THIRTY YEARS MONITORING THE FALL STANDING CROP BIOMASS OF MACROPHYTE COMMUNITIES IN HONEOYE LAKE

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INTRODUCTION

Macrophyte communities grow in the littoral zone of Honeoye Lake, a region where sufficient light is available along the bottom in the springtime to allow aquatic vegetation to develop from overwintering structures (e.g., bulbs, fragments, rhizomes, seeds, stolons, tubers, and turions), begin photosynthesizing, and grow upward in the water column. Some plants stay submerged in the water (submersed species), others have leaves floating on the surface (free-floating and floating attached species) and the remainder grow out of the water (emergent species). These habits of growth are often associated with decreasing water depth, respectively.

In Honeoye Lake, examples of submersed plants include water marigold (*Bidens beckii*), coontail (*Ceratophyllum demersum*), elodea (*Elodea canadensis*), water stargrass (*Heteranthera dubia*), Eurasian water milfoil (*Myriophyllum spicatum*), naiads, (*Najas* spp.), large-leaf pondweed (*Potamogeton amplifolius*), curly-leaf pondweed (*Potamogeton crispus*), sago pondweed (*Potamogeton pectinatus*), mall pondweed (*Potamogeton pusillus*), clasping-leaf pondweed (*Potamogeton richardsonii*), flat-stem pondweed (*Potamogeton zosterformis*), stiff white water buttercup (*Ranunculus longirostris*) and eelgrass (*Vallisneria americana*). Free-floating aquatic plants have their leaves just above the surface and roots hang free in the water beneath them. They are easily moved by winds and water currents. Common examples include lesser duckweed (*Lemna minor*), star-leaved duckweed (*Lemna trisulca*), greater duckweed (*Spirodela polyrhiza*), common bladderwort (*Utricularia vulgaris*), and the watermeals (*Wolffia* spp.). To the untrained eye, duckweeds and watermeals are often mistaken for green algae. Floating attached species have broad leaves at the water surface but they are rooted to the benthic substrate. Floating leaves are connected to the bottom by a petiole in water lilies (*Nuphar variegata* and *Nymphaea odorata*) or by stems with narrow underwater leaves in some pondweeds (*Potamogeton epihydrus* and *Potamogeton natans*). Emergent species are rooted in the shallow, shoreline waters where their basal portions are submerged but most leaves, branches and stems occur in the air directly above the water surface. Examples include button bush (*Cephalanthus occidentalis*), water willow (*Decodon verticillatus*), arrow arum (*Peltandra virginica*), pickerelweed (*Pontederia cordata*), and giant bur-reed (*Sparganium eurycarpum*). Most Honeoye Lake macrophyte communities are dominated by vascular plants but may also contain macro-algae like stoneworts (*Chara* spp.), aquatic mosses (*Fontinalis antipyretica*), and mosquito ferns (*Azolla caroliniana*). In recent years, quantities of filamentous green algae (e.g., *Hydrodictyon*, *Spirogyra*) have become more abundant as a matted growth on the lake bottom or as strands tangled with submersed vascular plants.

Diverse macrophyte communities are an essential component of healthy aquatic ecosystems. Their roots and other anchoring structures help keep bottom substrates in place. This reduces sediment re-suspension, thereby helping to minimize shoreline turbidity and benthic deposition that might otherwise have undesirable impacts on life stages of lake organisms, in particular, developing fish eggs residing on the lake bottom. Macrophyte stems and leaves can reduce wave energy thereby helping to protect lake shorelines from erosion. On a daily basis, macrophytes can enhance the dissolved oxygen supply in the water through their photosynthetic activity. Macrophytes may also improve water quality as they help control algal abundance by competitively "binding up" significant portions of a lake's nutrient budget. Most importantly, macrophytes are a critical habitat for many lake organisms, providing both food and shelter. Many invertebrates rely on aquatic plants during specific life history stages. Filter-feeders attach to plants as they ingest particles from surrounding waters. Insect larvae and nymphs cling to plant stems as they search for food. Algae attached to macrophytes are grazed on by snails and midges. Caddis fly and moth larvae feed directly on aquatic plant tissue. Habitat structure created by macrophytes provides food and shelter for juvenile and adult fish. Invertebrates living on aquatic plants are a fish food source. Some fish also graze directly on underwater leaves and stems. The architecture and density of aquatic plant cover influences the success of fish populations. For waterfowl and shorebirds, aquatic plants offer food, shelter and nesting materials. A diversity of plants can provide food throughout the seasons. Many waterfowl and shore birds consume invertebrates living on aquatic plants. Mammals, too, benefit from aquatic plants. River otters patrol the macrophyte communities hunting for food. Muskrats feed on shoreline emergents, especially giant bur-reed and cattail. Beaver dive down to dig out and feed on vegetation such as water lily tubers.

To assist the Ontario County Aquatic Vegetation Management program, this research provides recent information on aquatic plants within Honeoye Lake and, when compared with previous studies, helps to document long term ecological changes within the macrophyte communities. Specifically this report provides reliable and consistent data collected along multiple transects within the lake's littoral zone, documents patterns in fall standing crop biomass, identifies the relative importance of species that comprise the aquatic vegetation, brings particular emphasis on the changing role of aquatic invasive species, and compares 2014 data to similar data from 1984, 1994 and 2004.

LITERATURE REVIEW

Residing in one of several north-south glacially scoured valleys of western New York (Fairchild 1895), modern Honeoye Lake is a relic of a much larger Glacial Lake Honeoye that drained southward into Glacial Lake Naples when the retreating continental ice sheet margin blocked all north draining routes. By 11,500 years ago, a lake similar in surface dimensions to the modern lake was present in the valley but it was considerably deeper. Centuries of watershed erosion deposited silts and clays in the deeper waters of the lake, while coarse sands and gravels built points and beaches along the shoreline. The modern Honeoye Lake is the shallowest of the eleven Finger Lakes and has the second smallest surface area. Morphometric features of the lake are presented in TABLE 1.

European settlement in the Honeoye valley began the domestication of the lake's watershed lands. An excellent historical summary is presented in the opening chapter of The Honeoye Lake Book (Honeoye Lake Watershed Taskforce 1999). A year after its publication, FLCC was gifted the former Emil Muller home located in the southern Honeoye valley, soon to become the college's Muller Field Station. Shortly thereafter, faculty began a series of biological studies of the area including an extensive land use/land cover mapping project (Gilman 2004). Results of the mapping project and other watershed information are summarized in TABLE 2.

Water quality concerns and the formation of "lake protection" groups closely followed the rapid post-World War II development of the watershed. Historic photographs clearly depict an early 1900s agricultural landscape being replaced by residences and seasonal cottages. Abandoned hillside farmland began the slow process of natural succession back to forest cover. In these early decades, human activities negatively impacted the lake and left behind a legacy of nutrient pollution documented in bottom sediment cores (Gilman 2001). Due to the lake's shallow nature and frequent bouts of summer anoxia at depth, these legacy nutrients continue to represent a significant component (i.e., internal loading portion of the nutrient budget) of the lake's overall nutrient budget and contribute to its eutrophic condition. Hydrologic and nutrient models for Honeoye Lake (Princeton Hydro 2007, 2014) detail the challenge of nutrient management and set realistic goals for lake restoration. Macrophyte harvesting is one technique among the many best management practices being used to address the concerns of declining lake health (Gilman 1991). A summary of recent water quality data is presented in TABLE 3.

Relevant information on the historic composition and fall standing crop biomass of macrophyte communities of Honeoye Lake are presented in reports by Gilman (1985, 1994 and 2004). His intensive work in Honeoye Lake detected 18 aquatic plant species in 1984, 19 species in 1994 and 20 species in 2004. By comparison, similar macrophyte inventory work in the Wayne County Bays of Lake Ontario lists 13 species for East Bay, 17 species for Port Bay and 24 species for Sodus Bay (Gilman and Smith 1988). With the exception of heavily polluted Onondaga Lake, most central and western New York water bodies have similar species richness.

The maximum fall standing crop biomass determined for Honeoye Lake was 1373 g/m^2 in 1984, 513 g/m^2 in 1994, and 526 g/m^2 in 2004. These determinations fall within the range of values reported from other regional water bodies. Recent Owasco Lake research reports a maximum value of 1263 g/m^2 (Gilman et al. 2008). A maximum value of 1470 g/m^2 is listed for Conesus Lake (Makarewicz et al. 1991), and a maximum value of 1217 g/m^2 for Sodus Bay, 579 g/m^2 for Port Bay and 512 g/m^2 for East Bay (Gilman and Smith 1988). The maximum value for Canandaigua Lake was 719 g/m^2 (Gilman, unpublished data). After extensive milfoil herbivore defoliation in Waneta Lake the maximum fall standing crop biomass was 218 g/m^2 (Johnson et al. 2000). Fall standing crop biomass varies according to site conditions within lakes.

MATERIALS AND METHODS

Correct identification of macrophytes is a necessary prerequisite to their successful management. General guides appropriate for Honeoye Lake include Hotchkiss (1967), Rawinski et al. (1979), and Borman et al. (2014). Regional technical references include Ogden (1974), Ogden et al. (1976), and Hellquist and Crow (1985). Information on aquatic invasive species is available at websites of The New York Flora Association (www.nyfa.org), the New York State Federation of Lake Associations (www.nysfola.org), and the Finger Lakes Partnership for Regional Invasive Species Management (www.fingerlakesprism.org). Voucher specimens of most macrophyte species observed in Honeoye Lake were collected during the 2014 research, identified to species, and placed in the Finger Lakes Herbarium at FLCC. Vascular plant taxonomy follows Mitchell and Tucker (1997) with revisions recommended by the New York Flora Association.

One hundred aquatic macrophyte inventory stations were grouped five per transect following the protocol of previous research. The 20 transects were nearly equally spaced along the shoreline (FIGURE 1) and documented by GPS readings to facilitate return to each transect for future research. A preshrunk mooring line was temporarily anchored by grappling hook at the shoreline, then extended out perpendicularly towards the lake center and held in position by a heavy navy anchor. The line was kept afloat by four boat bumpers and a mast buoy. Each flotation device also served as the location of an inventory station. The first station was located about 3 meters (10 feet) from the shore and subsequent stations were equally spaced from the first at 30.5 meters (100 foot) intervals. Due to the high number of inventory stations, it was anticipated that most of the variability in littoral zone macrophyte communities would be sampled.

At each station, the standing crop biomass of aquatic plants was hand pulled at substrate level within a weighted ½ m^2 quadrat frame. The sampling process was facilitated by the use of snorkeling and SCUBA equipment. Each biomass sample was placed in a mesh bag underwater, rinsed in lake water, transferred to a plastic bag in the boat and labeled with site information. Biomass samples were returned to the college and temporarily refrigerated prior to laboratory sorting. Water depth was measured by staff gage or sounding line. Substrate quality was only visually assessed and recorded for each station. No sediment analyses were conducted based on the assumption that substrate conditions, which were tested for texture, pH and nutrient levels in previous research (Gilman 1984, 2001), were likely similar for this study year.

In the laboratory, biomass samples were sorted by species and any clinging, incidental sediment and large attached organisms like zebra mussels were removed from the plants. Sorted species were placed in individual brown paper bags, labelled, and transferred to the college greenhouse for air drying. If necessary, samples were brought to a stable weight by oven drying at 105 ºC prior to weighing on a top loading analytical balance. For all 100 inventory stations, fall standing crop biomass (g/m^2) was calculated by summing the dry weights of all component species within each sample. For the macrophyte community of the entire lake, a synthetic species importance value (IV) was computed as the mean of relative density and relative dominance derived from frequency of species occurrence and biomass totals, respectively. Comparison of IV scores across the four study years (1984, 1994, 2004, 2014) documents the long term variability of the macrophyte communities and might reveal directional changes in composition.

Additional ecological descriptions were determined individually for all 100 samples. These included the number of species detected (referred to as richness [n]), the degree to which all species in a sample were equally abundant (known as evenness and calculated as the J' index of Pielou), the concentration of dominance expressed as the fractional weight of the most abundant species compared to the weight of all species, and the overall sample diversity determined by calculation of Shannon's Index (H'). These statistical measures are commonly used to characterize species abundance relationships in natural communities.

To assure that transect locations were being replicated as closely as possible, individual site water depths for 1984, 1994, 2004 and 2014 were tested for similarity through regression analyses and tested for significance by calculation of correlation coefficients. This was deemed necessary as the 30 year project interval began prior to the availability of GPS coordinates and the time span captured a change from historic cottage numbers to a modern 911 emergency based numbering system.

RESULTS

Macrophyte communities in Honeoye Lake during 2014 were dominated by plants with a basal rosette of long, linear leaves, by short aquatic plants with small leaves, or by tall aquatic plants with flexuous stems and a concentration of reduced or finely dissected leaves. Of the 19 species detected, 17 were vascular plants, one was a moss, and one was an inclusive/collective algal category. The community composition was dominated by native species including eelgrass (*Vallisneria americana*), coontail (*Ceratophyllum demersum*), flat-stem pondweed (*Potamogeton zosteriformis*), water stargrass (*Heteranthera dubia*), small pondweed (*Potamogeton pusillus*), elodea (*Elodea canadensis*), star-leaved duckweed (*Lemna trisulca*), large-leaf pondweed (*Potamogeton amplifolius*) and clasping-leaf pondweed (*Potamogeton richardsonii*). Invasive species included Eurasian water milfoil (*Myriophyllum spicatum*) and curly-leaf pondweed (*Potamogeton crispus*). The fall abundance of aquatic plants in Honeoye Lake inventory stations is described in TABLE 4.

Twenty three of the 100 inventory stations had no vegetation and for 22 of them it was likely due to water depth so extreme that light intensity was not at the compensation level necessary to support aquatic plant photosynthesis. These stations ranged in water depth from 330 to 930 cm with a mean depth of 516 cm. The one station that was an exception to this explanation was a very shallow, near shore site (depth = 50 cm) strongly influenced by wave energy and rocky substrate, a combination that may hinder aquatic plant colonization and long-term persistence. In previous research, shallow depths at the south end of the lake basin contained emergent species including water willow (*Decodon verticillatus*), arrow arum (*Peltandra virginica*), pickerel weed (*Pontederia cordata*) and giant bur-reed (*Sparganium eurycarpum*) but these, although still present in 2014, were not found within the quadrat tosses. Spatial distribution of aquatic plants among the twenty transects is presented in TABLE 5.

Species richness per transect was greatest at the south end of the basin (transects A and T) where 15 macrophytes were detected, and in the northeastern corner of the lake (transects I, J and K) where 12-13 macrophytes were captured within the samples. Species richness per transect remained fairly high along the western shoreline, ranging from 8-11 macrophytes. The eastern shoreline was similar with the exception of transects E, F and G where macrophyte richness was lower, ranging from 1-6 species. This middle portion of the eastern shoreline corresponds to a region of the lake where benthic slope gradient is the greatest.

Eelgrass, coontail, flat-stem pondweed, Eurasian water milfoil, water stargrass, curly-leaf pondweed, small pondweed, elodea, star-leaved duckweed and large-leaf pondweed were widely distributed in Honeoye Lake during 2014. This dominance may result from their reproductive strategies. Eelgrass reproduces vegetatively with creeping stems called stolons which frequently root down forming large colonies in shallow lake bottom sites. It also produces a floating seed capsule at the top of a spiral stalk that may propagate the plant if the seeds are not consumed by migratory waterfowl. The basal rosette of long linear leaves moves flexuously with lake currents and leaf fragments may form by natural processes. These fragments do not form roots and, therefore, do not initiate new eelgrass beds. Coontail seldom roots to the lake bottom but instead grows tangled with other submersed aquatic plants, relying on their substrate attachment to hold itself in place. Coontail grows from overwintering fragments of the previous season. The pondweed species produce flowering spikes that emerge from the water surface, are pollinated by insects then form keeled seeds, but their persistence in the littoral plant communities is more strongly dependent on overwintering buds called turions. These are produced along branch tips at the end of the growing season. Curly pondweed and large-leaf pondweed grow in deeper waters, the former in the cold waters of springtime and the latter in the warm summer waters. Both grow quickly to the water surface and may then spread horizontally across it. Water stargrass forms dense but matted colonies that seldom reach the surface. It is especially abundant in protected coves along the shoreline. Elodea tolerates a range of water depths and will even grow stranded along the beach. Fragments quickly produce adventitious roots and propagate the plant. Flowering and seed production is rare in Elodea. The tiny but ubiquitous star-leaved duckweed floats beneath the surface amongst other macrophytes.

Macrophytes occurred out to a depth of 372 cm (12.2 feet) in August 2014. This depth closely correlates with the maximum depth of vegetation inferred by the Lowrance HDS GPS/depth finder sensing technique and interpretation provided by the Contour Innovations © Mapping Service (T. Gronwall, personal communication). Water depth for each inventory station is provided in TABLE 6. Water depth correlation coefficients among the sample years (TABLE 6) indicates a highly significant relationship and suggests excellent sample transect replication through time.

Fall standing crop biomass for each of the 100 inventory station is presented in TABLE 7 and results ranged from 0 to 518.64 g/m^2 (highest value at the middle inventory station, transect C). The mean fall standing crop biomass of all inventory stations was 105.22 g/m^2. Fall standing crop biomass for each of the 20 transects is summarized in TABLE 7 and results ranged from 0.39 to 264.52 g/m^2 (highest value for transect B which occurs within the New York State protected wetland at the southern end of the lake and were no vegetation harvesting is permitted). Individual inventory station biomass data was summarized to produce a depth distribution of the fall standing crop biomass with these results (TABLE 8): in the 0 – 100 centimeter zone, fall standing crop biomass averaged 113.95 g/m^2 (n=23 inventory stations), in the 101 – 200 centimeter zone, fall standing crop biomass averaged 198.98 g/m^2 (n=24), in the 201 – 300 centimeter zone, fall standing crop biomass averaged 122.73 g/m^2 (n=21 inventory stations), and in the 301 – 400 centimeter zone, fall standing crop biomass averaged 36.53 g/m^2 (n=15). Biomass was absent in the 401 – 500 centimeter zone (n=9), the 501 – 600 centimeter zone (n=5) and the 600+ centimeter zone (n=4). Based on lake bathymetry, the total 2014 lake wide fall standing crop biomass is estimated to have a dry weight of 412,067 kg.

Six submersed species (eelgrass, coontail, water stargrass, Eurasian water milfoil, elodea and large-leaf pondweed) accounted for approximately 95% of the macrophyte community fall standing crop biomass in 2014. Other species (small pondweed, star-leaved duckweed, curly-leaf pondweed, clasping-leaf pondweed) were as or more frequent but due to their small size or presence only as a vegetative propagule did not have significant biomass. Species occurrences were associated with water depth. Eelgrass was most abundant in shallow areas while elodea and coontail were found in intermediate depth zones. Water stargrass had maximum abundance in silt-rich substrates within bays off deltaic points. Eurasian water milfoil and large-leaf pondweed typified deeper zones but were also detected in intermediate depths. The combined importance values of eelgrass and coontail account for over 50% of the 2014 macrophyte community (TABLE 9).

Ecological indices, essentially a macrophyte community profile, are presented in TABLE 10. Based on submerged quadrat frame area (½ m^2), sample richness averaged 4.7 species. Of more interest to aquatic plant ecologists is how these species shared resources (i.e., the degree to which some species are common while others are quite rare) and how the submerged aquatic vegetation is structured (i.e., are there canopy-forming plants or other types of layering in the community). Resource sharing (Pielou's J' index) was low while concentration of dominance was high, suggesting that dominant species patches were larger than the frame area. Overall mean diversity (Shannon's H' index) was intermediate indicating limited numbers of rare species and few canopy-formers. The mean H' value detected here would also be used to describe a community of two equally common species, what biodiversity ecologists have termed the effective number of species. The maximum H' value measured, occurring in transect C, indicates more biodiversity, with an effective number of species equal to five. Sampling across the growing season would capture more submersed aquatic species due to species turnover (i.e., temporal partitioning of niche space) and enhance ecological indices of diversity.

DISCUSSION AND RECOMMENDATIONS

Similar investigations in 1984, 1994 and 2004 allow for long-term trend analyses in macrophyte community structure and function. Trends are hypothesized to result, in part, from changes in water quality following the installation of a perimeter sewer system in 1980 (Larsen 1971), the introduction and establishment of an invasive zebra mussel (*Dreissena polymorpha*) population in the late 1990s (Pearsall and Richardson 2001), and resource competition between macrophyte and phytoplankton communities driven in part by changes in internal nutrient loading associated with frequent summertime bouts of deep water benthic anoxia (Princeton Hydro 2007) as well as changes in external nutrient loading associated with an increased frequency of extreme storm events (Harvieux and Gilman, study in progress). These storm events can secondarily be coupled with poor runoff water quality as influenced by changing human land use practices in the watershed and the inability of natural systems to accommodate these storm intensities and total rainfall volumes.

The role of other factors and their potential regulatory effects on macrophyte community structure and function are poorly understood but may prove significant when relevant data becomes available. These include a phosphorus “pump” from the near-shore shallow sediments mediated by the planktonic cyanobacterium, *Gloeotrichia echinulata*, which has become increasing abundant in the recent decade. Although these near-shore sediments are normally oxic and trap phosphorus, the resting cells of *Gloeotrichia* are thought to have a luxury uptake of sediment phosphorus prior to their forming gas vesicles and rising up into the water column. When these blue-green algal cells die, their absorbed phosphorus is effectively released into the open water zone, stimulating the growth of other phytoplankton and, perhaps, limiting the light and nutrients available to the macrophyte community. Harvesting of macrophytes has been used as a management technique to improve lake-based recreational opportunities, and also to remove phosphorus in absorbed forms in the plant biomass. After careful study of macrophyte management alternatives (Honeoye Lake Watershed Taskforce 2008), mechanical harvesting was selected as the technique most environmentally acceptable, politically feasible and socially responsible. While successfully removing significant biomass, unanswered scientific questions remain about unintended consequences of harvesting. Fragments escaping from cutting operations may, in the case of some species, be viable propagules that could, if habitat space is available, initiate new stands of underwater vegetation. Cut stems still rooted to the bottom in harvested areas may leak plant sap into the water but it is unknown if this has a “fertilizer” effect within the macrophyte communities. The incidental capture of juvenile fish while harvesting has been studied (Gilman and Smith 1988) and judged inconsequential, but the impact on adult fish communities of opening the structure of the macrophyte beds when harvesting lanes are cut has not been examined in detail.

Over the 30 year period of these replicated studies, changes have been detected in the extent, composition and structure of the macrophyte communities. The community response to changes in water clarity (z_{sd}) has altered the maximum depth of the littoral zone during the years of record. The deep edge of the submerged plants was 4.30 meters in 1984, moved out to 5.70 meters by 1994, stood at 5.35 meters in 2004 and retreated back to 3.72 meters in 2014. The distribution of macrophyte biomass prior to mechanical harvesting (1984) peaked in the 1 – 2 meter depth zone but this has been consistently cut by one third with harvesting (1994, 2004, 2014) in this zone (FIGURE 2). In subsequent decades, biomass shifted to deeper waters as clarity improved but in 2014 has returned to shallower waters reminiscent of the 1984 graph profile. This may be a response to reduced clarity brought on by the increase in blue-green algae as well as increases in inorganic turbidity associated with more frequent, intense storm events. Thirty year transect dry weight fall standing crop biomass totals (FIGURE 3) follow the pattern of the lake-wide data with few exceptions. These exceptions, where higher than anticipated biomass was detected in 2014, included transect H just south of Trident Marine along the east side of the lake, transect O in the Twin Bay region north of California Point along the west side of the lake (mechanical harvesting is not possible in this location due to numerous tree stumps in the water) and transect Q just south of California Point. As the area inhabited by macrophytes has shifted and the depth distribution of their biomass has changed, so has the estimated total lake wide plant biomass. The fall dry weight standing crop biomass was estimated at 527,359 kg in 1984, dropping to 333,443 kg in 1994, rising to 463,720 kg in 2004 and stabilizing at 412,067 kg in 2014. Variability in the extent, composition, and structure of macrophyte communities appears to be the norm and predictions concerning their future structure and function should take this variability into account. Ongoing assessment of macrophyte communities (e.g., annual rake toss studies, collection of side scan sonar information and periodic, 10 year fall standing crop biomass research) is recommended. Continuation of a boat launch steward program is also recommended as an efficient, educational practice for quickly discovering the introduction of new aquatic invasive species. Such an early warning system is especially critical with the highly invasive plant, *Hydrilla verticillata*, already growing in nearby Cayuga Lake and the New York State barge canal system.

Anecdotal evidence regarding macrophyte community composition is known back to 1946 (TABLE 11). While there may be bias in the early years of this dataset caused by taxonomic ambiguities, sampling intensities and locations surveyed, all studies show dominance by eelgrass. Species that increased over the years include small pondweed, flat-stem pondweed, elodea, star-leaved duckweed, water stargrass and white water buttercup. Coontail, curly leaf pondweed and large leaf pondweed have remained fairly constant while Eurasian water milfoil and water marigold appear to be decreasing. The overall richness of the macrophyte communities has remained remarkably similar since 1984 when a precise sampling protocol was first used and repeated every decade thereafter. This consistent, long-term biological dataset is unmatched in the Finger Lakes of New York State.

Long-term changes in dry weight fall standing crop biomass for dominant species are presented in TABLE 12. While eelgrass remains as the biomass leader, coontail and water stargrass have seen notable increases during the last two decades while water marigold and Eurasian water milfoil have dropped precipitously. In the latter case, herbivores have been verified feeding on submerged leaves and, perhaps, contributing to the biomass decline (Bob Johnson, personal communication). The scientific literature has also suggested that Eurasian water milfoil may experience an autoantibiosis, that is, over time its decaying remains may modify the substrate in a way that hinders or inhibits future milfoil growth. No experiments have been performed on Honeoye Lake sediment to confirm this hypothesis.

The combined importance value of invasive species (Eurasian water milfoil, curly leaf pondweed, various leaved water milfoil) rose from 9.2% in 1984 to 39.0% in 1994 but then began a steady decline to 14.5% in 2004 and finally 11.0% in 2014. Over the same time period, the combined importance values of eelgrass, coontail, water stargrass, Eurasian water milfoil, elodea and large-leaf pondweed have consistently accounted for 76-82% of the community total. This suggests the inertia for plant production is consistently high in eutrophic Honeoye Lake, but the partitioning of biomass among individual species is driven by local conditions that are subject to change annually. Relative dominance values (FIGURE 4) best demonstrate this annual variability.

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Table 1

MORPHOMETRIC FEATURES		
Watershed area	38.3 sq. mile (24497 acres)	99.14 km^2 (9914 hectares)
Lake area	2.8 sq. mile (1804 acres)	7.30 km^2 (730 hectares)
Lake length	4.1 miles	6.60 kilometers
Lake width	0.88 miles	1.49 kilometers
Maximum depth	31.6 feet	9.6 meters
Mean depth	16.1 feet	4.9 meters
Lake volume	10.2 billion gallons	38.6 million cubic meters

ADDITIONAL DESCRIPTIVE INFORMATION	
Hydraulic retention time	estimated at 292-352 days
Surface elevation	803 feet (244.8 meters)
Length of shoreline	9.6 miles (15.45 kilometers)
Annual lake discharge	estimated at 7.58 billion gallons
Perennial tributaries	Honeoye Inlet, Briggs Gully, Bray Gully, Affolter Creek complex

Table 2

LAND USE AND LAND COVER		
Lacustrine cover types	Natural lakes and ponds	1841 acres
	Man-made ponds	84 acres
Palustrine cover types	Forested mineral soil wetlands	876 acres
	Open mineral soil wetlands	107 acres
Terrestrial cover types	Barrens and woodlands	42 acres
	Forested uplands	15551 acres
	Open uplands	2200 acres
	Cultural	3783 acres

Terrestrial cultural land uses include 1360 acres of residential land, 1132 acres of conifer plantation, 985 acres of cropland, 112 acres of outdoor recreation, 105 acres of pasture, and miscellaneous smaller human uses.

(detailed descriptive land use/land cover categories in Gilman (2004).

Table 3

LAKE WATER QUALITY		
Nutrients	total phosphorus	10-450 µg/L
	nitrate nitrogen	0.1-2.2 mg/L
	total kjeldahl nitrogen	200-930 µg/L
Buffer capacity	moderate	55-75 mg $CaCO_3$/L
Specific conductance	moderate	190-225 µmhos/cm
Active acidity (pH)	slightly alkaline	7.45-8.69
Major dissolved ions	cations: Ca, Mg, Na	anions: HCO_3, SO_4, Cl, CO_3
Water clarity (z_{sd})	low to moderate	1.0-5.0 meters
Algal abundance	chlorophyll *a* concentration	10-25 µg/L, locally higher
Trophic status	Carlson Trophic State Index	usually > 51, eutrophic

Table 4

FALL 2014 ABUNDANCE OF MACROPHYTES IN HONEOYE LAKE			
		% occurrence	
Common name	Scientific name	All sites	Vegetated sites
Eel grass	*Vallisneria americana*	63	82
Coontail	*Ceratophyllum demersum*	60	78
Flat-stem pondweed	*Potamogeton zosteriformis*	47	61
Eurasian water milfoil	*Myriophyllum spicatum*	46	60
Water stargrass	*Heteranthera dubia*	37	48
Curly-leaf pondweed	*Potamogeton crispus*	35	45
Small pondweed	*Potamogeton pusillus*	35	45
Elodea	*Elodea canadensis*	34	44
Star-leaved duckweed	*Lemna trisulca*	32	42
Large-leaf pondweed	*Potamogeton amplifolius*	26	34
Clasping-leaf pondweed	*Potamogeton richardsonii*	17	22
Attached algae		7	9
Southern naiad	*Najas guadalupensis*	7	9
Whorled water milfoil	*Myriophyllum verticillatum*	6	8
White water buttercup	*Ranunculus longirostris*	6	8
Sago pondweed	*Potamogeton pectinatus*	5	6
Slender naiad	*Najas flexilis*	3	4
Various-leaved milfoil	*Myriophyllum heterophyllum*	2	3
Aquatic moss	*Fontinalis antipyretica*	1	1

Table 5

FALL 2014 SPATIAL DISTRIBUTION OF MACROPHYTES IN HONEOYE LAKE																					
	Transect code																				Total
Common name	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	Transects
Eel grass	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	20
Coontail	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	17
Flat-stem pondweed	X	X	X	X		X		X	X	X	X	X	X	X	X	X	X	X	X	X	18
Eurasian water milfoil	X	X	X	X		X		X	X	X	X		X	X	X	X	X	X	X	X	17
Water stargrass	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
Curly-leaf pondweed	X		X	X				X	X	X	X	X	X	X	X		X	X	X	X	15
Small pondweed	X			X		X	X	X	X	X	X	X	X	X	X		X	X		X	15
Elodea	X	X	X			X		X	X	X	X		X		X	X	X	X	X	X	15
Star-leaved duckweed	X	X	X					X	X	X	X	X	X	X	X	X	X			X	14
Large-leaf pondweed						X	X	X	X	X		X			X	X	X	X	X	X	12
Clasping-leaf pondweed	X	X	X	X							X									X	6
Attached algae	X		X							X	X				X					X	6
Southern naiad	X										X					X				X	4
Whorled water milfoil								X	X	X	X	X									5
White water buttercup	X	X	X						X												4
Sago pondweed			X									X	X			X				X	5
Slender naiad	X		X						X												3
Various-leaved milfoil	X																				1
Aquatic moss																				X	1

Table 6

FALL 2014 WATER DEPTH (cm) FOR MACROPHYTE INVENTORY STATIONS					
	Distance from shoreline (meters)				
Transect	3	33.5	64	94.5	125
A	60	98	111	126	148
B	45	136	198	262	320
C	21	80	132	276	360
D	28	170	372	490	530
E	50	270	610	855	930
F	40	192	390	530	740
G	54	220	310	351	442
H	53	182	218	251	282
I	51	189	232	263	293
J	50	149	198	253	265
K	43	71	131	197	232
L	31	158	279	320	330
M	35	246	320	370	420
N	41	271	340	400	447
O	32	111	161	229	266
P	29	273	488	570	600
Q	55	180	260	320	355
R	35	159	308	495	547
S	41	192	252	405	449
T	70	118	150	178	197

CORRELATION COEFFICIENT (r) FOR WATER DEPTH BETWEEN SAMPLE YEARS			
	1984	1994	2004
1994	0.93	-	-
2004	0.94	0.93	-
2014	0.92	0.90	0.93
r = 0.20 (p < .05), r = 0.26 (p < .01)			

Table 7

FALL 2014 TOTAL DRY WEIGHT FALL STANDING CROP BIOMASS (g/m^2) FOR MACROPHYTE INVENTORY STATIONS								
	Distance from shoreline (meters)						Mean	
Transect	3	33.5	64	94.5	125		all sites	vegetated
A	325.27	308.72	220.78	137.23	135.03		225.41	225.41
B	194.05	325.80	350.38	240.06	212.31		264.52	264.52
C	28.53	140.03	518.64	300.58	7.14		193.28	193.28
D	38.52	24.55	0.58	0.00	0.00		12.73	21.22
E	0.87	1.06	0.00	0.00	0.00		0.39	0.97
F	134.91	151.97	0.00	0.00	0.00		57.38	143.44
G	0.81	29.95	15.38	0.00	0.00		9.23	15.38
H	241.79	174.91	81.52	255.33	85.13		167.74	167.74
I	106.10	256.79	179.08	147.68	3.36		138.60	138.60
J	0.00	282.89	212.96	44.24	128.39		133.70	167.12
K	37.04	4.03	54.51	96.14	40.97		46.54	46.54
L	25.51	243.31	3.26	0.88	0.00		54.59	68.24
M	31.53	251.03	1.49	0.55	0.00		56.92	71.15
N	56.00	34.46	0.00	0.00	0.00		18.09	45.23
O	228.55	19.93	394.64	299.85	205.16		229.63	229.63
P	86.15	21.08	0.00	0.00	0.00		21.45	53.62
Q	205.59	209.49	146.88	245.67	17.28		164.98	164.98
R	213.68	189.63	46.67	0.00	0.00		90.00	150.00
S	79.66	390.40	78.17	0.00	0.00		109.65	182.74
T	133.48	187.73	57.45	45.00	95.73		103.88	103.88

Table 8

FALL 2014 TOTAL DRY WEIGHT FALL STANDING CROP BIOMASS (g/m^2) OVER WATER DEPTH GRADIENT		
Water depth (cm)	Biomass (g/m^2)	Sample size (n)
0-100	113.95	23
101-200	198.98	24
201-300	122.73	24
301-400	36.53	15
401-500	0	8
501-600	0	5
600+	0	4

Table 9

FALL 2014 MACROPHYTE COMMUNITY PROFILE FOR DOMINANT SUBMERSED SPECIES IN HONEOYE LAKE						
Species	Fall standing crop biomass	Occurrences	Relative dominance	Relative frequency		Importance value
Eelgrass	50.31 g/m^2	63	47.9%	13.5%		30.7%
Coontail	30.92	60	29.4	12.8		21.1
Water stargrass	9.47	37	9.0	7.9		8.5
Eurasian water milfoil	4.53	46	4.3	9.9		7.1
Flat-stem pondweed	2.03	47	1.9	10.1		6.0
Elodea	2.39	34	2.3	7.3		4.8
Small pondweed	0.93	35	0.9	7.5		4.2
Curly pondweed	0.39	35	0.4	7.5		3.9
Large-leaf pondweed	1.94	26	1.8	5.6		3.7
Star-leaved duckweed	0.12	32	0.1	6.9		3.5

Table 10

FALL 2014 DIVERSITY INDICIES FOR THE MACROPHYTE COMMUNITY IN HONEOYE LAKE DERIVED FROM 100 SUBMERGED QUADRAT (½ m^2) SAMPLES				
Index	Mean		Minimum	Maximum
Richness (n)	4.7		0	13
Evenness (J’)	0.4056		0.0028	0.8941
Dominance	0.7342		0.3656	0.9998
Diversity (H’)	0.7286		0.0019	1.6690

Table 11

HISTORICAL RECORDS OF AQUATIC PLANT OCCURRENCES IN HONEOYE LAKE. ABUNDANT (a), COMMON (c), FAIRLY COMMON (fc), PRESENT (p) AND NO DATA (-) AS NOTED IN THE SCIENTIFIC LITERATURE.							
Species	1946	1952	1970	1984	1994	2004	2014
Eelgrass	a	a	a	a	a	a	a
Large-leaf pondweed	a	fc	-	c	c	c	c
Curly-leaf pondweed	-	fc	-	c	c	c	c
Small pondweed	-	-	-	-	fc	c	c
Sago pondweed	-	-	p	p	-	p	p
Clasping-leaf pondweed	c	fc	p	p	p	fc	fc
Flat-stem pondweed	-	-	p	fc	a	a	a
Slender naiad	c	-	c	p	fc	p	p
Southern naiad	-	-	-	-	fc	p	p
Elodea	c	-	c	fc	a	a	a
Star-leaved duckweed	-	-	-	fc	c	a	a
White water buttercup	-	-	-	-	p	fc	c
Coontail	c	c	fc	fc	a	a	a
Water stargrass	fc	-	p	c	c	c	c
Native milfoil	-	-	-	-	p	p	p
Eurasian water milfoil	c	-	-	c	a	c	fc
Great bladderwort	-	-	-	p	p	p	p
Water marigold	-	-	-	fc	fc	fc	p
	1946 study by Stone and Pesko (cited in Larsen 1971)						
	1952 study by Reed and Carpenter (cited in Larsen 1971)						
	1970 study by Forest (cited in Larsen 1971)						
	1984 study by Gilman						
	1994 study by Gilman						
	2004 study by Gilman and Foust						
	2014 study by Gilman, Foust and Hanselman						
In addition, these vascular species have been collected in Honeoye Lake during the last three decades: common water starwort (*Callitriche palustris*), lesser duckweed (*Lemna minor*), various- leaved milfoil (*Myriophyllum heterophyllum*), ribbon-leaf pondweed (*Potamogeton epihydrus*), brown pondweed (*Potamogeton natans*), greater duckweed (*Spirodela polyrhiza*) and water meal (*Wolffia* spp.). The following species are only known historically: shining pondweed (*Potamogeton illinoensis*) and white-stemmed pondweed (*Potamogeton praelongus*).							

Table 12

LONG-TERM CHANGES IN DRY WEIGHT FALL STANDING CROP BIOMASS (g/m^2) OF DOMINANT SPECIES IN HONEOYE LAKE, 1984-2014.					
Species	Dry weight standing crop biomass (g/m^2)				
	1984	1994	2004	2014	net change
eelgrass	60.77	16.28	23.74	50.31	-10.46
coontail	8.95	10.49	39.24	30.92	+21.97
elodea	5.48	4.65	10.63	2.39	-3.09
water stargrass	5.27	5.15	16.13	9.47	+4.20
water marigold	4.03	1.27	1.44	0.00	-4.03
large-leaf pondweed	3.86	5.98	12.98	1.94	-1.92
Eurasian water milfoil	2.79	57.49	18.08	4.53	+1.74
star-leaved duckweed	0.33	1.82	3.56	2.03	+1.70
curly-leaf pondweed	0.21	0.39	1.87	0.12	-0.09
clasping-leaf pondweed	0.15	0.10	1.10	0.93	+0.78
flat-stem pondweed	0.05	0.31	0.13	1.27	+1.22
small pondweed	0.00	0.50	0.30	0.39	+0.39

Table 13

LONG-TERM CHANGES IN IMPORTANCE VALUES OF DOMINANT SPECIES IN HONEOYE LAKE, 1984-2014.					
Species	Importance value (%)				
	1984	1994	2004	2014	net change
eelgrass	44.2	12.7	15.0	30.7	-13.5
coontail	8.6	9.9	22.1	21.1	+12.5
elodea	6.5	7.3	10.0	4.8	-1.7
water stargrass	8.0	5.2	11.4	8.5	+0.5
water marigold	6.0	1.5	1.6	0.0	-6.0
large-leaf pondweed	7.3	7.0	10.1	3.7	-3.6
Eurasian water milfoil	6.2	34.9	13.8	7.1	+0.9
star-leaved duckweed	3.8	3.4	3.5	3.5	-0.3
curly-leaf pondweed	3.0	4.1	0.7	3.9	+0.9
clasping-leaf pondweed	0.6	0.6	0.4	2.4	+1.8
flat-stem pondweed	1.6	5.8	4.7	6.0	+4.4
small pondweed	0.0	0.9	1.3	4.2	+4.2

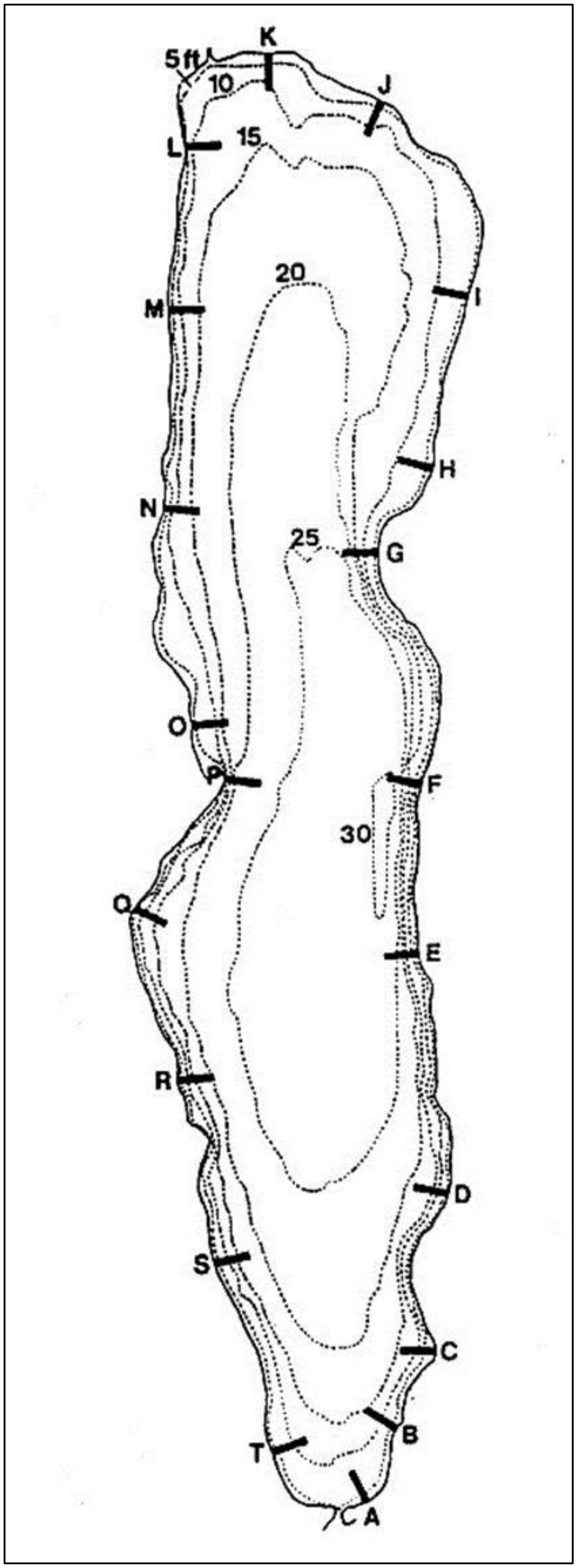


FIGURE 1

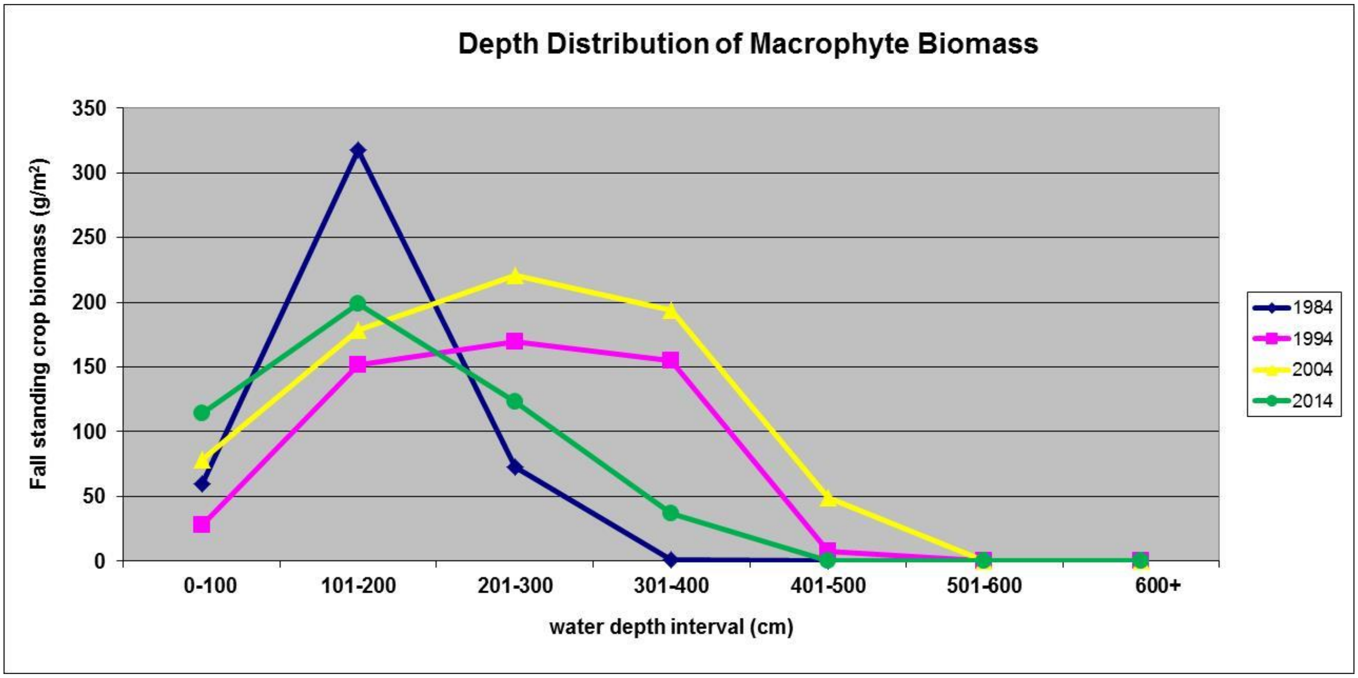


FIGURE 2

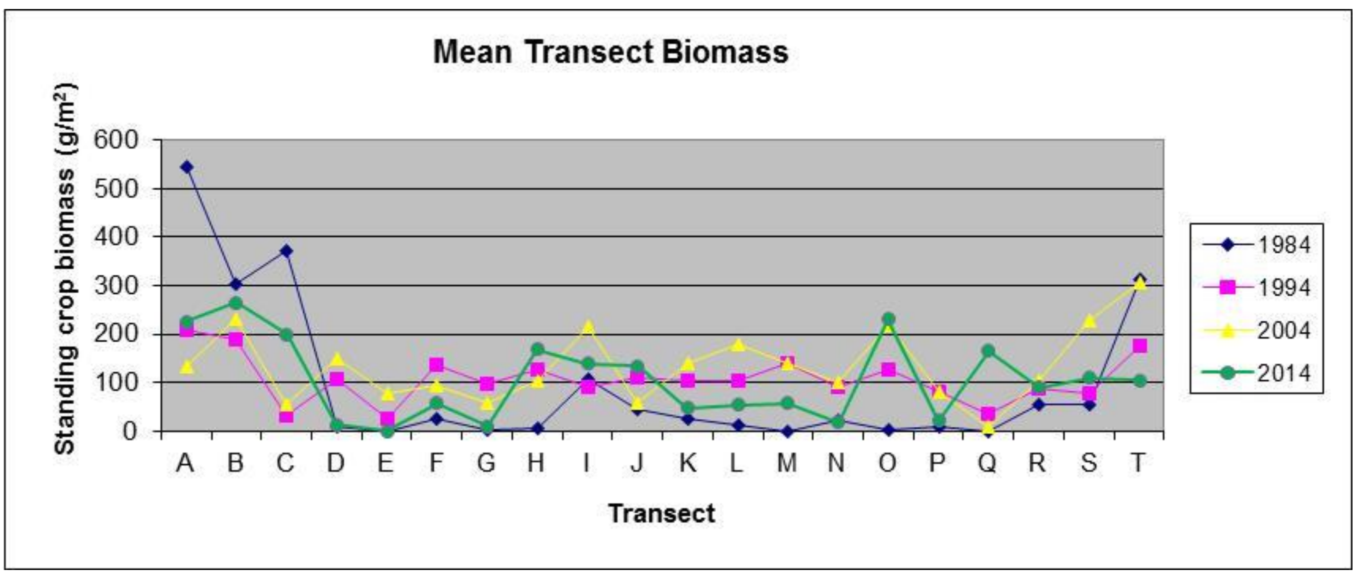
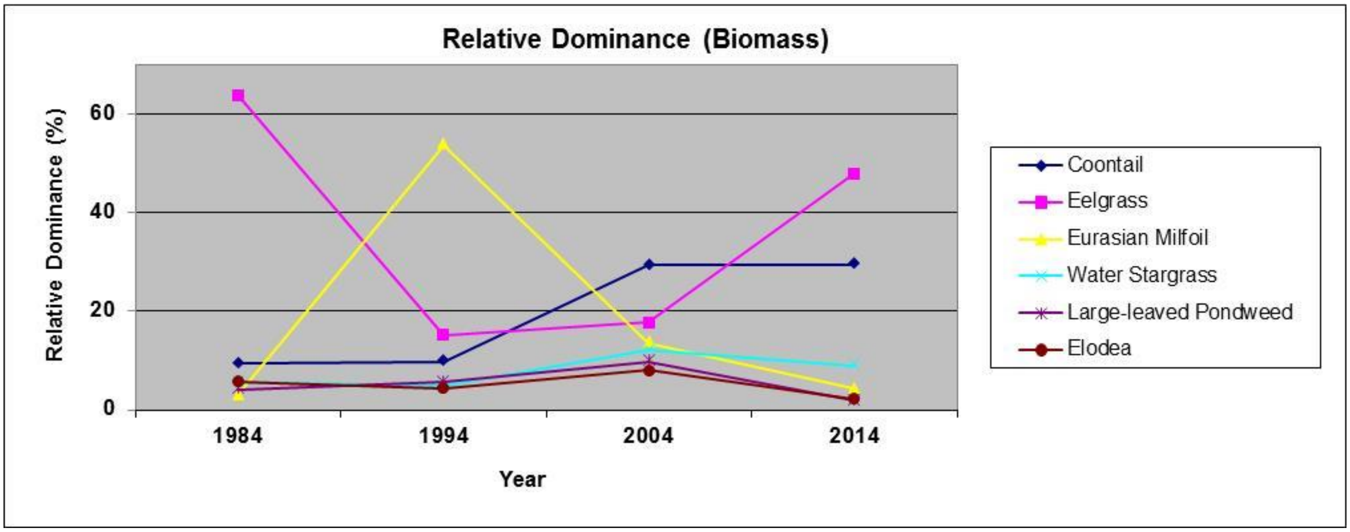
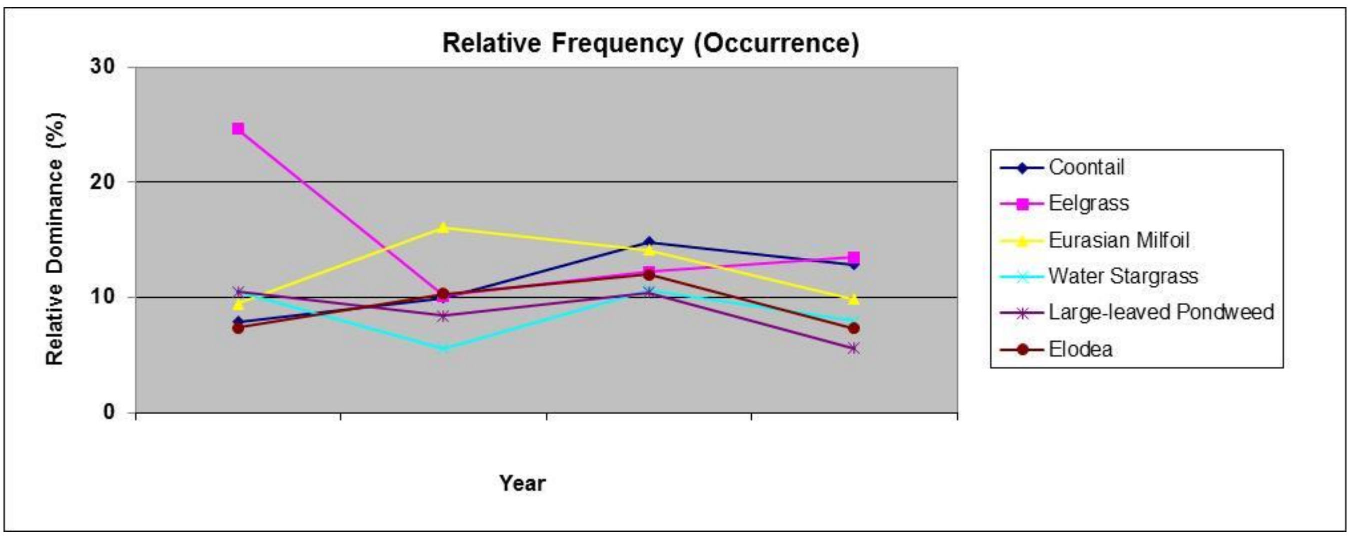


FIGURE 3


Relative Dominance (Biomass)
Relative Dominance (%)
0
20
40
60
1984
1994
2004
2014
Year
Coontail
Eelgrass
Eurasian Milfoil
Water Stargrass
Large-leaved Pondweed
Elodea


Relative Frequency (Occurrence)
Relative Dominance (%)
0
10
20
30
Year
Coontail
Eelgrass
Eurasian Milfoil
Water Stargrass
Large-leaved Pondweed
Elodea

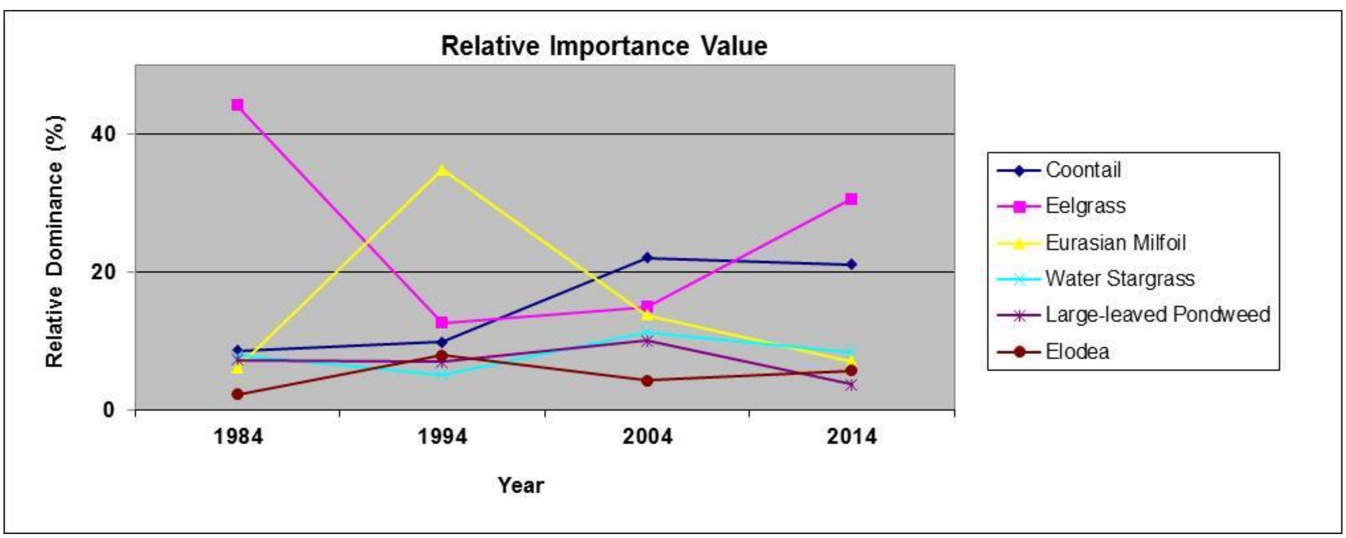

Relative Importance Value
Relative Dominance (%)
0
20
40
1984
1994
2004
2014
Year
Coontail
Eelgrass
Eurasian Milfoil
Water Stargrass
Large-leaved Pondweed
Elodea

FIGURE 4