampling did (14 taxa, 715 individuals). Macroinvertebrate samples from Hester-Dendy sampling showed a significant result for diversity in the ANOVA model (p = 0.014), but no significant pairwise differences (Table 4). Both meadow (p = 0.068) and submerged (p = 0.099) communities trend higher in macroinvertebrate diversity compared to the *Typha* and *Typha* + EFB communities. The submerged community had significantly higher species richness than the *Typha* community but was not significantly different from the other plant communities (p = 0.004, Table 4). Macroinvertebrate abundance (p = 0.127) or biomass (p = 0.409) did not differ between any plant communities for Hester-Dendy samplers (Table 4).

Table 4. Macroinvertebrate variables (mean ± SE) collected from dipnet sampling in July and September 2020 and from Hester-Dendy samplers deployed for six weeks in Munuscong Bay, Michigan separated by plant community (meadow, submerged, *Typha* + EFB, *Typha*; n = 8). Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities as determined by ANOVA and Tukey's HSD. Data were log transformed when necessary to meet model assumptions. Differences in non-parametric data were determined using a Kruskal-Wallis and Wilcox test. Hester-Dendy H' significantly differed between plant communities, but none of the pairwise comparisons were significantly different.

Variable	Meadow	Submerged	*Typha* + EFB	*Typha*	*p*
July					
H'	1.29 ± 0.16	1.54 ± 0.09	1.27 ± 0.21	0.99 ± 0.26	0.263
Richness	8.75 ± 0.45	7.75 ± 0.90	8.00 ± 0.60	6.25 ± 1.14	0.204
Abundance (no/m^2)	115.00 ± 34.94^{a}	39.75 ± 7.43^{b}	47.13 ± 8.51^{ab}	62.63 ± 14.83^{ab}	0.049
Biomass (mg/m^2)	62.20 ± 13.75	56.47 ± 20.39	83.91 ± 51.63	36.16 ± 8.77	0.631
September					
H'	1.44 ± 0.16	1.38 ± 0.09	1.15 ± 0.18	0.92 ± 0.13	0.071
Richness	9.00 ± 1.05	7.63 ± 0.60	7.38 ± 0.56	6.50 ± 0.68	0.151
Abundance (no/m^2)	64.88 ± 16.69	65.50 ± 15.25	65.00 ± 13.94	76.88 ± 18.25	0.939
Biomass (mg/m^2)	101.51 ± 27.45	57.40 ± 8.44	100.75 ± 38.22	69.79 ± 14.28	0.782
Hester-Dendy					
H'	1.01 ± 0.10	0.98 ± 0.11	0.58 ± 0.16	0.58 ± 0.08	0.014
Richness	3.75 ± 0.45^{ab}	4.25 ± 0.31^{a}	2.75 ± 0.53^{ab}	2.25 ± 0.16^{b}	0.004
Abundance (no/m^2)	15.88 ± 3.99	30.50 ± 5.11	14.75 ± 4.69	28.25 ± 9.22	0.127
Biomass (mg/m^2)	17.79 ± 10.81	23.51 ± 5.53	16.01 ± 8.32	30.69 ± 10.52	0.409

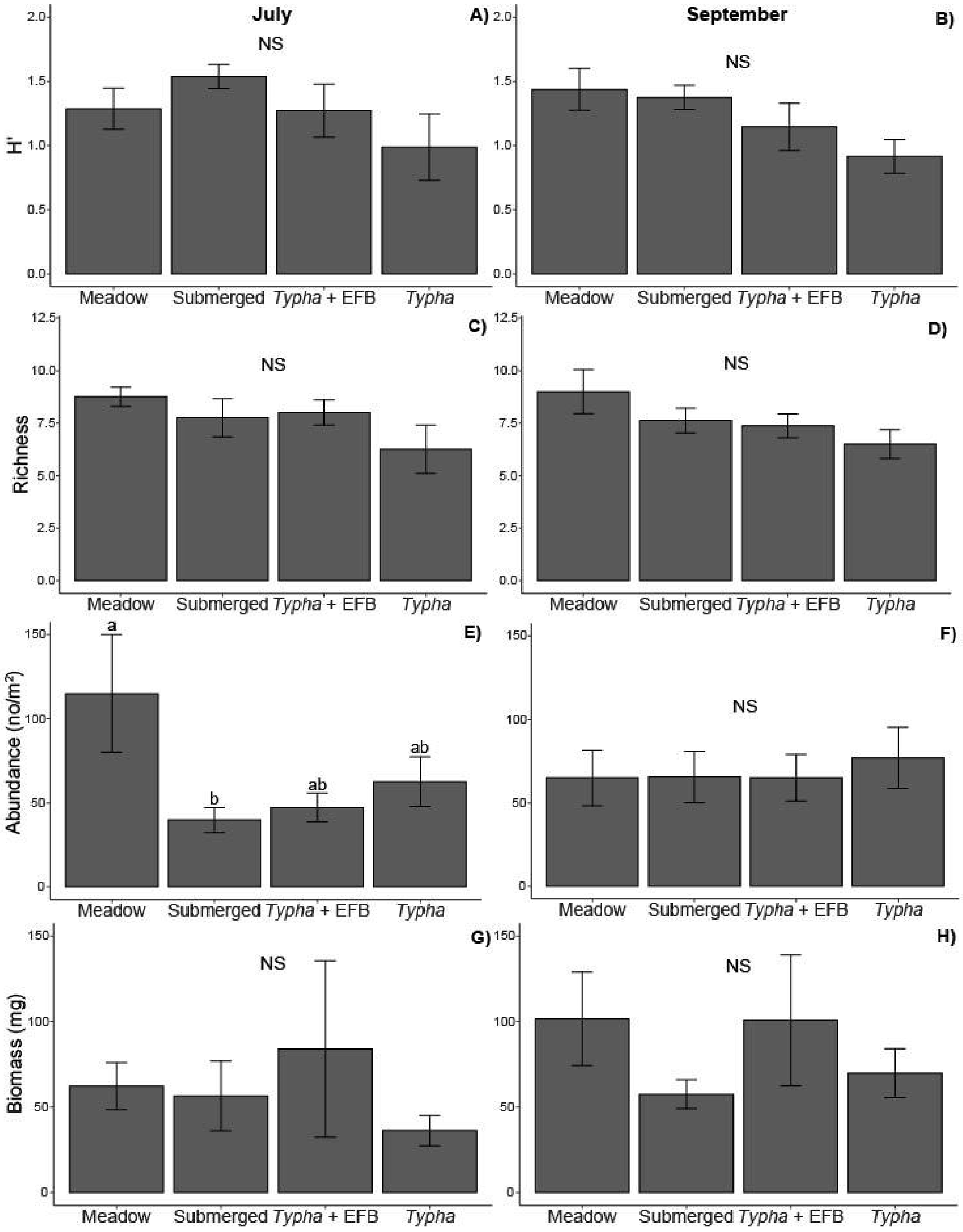


Figure 6. Mean macroinvertebrate Shannon-Wiener diversity (a, b), richness (c, d), abundance (e, f), and biomass (g, h) from Munuscong Bay, Michigan in July (a, c, e, g) and September (b, d, f, h) 2020 by plant community (n = 8). Error bars represent ± 1 SE. Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities, NS = no significant differences.

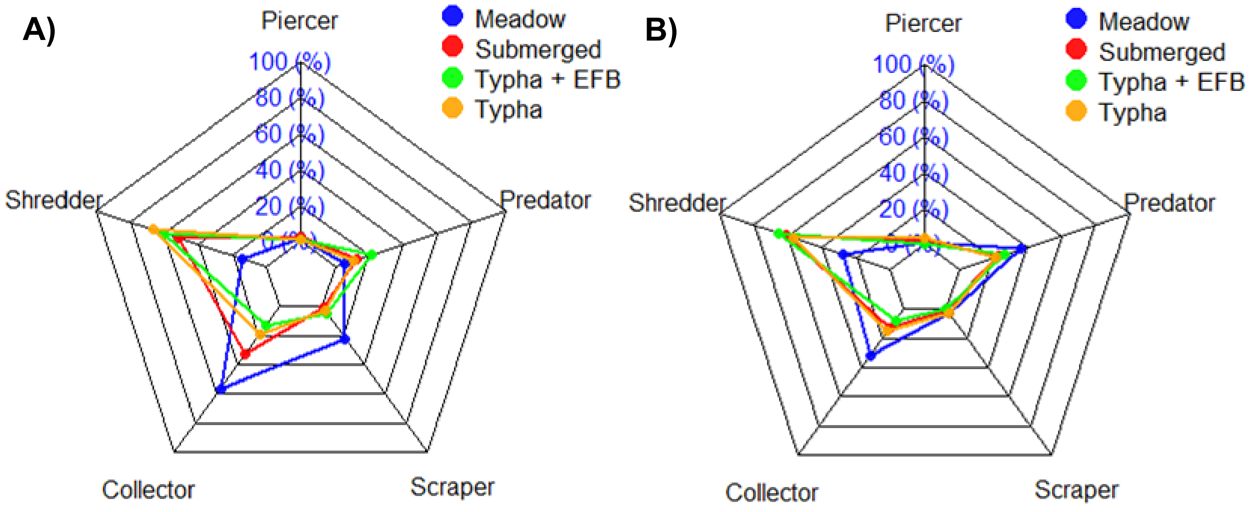


Figure 7. Proportion of different macroinvertebrate functional feeding groups present in Munuscong Bay, Michigan in a) July and b) September 2020 by plant community (meadow, submerged, *Typha* + EFB, *Typha*; n = 8). Proportions are based on abundance data for all taxa present at the plot-level.

I found significant differences in macroinvertebrate functional feeding group composition in July and September. The proportion of collectors in the meadow community was significantly higher than the *Typha* and *Typha* + EFB communities in July ($p = <0.001$, Table 5, Fig. 7a), while in September collector abundance in the meadow community was trending higher compared to other plant communities ($p = 0.191$, Table 5, Fig. 7b). In both July and September, Shredders were significantly more abundant in submerged, *Typha*, and *Typha* + EFB communities compared to the meadow community ($p = <0.001$), except in September there was no significant difference in shredder abundance between the meadow and *Typha* communities ($p = 0.099$, Fig. 7b). Scrapers were significantly more abundant in the meadow community compared to all other plant communities in July ($p = <0.001$, Table 5, Fig. 7a), although there was no significant difference in scraper abundance between the meadow and *Typha* communities in September ($p = 0.282$, Table 5, Fig. 7b). There was no significant difference in piercer and predator abundance between plant communities in July or September (Table 5, Fig. 7).

Table 5. Proportion data (%) of macroinvertebrate functional feeding group abundance (mean ± SE) in July and September 2020 from Munuscong Bay, Michigan separated by plant community (meadow, submerged, *Typha* + EFB, *Typha*; n = 8). Non-overlapping letters represent significant differences ($p < 0.05$) between plant communities as determined by ANOVA and Tukey's HSD. Data were square root transformed when necessary to meet model assumptions. Differences in non-parametric data were determined using a Kruskal-Wallis and Wilcox test.

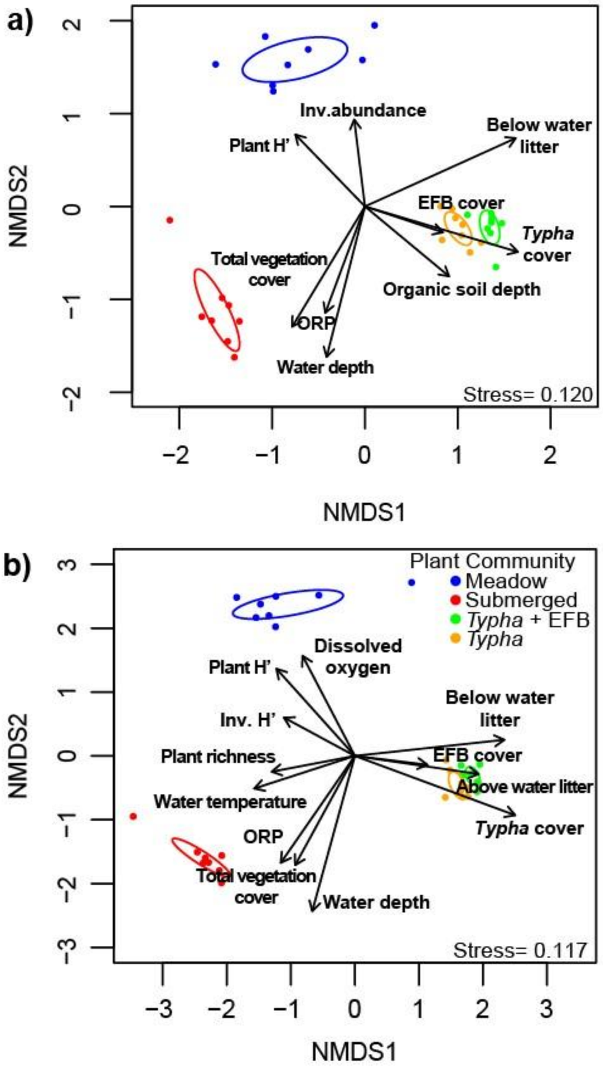
Variable	Meadow	Submerged	*Typha* + EFB	*Typha*	*p*
July					
Collectors	56.08 ± 9.09^{a}	32.62 ± 3.10^{ab}	13.25 ± 5.28^{b}	19.20 ± 7.56^{b}	<0.001
Shredders	14.39 ± 7.08^{a}	51.13 ± 4.50^{b}	59.96 ± 9.67^{b}	66.60 ± 10.73^{b}	<0.001
Piercers	1.69 ± 0.83	2.56 ± 1.70	1.08 ± 0.61	0.73 ± 0.41	0.803
Scrapers	21.90 ± 5.53^{a}	0.80 ± 0.61^{b}	4.43 ± 1.28^{b}	2.84 ± 1.57^{b}	<0.001
Predators	5.94 ± 1.58	12.89 ± 2.63	21.28 ± 6.78	10.62 ± 5.21	0.127
September					
Collectors	31.74 ± 10.76	13.14 ± 3.58	7.37 ± 2.71	15.27 ± 5.63	0.191
Shredders	27.45 ± 8.44^{a}	61.41 ± 5.45^{b}	65.37 ± 9.15^{b}	57.04 ± 10.89^{ab}	0.018
Piercers	1.56 ± 0.91	1.94 ± 1.77	0.21 ± 0.14	3.87 ± 1.34	0.069
Scrapers	2.78 ± 0.68^{a}	0.42 ± 0.33^{b}	0.00^{b}	2.49 ± 1.55^{ab}	0.004
Predators	36.47 ± 9.29	23.08 ± 5.18	27.05 ± 7.21	21.34 ± 10.27	0.443

Multivariate Community Analysis

Using multivariate analysis of plant species assemblage in each plant community, I found significant differences in community composition between plant communities in July and September. PERMANOVA results confirmed plant species composition was different in July (F = 19.99, $p = 0.01$) and September (F = 20.03, $p = 0.01$). Through PERMANOVA pairwise comparisons, I found that plant species composition of all plant communities were significantly different ($p < 0.05$) from one another across both time periods. NMDS plots illustrated clear separation in plant species composition between each plant community in both July (Fig. 8a) and September (Fig. 8b) with the meadow and submerged communities diverging from all other plant communities and the *Typha* and *Typha* + EFB communities showing less separation. The NMDS plots showed a good fit to the data with a stress of 0.120 in July and 0.117 in September (Clarke 1993). Fitted vectors for the July plant NMDS showed plant diversity, macroinvertebrate abundance, below water litter, EFB cover, *Typha* cover, organic soil layer depth, water depth, ORP, and total vegetation cover were significant factors that covaried with plant communities (Fig. 8a). Fitted vectors for the September plant NMDS showed plant diversity, DO, below water litter, above water litter, EFB cover, *Typha* cover, water depth, total vegetation cover, ORP, water temperature, plant richness, and macroinvertebrate diversity were significant factors that covaried with plant communities (Fig. 8b).

Macroinvertebrate community composition between plant communities also differed by plant community. PERMANOVA results in July (F = 5.39, $p = 0.01$) and September (F = 1.98, $p = 0.04$) confirm differences in macroinvertebrate community composition between plant communities. I found through PERMANOVA pairwise comparisons of July macroinvertebrate data that macroinvertebrate community compositions in all plant communities were significantly different ($p < 0.05$) from one another except the *Typha* and *Typha* + EFB communities ($p = 0.70$). NMDS plots illustrated separation between macroinvertebrate communities in each plant community. In July, the meadow and submerged communities diverged from all other plant communities while the *Typha* and *Typha* + EFB communities overlapped (Fig. 8c). The NMDS showed a good fit to the data with a stress of 0.158 (Clarke 1993). Fitted vectors for the July macroinvertebrate NMDS showed macroinvertebrate diversity, total vegetation cover, ORP, water depth, plant diversity, macroinvertebrate abundance, below water litter, and *Typha* cover were significant factors that covaried with plant communities (Fig. 8c).

PERMANOVA pairwise comparison of September macroinvertebrate data found macroinvertebrate community composition in the submerged community was significantly different from the meadow (F = 2.02, $p = 0.04$) and *Typha* (F = 3.51, $p = 0.04$) communities, while it did not differ from the *Typha* + EFB community (F = 0.93, *p* = 0.41). Macroinvertebrate community composition in the meadow community was not significantly different from the *Typha* + EFB (F = 1.90, *p* = 0.06) and *Typha* (F = 2.07, *p* = 0.08), and the *Typha* and *Typha* + EFB communities did not differ from each other as well (F = 1.43, *p* = 0.20). There was more overlap in macroinvertebrate community composition between all plant communities in the September NMDS (Fig. 8d) compared to July, with greater divergence between the *Typha* and *Typha* + EFB communities and more overlap between the meadow community and all other plant communities. The submerged and *Typha* + EFB communities also had more overlap between them. The September macroinvertebrate NMDS showed a good fit to the data with a stress of 0.149 (Clarke 1993). Fitted vectors for the September macroinvertebrate NMDS showed total vegetation cover, pH, water depth, macroinvertebrate diversity, water temperature, macroinvertebrate abundance, and macroinvertebrate biomass were significant factors that covaried with plant communities (Fig. 8d).


a)
NMDS1
NMDS2
Inv.abundance
Plant H'
Below water litter
EFB cover
Typha cover
Organic soil depth
Total vegetation cover
ORP
Water depth
Stress= 0.120
b)
Plant Community
Meadow
Submerged
Typha + EFB
Typha
Dissolved oxygen
Plant H'
Inv. H'
Plant richness
Water temperature
ORP
Total vegetation cover
Water depth
Below water litter
EFB cover
Above water litter
Typha cover
Stress= 0.117

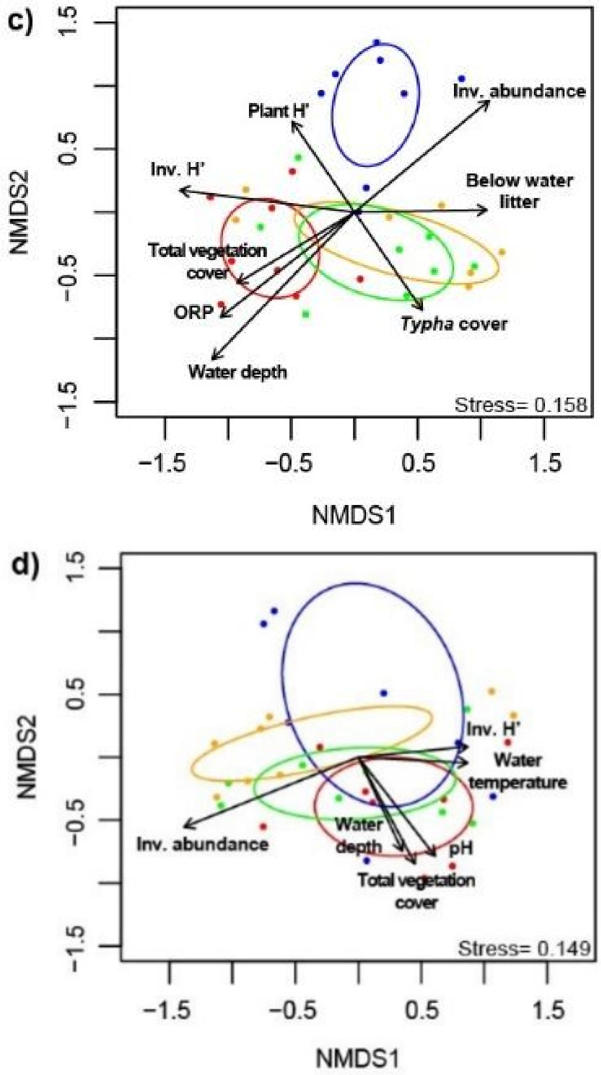


Figure 8. Non-metric multidimensional scaling ordination plots of 2020 plant (a, b) and macroinvertebrate (c, d) communities from July (a, c) and September (b, d) by plant community (meadow, submerged, *Typha* + EFB, *Typha*) at Munuscong Bay, Michigan (n = 8). Points represent percent cover for plant community ordination plots and abundance for macroinvertebrate community ordination plots of all species present in each 1 × 1 m plot and ovals represent one standard deviation around the mean location of each group. Fitted vectors are significant ($p < 0.05$) and their length is proportional to their explanatory strength. Inv. = macroinvertebrate.

Using indicator species analysis, I found that several plant species were significantly associated with each plant community. In July, *Calamogrostis canadensis*, *Carex stricta*, *C. lacustris*, *Phalaris arundinacea*, and *Persicaria amphibia* corresponded with the meadow community; *Nymphaea odorata*, *Ceratophyllum demersum*, *Myriophyllum sibiricum*, *Potamogeton gramineus* and *Potamogeton* spp. corresponded with the submerged community; *Hydrocharis morsus-ranae* and *Typha* × *glauca* corresponded with the *Typha* + EFB community; and *Typha* × *glauca* and *Equisetum fluviatile* corresponded with the *Typha* community (Table 6). *Utricularia vulgaris* was an indicator species in each plant community except the *Typha* + EFB community. In September, *C. canadensis*, *C. stricta*, *P. arundinacea*, and *U. vulgaris* corresponded with the meadow community; *N. odorata*, *C. demersum*, *M. sibiricum*, *Nuphar variegata*, *P. gramineus* and *Lemna trisulca* corresponded with the submerged community; *H. morsus-ranae* and *Typha* × *glauca* corresponded with the *Typha* + EFB community; and *Typha* × *glauca* and *U. vulgaris* corresponded with the *Typha* community (Table 6).

Indicator species analysis also found macroinvertebrate taxa that were significantly associated with each plant community. In July, *Planorbula* spp., Chironomids, and *Bezzia* spp. corresponded with the meadow community and *Holocentropus* spp. corresponded with the submerged community, while there were no significant taxa that were associated with the *Typha* and *Typha* + EFB communities (Table 6). In September, there were only two taxa that were significantly associated with any plant communities: *Planorbula* spp. corresponded to both the meadow and *Typha* communities while *Epitheca* spp. corresponded to the submerged and *Typha* + EFB communities (Table 6). Indicator species analysis of macroinvertebrates collected by Hester-Dendy samplers found that *Planorbula* spp. corresponded with the meadow community (indicator value = 0.674, $p = 0.01$) and *Holocentropus* spp. corresponded with the submerged community (indicator value = 0.791, $p = 0.01$).

Table 6. Indicator species analysis results for plant and macroinvertebrate data from Munuscong Bay, Michigan in July and September 2020 shown by plant community (meadow, submerged, *Typha* + EFB, *Typha*; n = 8). All taxa shown are significant ($p < 0.05$). Indicator values range from 0 (no indication) to 1.0 (perfect indication).

	July		September	
Taxa	Indicator Value	*p*	Indicator Value	*p*
Meadow				
Macroinvertebrate				
Planorbula spp.	0.966	0.005	0.707	0.01
Chironomidae	0.922	0.04		
Bezzia spp.	0.707	0.015		
Plant				
Calamagrastis canadensis	1	0.005	0.935	0.005
Carex stricta	0.93	0.005	0.932	0.005
Carex lacustrus	0.707	0.015		
Phalaris arundinacea	0.707	0.01	0.707	0.015
Persicaria amphibia	0.612	0.025		
Utricularia vulgaris	0.798	0.045	0.668	0.05
Submerged				
Macroinvertebrate				
Holocentropus spp.	0.848	0.025		
Epitheca spp.			0.612	0.035
Plant				
Nymphaea odorata	0.935	0.005	0.935	0.005
Ceratophyllum demersum	0.836	0.005	0.98	0.005
Utricularia vulgaris	0.798	0.045		
Myriophyllum sibiricum	0.791	0.005	0.866	0.005
Nuphar variegata			0.707	0.02
Potamogeton gramineus	0.779	0.005	0.685	0.015
Lemna trisulca			0.671	0.035
Potamogeton spp.	0.612	0.05		
Typha + EFB				
Macroinvertebrate				
Epitheca spp.			0.612	0.035
Plant				
Typha × glauca	1	0.005	1	0.005
Hydrocharis morsus-ranae	0.977	0.005	0.971	0.005
Typha				
Macroinvertebrate				
Planorbula spp.			0.707	0.01
Plant				
Typha × glauca	1	0.005	1	0.005
Utricularia vulgaris	0.798	0.045	0.668	0.05
Equisetum fluviatile	0.624	0.02		

Environmental Factors Affecting Macroinvertebrates

In July, macroinvertebrate diversity tended to increase with increasing DO in July ($r^2 = 0.21$, $p = 0.005$, Fig. 9a) and ORP ($r^2 = 0.11$, $p = 0.039$) while macroinvertebrate abundance tended to decrease with increasing water depth ($r^2 = 0.34$, $p < 0.001$, Fig. 10a).

Macroinvertebrate diversity, richness, abundance, and biomass had no relationships with any other plant or environmental variables in July (Fig. 9c, 9e, 9g). The proportion of collectors sampled in July tended to increase with increasing plant diversity ($r^2 = 0.16$, $p = 0.013$, Fig. 10c) while the proportion of shredders sampled tended to decrease with increasing plant diversity ($r^2 = 0.24$, $p = 0.003$, Fig. 10e), and the proportion of scrapers sampled tended to decrease with increasing floating vegetation cover ($r^2 = 0.21$, $p = 0.005$, Fig. 10g).

In September, macroinvertebrate diversity tended to increase with increasing DO ($r^2 = 0.18$, $p = 0.01$, Fig. 9b) as well as increasing total vegetation cover ($r^2 = 0.11$, $p = 0.01$, Fig. 9d), plant diversity ($r^2 = 0.22$, $p = 0.004$, Fig. 9f), plant richness ($r^2 = 0.14$, $p = 0.02$), and water temperature ($r^2 = 0.14$, $p = 0.022$, Fig. 9h). In contrast to July, macroinvertebrate abundance did not show any significant relationship to water depth in September ($r^2 = 0.01$, $p = 0.269$, Fig. 10b). Macroinvertebrate richness also tended to increase with increasing DO ($r^2 = 0.11$, $p = 0.035$) and increasing plant richness ($r^2 = 0.10$, $p = 0.043$) in September. The proportion of collectors sampled in September had no significant relationship with plant diversity ($r^2 = 0.01$, $p = 0.24$, Fig. 10d) while the proportion of shredders sampled continued to decrease with increasing plant diversity ($r^2 = 0.18$, $p = 0.01$, Fig. 10f), and the proportion of scrapers sampled had no significant relationship with floating vegetation cover ($r^2 = 0.06$, $p = 0.093$, Fig. 10h). Submerged vegetation cover had no significant effects on any macroinvertebrate metrics across both time periods.

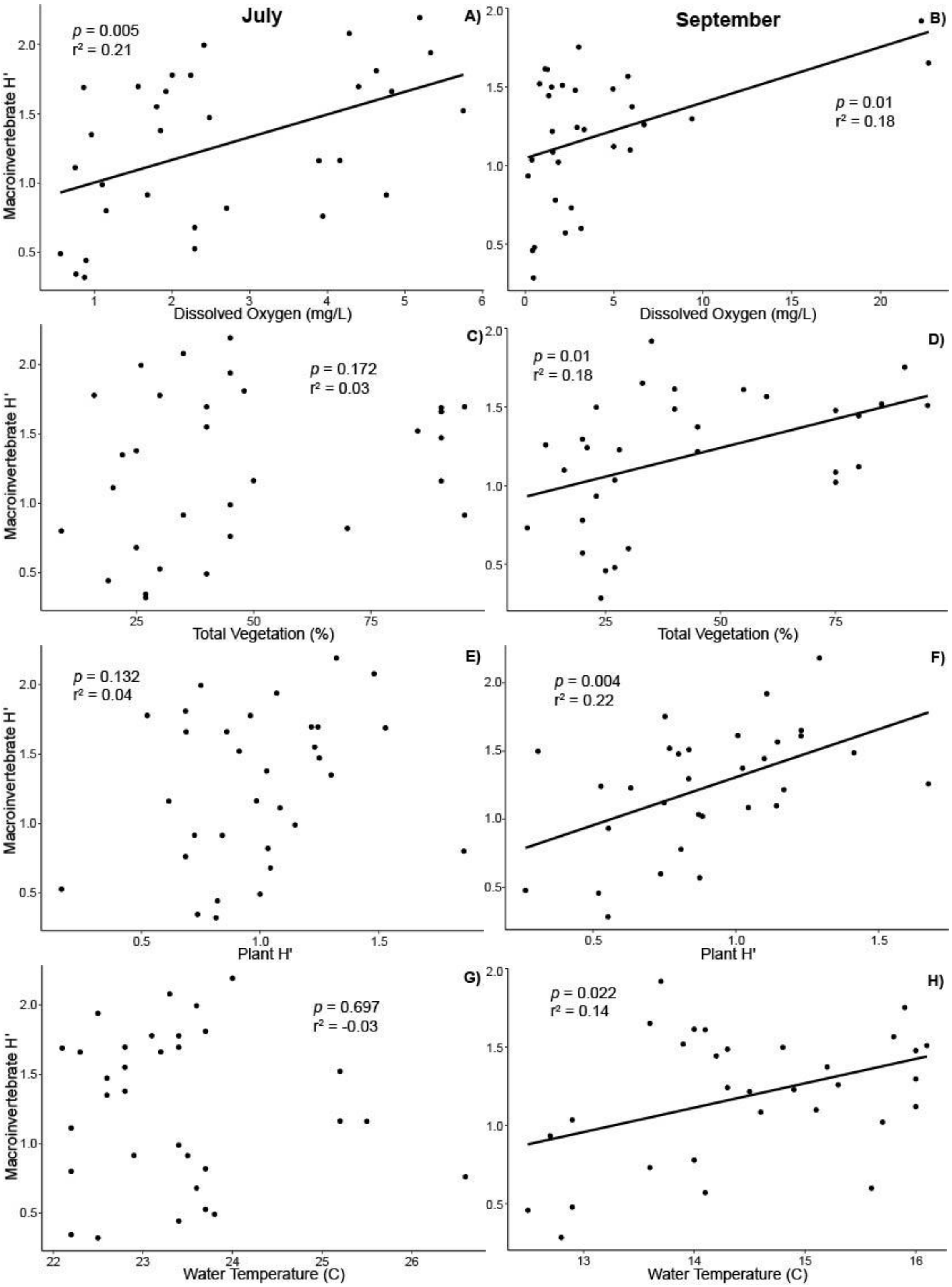


Figure 9. Correlations for macroinvertebrate Shannon-Wiener diversity and dissolved oxygen (a, b), total vegetation (c, d), plant diversity (e, f), and water temperature (g, h) in July (a, c, e, g) and September (b, d, f, h) 2020 at Munuscong Bay, Michigan (n = 32). Data were log or square root transformed when necessary to meet model assumptions. R^2 correlation coefficients and *p*-values are shown. Black lines show significant linear models.

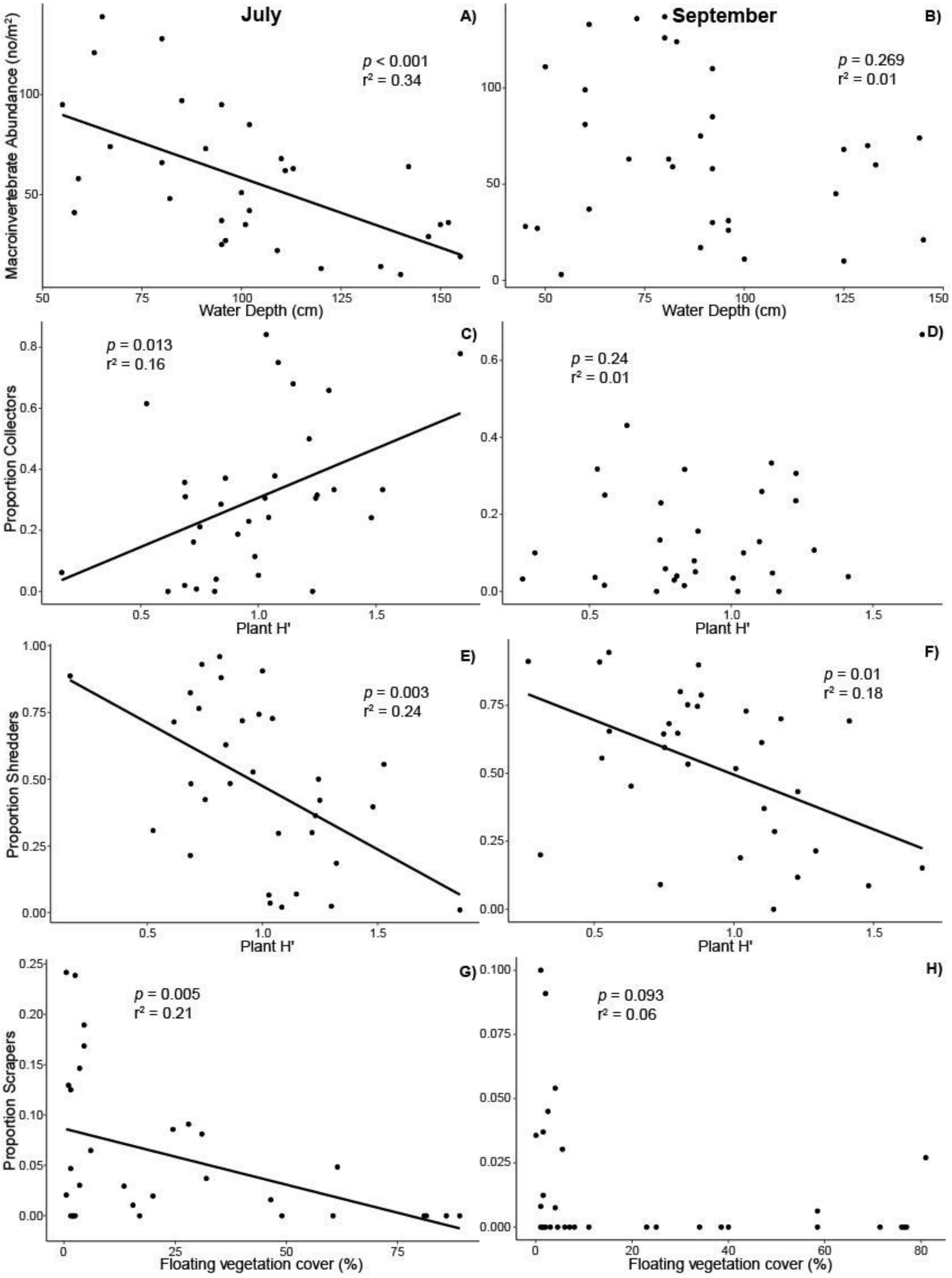


Figure 10. Correlations for macroinvertebrate abundance and water depth (a,b), collectors and plant diversity (c, d), shredders and plant diversity (e, f), and scrapers and floating vegetation cover in July (a, c, e, g) and September (b, d, f, h) 2020 from Munuscong Bay, Michigan (n = 32). Data were square root transformed when necessary to meet model assumptions. R^2 correlation coefficients and *p*-values are shown. Black lines show significant linear models.

DISCUSSION

This study investigated plant and macroinvertebrate community responses to a secondary invasion of EFB in a *Typha*-dominated Great Lakes coastal wetland. Secondary EFB invasion increases total vegetation cover within *Typha* and reduces submerged vegetation cover, shifting plant community composition compared to *Typha* communities. EFB invasion is also associated with extremely low DO concentrations. Macroinvertebrate diversity, richness, abundance, biomass, or community composition did not change in response to EFB invasion. However, macroinvertebrate diversity had varying relationships with total vegetation cover, plant diversity, and DO which indicate that EFB does affect macroinvertebrate communities. Macroinvertebrates that depend on submerged vegetation or that are not hypoxia-tolerant are most likely to be negatively affected by EFB invasion. This is the only study that has documented the effects of EFB on macroinvertebrates in the Great Lakes. Zhu et al. (2015) investigated the effects of EFB on macroinvertebrates in Oneida Lake, New York and compared areas invaded by EFB to unvegetated areas that would be left behind after EFB removal. My study compared an area invaded by both *Typha* and EFB to three other plant communities to assess the effects of EFB invasion and plant community structure on macroinvertebrates.

Plant Community Responses to EFB Invasion

EFB appears to have a profound effect on submerged plants as there was significantly less submerged vegetation cover in the *Typha* + EFB community compared to all other plant communities. Total vegetation cover nearly doubled in the *Typha* + EFB community compared to the *Typha* community, mainly due to a >25% increase in floating vegetation cover in the *Typha* + EFB community driven by EFB (Fig. 5). *Utricularia vulgaris* was the most common submerged species in the *Typha* community and was largely absent from the *Typha* + EFB community, which was the only plant community where *Utricularia vulgaris* was never an indicator species (Table 6). Catling et al. (1988) found that EFB has a deleterious effect on *Utricularia vulgaris*, and that *Utricularia vulgaris* cover declined to 1/8 of its typical cover in the presence of EFB. Increased floating vegetation cover from EFB displaces submerged vegetation and restructures plant communities within *Typha* stands. The loss of highly dissected submerged vegetation, such as *Utricularia vulgaris*, within *Typha* stands may reduce macroinvertebrate abundance (Schultz and Dibble 2012), particularly for taxa such as *Holocentropus*, *Acentria*, and *Parapoynx* that shelter in submerged plants. However, submerged vegetation cover within *Typha* stands is already relatively low (Lawrence et al. 2016) and highly dissected plant species do not always support greater macroinvertebrate abundance compared to broad leaved species (Cyr and Downing 1988a). Therefore, the reduction of submerged vegetation cover within *Typha* due to EFB invasion likely negatively affects specific macroinvertebrate taxa rather than the whole macroinvertebrate community.

Plant species composition was significantly different between all four plant communities in this study, including between the *Typha* and *Typha* + EFB communities (Fig. 8). Plant community types corresponded to the water depth gradient with the submerged community at the lowest elevations, followed by *Typha* and *Typha* + EFB communities at a medium elevation, and the meadow community at the highest elevation. The difference in community composition between the *Typha* and *Typha* + EFB communities is driven by the reduction of *Utricularia vulgaris* and *Equisetum fluviatle* cover while other lemnid plants such as *Spirodella polyrhiza* increased in cover in the *Typha* + EFB community. The stratification of plant communities by water depth is consistent with Keddy and Ellis (1985) as plant species grow according to their water-depth tolerance. However, in contrast with my study, Thomas and Daldorph (1991) found that plant community structure in enclosure-exclosure experiments was unaffected by EFB introduction after six months. EFB has been present in Munuscong Bay for over 10 years, indicating that older EFB populations affect plant community composition more severely. Long-term EFB dominance in *Typha*-dominated wetlands likely reduces submerged vegetation cover and affects plant community composition more than what could be observed in a short-term mesocosm study.

Macroinvertebrate Response to Plant Communities

I found no significant differences in macroinvertebrate diversity, richness, or biomass in dipnet sampling between plant communities despite significant differences in plant diversity, vegetation cover, and plant community composition (Fig. 6). Only macroinvertebrate abundance in July was significantly different between the meadow and *Typha* communities because of high Chironomid abundance in the meadow community. Although there were no differences in macroinvertebrate diversity, NMDS (Fig. 8), indicator species analysis (Table 6), and functional feeding group composition (Fig. 7, Table 5) highlight that macroinvertebrate communities varied between plant communities. These results are consistent with other studies that plant community composition in wetlands affects macroinvertebrate community composition (Burton et al. 2002, Voights 1976, Walker et al. 2012). The similarities in macroinvertebrate metrics and community composition between *Typha* and *Typha* + EFB communities indicate that *Typha* may have a stronger effect on macroinvertebrate communities than EFB. Lawrence et al. (2016) and Lishawa et al. (2010) found that *Typha* homogenizes plant communities and structural diversity, indicating similar habitat structure between *Typha* and *Typha* + EFB communities. In addition to this, invasive *Typha* has been established in Munuscong Bay over 20 years longer than EFB, and litter accumulation and soil organic matter increase with *Typha* stand age while plant diversity decreases with stand age (Lishawa et al. 2014, Tuchman 2009, Vaccaro et al. 2009). My data show that EFB appears to exacerbate some of the ecological impacts of *Typha* (i.e., reduced DO and submerged vegetation cover) rather than introduce new ecological impacts.

Linear regression models found that macroinvertebrate diversity increased with increasing total vegetation cover and plant diversity in September, indicating that the secondary invasion of EFB within *Typha* should increase macroinvertebrate diversity. It is common for macroinvertebrate diversity to increase when habitat heterogeneity increases due to greater plant diversity, and macroinvertebrates also respond positively to increased vegetation cover with increased abundance and biomass (Cyr and Downing 1988b, Schultz and Dibble 2012). Low plant diversity in the *Typha* community in conjunction with relatively low vegetation cover is indicative of greater habitat homogeneity, resulting in poor macroinvertebrate habitat. Other invasive plants like *Trapa natans*, an aquatic plant with submerged stalks and floating leaves similar to EFB, show similar trends where increasing vegetation cover corresponded with increased macroinvertebrate diversity. Strayer et al. (2003) and Kornijów et al. (2010) hypothesized that mats of *Trapa natans* in the Hudson River increased plant biomass and could support greater macroinvertebrate abundance and diversity compared to beds of native *Vallisneria americana*. Increased vegetation cover resulting from EFB invasion could increase macroinvertebrate diversity by increasing plant biomass that is available to support macroinvertebrate populations within *Typha* stands. Contrary to previous literature however, I found no significant trends in macroinvertebrate abundance or biomass related to vegetation cover or plant diversity.

The results of this study partially supported my hypothesis that functional feeding group composition in native plant communities would be more centered around algae and fine organic matter (i.e., more collectors and scrapers and less shredders) as functional feeding group composition in the submerged community was more similar to the *Typha* and *Typha* + EFB communities (Figure 7, Table 5). Observing functional feeding group composition reflects the relative availability of different food sources within a habitat as those mechanisms increase intake efficiency for specific foods (Cummins and Klug 1979). Differences between sedge and *Typha* leaf litter quality may explain differences in functional feeding group composition between plant communities. Leroy and Marks (2006) found that leaf litter quality and diversity affect litter decomposition rates, with high quality and diverse litter mixtures decomposing faster than low quality single species litter. These findings support my data as the meadow community had the highest plant diversity with high quality litter and supported a greater abundance of collectors that feed on fine particulate organic matter. The low quality *Typha* litter in *Typha* and *Typha* + EFB communities (Table 2) provided an abundant food source for shredders, although decomposed into fine particulate organic matter slower. Therefore, litter decomposition rates are faster in meadow communities, and they support more collectors compared to *Typha*-dominated communities.

Scraper abundance was relatively low in all plant communities in this study except the meadow community in July. Floating vegetation cover particularly affected scraper abundance as plots with little to no floating vegetation cover had the greatest abundance of scrapers (Fig. 10g).

Algae and biofilms play an important role in providing food for scraper macroinvertebrates (Campeau et al. 1994). Cattaneo et al. (1998) found that floating vegetation in a lake reduced light transmission to 7% and subsequently supported two to eight times less algal biomass and two to ten times fewer macroinvertebrates than submerged vegetation. In an inclusion-exclusion experiment, Catling et al. (1988) found that floating EFB mats decreased mean algae cover in July from 1.51% to 0.03% due to reduced light availability. These studies support my results, as an open canopy and little to no floating vegetation likely increased algal productivity in the meadow community while greater floating vegetation cover in the submerged and *Typha* + EFB communities reduced algal productivity. Therefore, increases in floating vegetation cover due to EFB invasion will decrease light availability and algal cover, reducing scraper macroinvertebrate abundance.

Dissolved Oxygen Dynamics

DO was relatively low throughout Munuscong Bay, measuring <5 mg/L in all plant communities except the meadow community in September (Fig. 4, Table 1). DO concentrations in September in the *Typha* + EFB community averaged <1 mg/L with the lowest concentration being 0.38 mg/L, over 1 mg/L lower than the previously lowest recorded DO concentration of 1.9 mg/L in Oneida Lake (Zhu et al. 2008). EFB mats may limit DO concentrations through multiple mechanisms. Floating wetland plants such as *Lemna minor*, *Trapa natans*, and *Hydrocotyle ranunculoides* reduce atmospheric gas exchange when they form dense mats (Morris and Barker 1977, Stiers et al. 2011, Strayer et al. 2003). However, the decrease in DO associated with the *Typha* + EFB community in September indicates that seasonal die-offs and subsequent decomposition of EFB in the fall reduces DO. Rose and Crumpton (1996) found that biomass additions from vegetation increase the pool of organic carbon in wetlands which increases oxygen demand. Lastly, decreased light availability and reduced submerged vegetation from high EFB cover would reduce oxygen production from photosynthesis in the water column (Rose and Crumpton 1996). The formation of dense EFB mats within *Typha* stands may exacerbate hypoxic conditions due to reducing gas exchange, increasing oxygen demand, and reducing photosynthetic rates.

I expected reduced macroinvertebrate diversity in the *Typha* + EFB community due to reduced DO (Fig. 9b). However, macroinvertebrate diversity was not reduced in the *Typha* + EFB community. Reduced DO in *Typha* + EFB communities could restructure macroinvertebrate communities, selecting for hypoxic-tolerant taxa that could survive such low DO concentrations (Spieles and Mitsch 2003). The macroinvertebrates collected from Munuscong Bay possess a variety of behavioral and physiological respiratory strategies that allow them to tolerate low DO conditions, including respiratory pigments such as hemoglobin, the use of atmospheric oxygen through collecting and carrying air bubbles or through movement to the well oxygenated surface of the water column to respire, flattened or small bodies with high surface-to-volume ratio to maximize cutaneous respiration, and elongated respiratory siphons that extend out of the water (Merritt et al. 2019). Macroinvertebrates may also use oxygen exuded from EFB roots to survive hypoxic conditions under EFB mats, a strategy used by macroinvertebrates under *Trapa natans* mats (Strayer et al. 2003, Kornijów et al. 2010). The low DO conditions in the *Typha* and *Typha* + EFB communities may discourage fish predation of macroinvertebrates as many fish species cannot tolerate low DO, benefitting macroinvertebrate communities and encouraging the colonization of hypoxic-tolerant macroinvertebrate taxa (Murkin et al. 1992, Schrank and Lishawa 2019, Wellborn et al. 1996). Therefore, the hypoxic conditions resulting from secondary

EFB invasion does not negatively affect wetland macroinvertebrates due to their adaptations for low DO conditions.

Effects of Water Depth on Plant and Macroinvertebrate Communities

Although my results did not support any relationship between macroinvertebrate diversity and water depth, I found that macroinvertebrate abundance was negatively related to water depth in July. Consistent with my results, Cyr and Downing (1988b) observed that macroinvertebrate abundance is negatively related to water depth. However, flooding regime, temperature, DO, water chemistry, wave energy, and litter dynamics can affect macroinvertebrate metrics in addition to water depth (Gathman and Burton 2011). Lake Michigan-Huron water levels at the time of this study were at a historic record high and averaged approximately 1 m greater than the long-term average annual water depth (USACE 2021). Record-high water levels likely affected macroinvertebrate metrics and abundance, diversity, or biomass may have been higher under lower water conditions. Record-high water levels in Lake Ontario coastal wetlands in 2017 and 2019 reduced total vegetation cover with most of the vegetation cover loss occurring in meadow communities (Smith et al. 2021). High water levels likely affected the plant community in Munuscong Bay and reduced vegetation cover in the meadow community, which may have lowered macroinvertebrate diversity or other metrics due to lost habitat structure.

Macroinvertebrate taxa in Munuscong Bay demonstrated a shift upslope in positioning, as high flooding likely reduced the abundance of high-elevation specialists (i.e., low water depth) such as *Bezzia* (Ceratopogonidae), *Neoscutopterus* (Dytiscidae), *Limnephilus* (Limnephilidae), and *Planorbula* (Planorbidae), while chironomid abundance increased in the meadow community as they are characterized as rapid-reversers that quickly colonize the meadow under high water. Flooding regimes and water depth gradients affect macroinvertebrate community structure directly by limiting taxa present to only those with life history and behavioral traits that are adapted to flooded conditions (Baumgärtner et al. 2008, Schneider and Frost 1996), and indirectly by driving changes in plant communities and water chemistry (Wilcox and Nichols 2008). Gathman and Burton (2011) found that water level is a stronger driver of macroinvertebrate positioning and communities than vegetation zonation, and that most taxa shift or expand their distributions upslope during high-water periods. Macroinvertebrate community composition in Munuscong Bay was likely shifted under high-water conditions that favored flood-adapted taxa.

CONCLUSION

Implications for Great Lakes Macroinvertebrates

Within *Typha* stands, the secondary invasion of EFB impacts plant communities. *Typha* + EFB communities have altered plant community composition, increased total vegetation cover, and reduced submerged vegetation cover compared to *Typha* communities. The structure provided by EFB does not appear to fully restore the functional structure of native submerged vegetation within *Typha* as there were seasonal differences in macroinvertebrate community composition between the submerged and *Typha* + EFB communities. However, secondary EFB invasion does not reduce total macroinvertebrate abundance, diversity, biomass, or alter macroinvertebrate community composition compared to *Typha* communities, which is consistent with the conclusion of Zhu et al. (2018) that the effects of EFB on macroinvertebrates are not as serious as previously thought. The similarity of the macroinvertebrate communities between the *Typha* and *Typha* + EFB communities suggest that the ecological impacts of *Typha* overshadow the impacts of EFB. While submerged vegetation was reduced under EFB, the overall increases in total vegetation cover are associated with increases to macroinvertebrate abundance and diversity. In addition to this, the low DO conditions associated with not only EFB, but also *Typha*, sedge meadows, and submerged vegetation, are not very impactful as most wetland macroinvertebrates possess multiple respiratory strategies to tolerate the low DO conditions. However, my study suggests that EFB invasion affects specific macroinvertebrate taxa rather than the whole community, such as taxa that feed on algae, shelter in exclusively submerged vegetation, and cannot tolerate hypoxia. GLCWs invaded by EFB will likely experience decreases in gastropods and other scraper taxa, as well as some Trichopteran and Crambid species.

This study was limited to two sampling events in one GLCW within a year, and further long-term studies in other GLCWs are needed to confirm the results of this study. This study was also unable to observe the ecological impacts of EFB separately from *Typha*. Future studies on EFB invasion in native plant communities are needed to determine the ecological impacts of EFB on macroinvertebrates without the influence of *Typha*. In addition to this, data on light transmission and algal biomass under EFB mats along with scraper abundance in future studies would confirm the hypothesis that EFB reduces algae cover and strongly affects scrapers. Lastly, record-high water levels in the Great Lakes likely affected the plant and macroinvertebrate community in this study. Future studies on macroinvertebrate communities in GLCWs should take water-level fluctuations and their impacts on macroinvertebrates and vegetation into account.

Implications for Management

Invasive *Typha* is widespread throughout the Great Lakes and is the dominant vegetation in ~28,000 ha of GLCW (Carson et al. 2018). Because *Typha* facilitates EFB invasion, EFB has a large potential invasion range in the Great Lakes basin (Monks et al. 2019). Current strategies for EFB management include frequent hand-pulling, shading with a shade cloth at 70% shade or higher, and herbicide treatment (Zhu et al. 2014, 2015, 2018). Hand-pulling and shading both reduce vegetation cover and create frequent disturbances that decrease macroinvertebrate habitat quality. Zhu et al. (2014, 2015) found that shading decreases amphipod density and reduces submerged vegetation biomass. The results of my study along with other studies (Cyr and Downing 1988b, Schultz and Dibble 2012) indicate that reductions in total vegetation cover from EFB management methods would reduce macroinvertebrate abundance and diversity. Management of established EFB populations within *Typha* stands without addressing the *Typha* would likely cause more harm than good to the macroinvertebrate community as EFB could invade into the *Typha* again.

Management of *Typha* is crucial for managing the spread of EFB and preventing new invasions, and it is the most effective and cost-efficient control method available (Monks et al. 2019, Zhu et al. 2018). Harvesting *Typha* biomass creates a large disturbance that temporarily reduces plant cover but increases plant diversity and decreases *Typha* dominance and biomass (Lishawa et al. 2015). A decrease in *Typha* dominance from harvesting would reduce the facilitation of EFB and effectively control its spread, and my results show that increased plant diversity and DO from reducing *Typha* and EFB cover would increase macroinvertebrate diversity. My study implies that harvesting *Typha* biomass and restoring native plant communities would be the most beneficial EFB management method for alleviating environmental stressors and supporting diverse and abundant macroinvertebrate communities that fish and waterfowl populations can utilize.

APPENDIX A

LIST OF MACROINVERTEBRATE TAXA

- **Amphipoda**
  - Crangonyctidae
    - *Crangonyx* sp.
- **Araneae**
- **Coleoptera**
  - Dytiscidae
    - *Neoscutopterus* sp.
  - Haliplidae
    - *Haliplus* sp.
- **Diptera**
  - Ceratopogonidae
    - *Bezzia* sp.
  - Chironomidae
  - Culicidae
    - *Culex* sp.
    - *Mansonia* sp.
  - Dixidae
    - *Dixella* sp.
  - Limnoiidae
    - *Eloeophila* sp.
  - Ptychopteridae
    - *Bittacomorpha* sp.
  - Stratiomyidae
    - *Stratiomys* sp.
- **Ephemeroptera**
  - Baetidae
    - *Neocloeon* sp.
  - Caenidae
    - *Caenis* sp.
- **Gastropoda**
  - Physidae
    - *Physella* sp.
  - Planorbidae
    - *Planorbula* sp.
- **Hemiptera**
  - Corixidae
    - *Hesperocorixa* sp.
  - Belostomatidae
    - *Belostoma* sp.
  - Nepidae
    - *Ranatra* sp.
  - Pleidae
    - *Neoplea* sp.
  - Notonectidae
    - *Notonecta* sp.
  - Gerridae
    - *Trepobates* sp.
  - Mesoveliidae
    - *Mesovelia* sp.
- **Hirudinea**
- **Isopoda**
  - Asellidae
    - *Caecidotea* sp.
- **Lepidoptera**
  - Crambidae
    - *Acentria* sp.
    - *Paraponyx* sp.
- **Odonata**
  - Aeshnidae
    - *Anax* sp.
  - Coenagrionidae
    - *Enallagma* sp.
    - *Ischnura* sp.
  - Corduliidae
    - *Cordulia* sp.
    - *Epitheca* sp.
  - Libellulidae
    - *Leucorrhinia* sp.
    - *Sympetrum* sp.
- **Oligochaeta**
  - Lumbriculidae
- **Trichoptera**
  - Phryganeidae
    - *Banksiola* sp.
    - Fabria sp.
  - Polycentropodidae
    - *Holocentropus* sp.
  - Leptoceridae
    - *Oecetis* sp.
  - Limnephilidae
    - *Limnephilus* sp.
- **Trombidiformes**
  - Hydrachnidia

APPENDIX B

LIST OF PLANT SPECIES

Bidens beckii

Calamogrostis canadensis

Carex aquatilis

Carex lacustris

Carex stricta

Ceratophyllum demersum

Elodea canadensis

Equisetum fluviatile

Lathyrus palustris

Lemna minor

Lemna trisulca

Myriophyllum sibiricum

Nymphaea odorata

Nuphar variegata

Persicaria amphibia

Phalaris arundinacea

Phragmites australis

Potamogeton natans

Potamogeton gramineus

Potamogeton spp.

Ricciocarpus natans

Riccia fluitans

Schoenoplectus acutus

Spirodela polyrhiza

Utrichularia minor

Utrichularia vulgaris

Valisneria americana

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VITA

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