Integrated plant management of Eurasian watermilfoil: The role of grass carp and drawdowns in the Candlewood Lake, CT system

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ABSTRACT

Eurasian watermilfoil (*Myriophyllum spicatum*) has been a persistent management challenge in Candlewood Lake and Squantz Pond, Connecticut. Two system-scale interventions, annual winter drawdowns since the 1980s and the introduction of triploid grass carp (*Ctenopharyngodon idella*) in 2015 and 2017, were evaluated using 17 yr (2008 to 2024) of macrophyte survey data. Statistical analyses showed that drawdown duration was a significant negative predictor of Eurasian watermilfoil abundance, with earlier, longer, and deeper drawdowns more effective when coinciding with freezing conditions. However, drawdown initiation shifted from late November (1984 to 1993 mean = day 27) to early January (2007 to 2024 mean = day 64), reducing freezing-day exposure by up to 212% in some years and diminishing overall efficacy. Grass carp biomass also significantly reduced macrophyte abundance, with stronger suppression of Eurasian watermilfoil relative to native coontail (*Ceratophyllum demersum*), particularly in shallow habitats and Squantz Pond. Peak impacts occurred 6 yr after initial stocking, coinciding with maximum estimated biomass (~46,569 kg in 2021). By 2024, macrophyte occurrence across transects reached historically low levels, with invasive richness declining below native richness. Although winter drawdowns provided measurable but inconsistent suppression, grass carp herbivory accounted for the more substantial long-term reductions. These findings highlight that regulating grass carp biomass while restoring earlier drawdown initiation can strengthen long-term management of Eurasian watermilfoil in the Candlewood Lake system.

Key words: aquatic invasive species, biocontrol, case study, ecosystem management, herbivory effects, submerged vegetation.

INTRODUCTION

Invasive species exert profound impacts on ecosystems, economies, and human welfare. The cumulative cost of biological invasions in the United States has reached approximately $4.5 trillion over six decades, with annual costs rising from $2 billion in the 1960s to $21 billion in recent decades (Fantle-Lepczyk et al. 2022). Although terrestrial invasions account for the majority of national costs, an estimated $644 billion compared to $13.5 billion for aquatic invasions, this broad comparison obscures important regional differences. In the northeastern United States, aquatic ecosystems incur disproportionately high invasion costs relative to terrestrial systems, largely because of the combination of dense population centers, interconnected waterways, and extensive recreational and commercial use (Fantle-Lepczyk et al. 2022).

In Connecticut, data from 20 years of aquatic plant surveys indicate that 56% of lakes and ponds have at least one invasive macrophyte species (Connecticut Agricultural Experiment Station Office of Aquatic Invasive Species [CAES OAIS] 2025). This contrasts with other New England states such as Maine, where only 1% of the waterbodies are reported to have one or more aquatic invasive species (Blanchette and Schaffner 2017). Consequently, Connecticut represents an important pathway for the spread of aquatic invasive species into New England and the New York City Tri-State area.

Native to Europe, Asia, and northern Africa, Eurasian watermilfoil (*Myriophyllum spicatum* L.) has spread to all continents except Antarctica, including 48 states in the United States and four Canadian provinces (USDA-NRCS 2025). Once established, the plant can form dense monostands that reach the surface, adversely affecting communities of native species, recreation, real estate values, water intakes, and fisheries (Madsen et al. 1994, Fishman et al. 1998, Eiswerth et al. 2017). In Connecticut, Eurasian watermilfoil is the most common aquatic invasive plant, infesting nearly a quarter of all surveyed lakes (CAES OAIS 2025). It is a perennial macrophyte that spreads primarily by fragmentation, root crowns, and runners (Kimbel 1982, Madsen et al. 1988). Although viable seeds are common, they are not considered a significant source of spread (Hartleb et al. 1993, Madsen et al. 1998). Eurasian wate-rmilfoil typically grows at depths of 1 to 4 m, with a maximum depth of 12 m (Smith and Barko 1990, USDA-NRCS 2025).

Candlewood Lake (2,046 ha) and Squantz Pond (108 ha) make up Connecticut's largest lake system (2,154 ha). The

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system has a mean depth of 10 m and a maximum depth of 27 m (Jacobs and O'Donnell 2002). Squantz Pond is connected to Candlewood Lake via a culvert under a causeway, allowing for equalization of water levels and exchange of vegetative propagules, fish, and other aquatic organisms (Figure 1). The Candlewood Lake system is a man-made impoundment, constructed over existing forest, ponds, small streams, and the Rocky River in the 1920s. The lake system serves as the first large-scale hydroelectric project in the United States and the first pumped storage hydro project there. During periods of low electricity demand, water is pumped uphill from the Housatonic River to Candlewood Lake, storing energy for later use. Candlewood Lake's winter drawdowns, managed by FirstLight Power Resources, are used, in part, to control aquatic nuisance vegetation, protect shoreline structures from ice damage, and accommodate hydro facility maintenance and ISO New England's winter generation capacity test. During high-demand periods, the stored water is released through turbines to generate electricity (Murphy and Smolen 2005). This hydroelectric process allows considerable control over the water level and has promoted water level manipulation for the control of nuisance aquatic vegetation since the 1980s. Typically, shallow winter drawdowns (2–3 m) in one year were alternated with deep drawdowns (3–4 m) the next. Eurasian watermilfoil has been present in Candlewood Lake since the early 1970s (Siver et al. 1986). From 1983 to 1995, the target drawdown depth was consistently reached between mid-December and early January and maintained until the end of February. After 1995, however, drawdowns often did not achieve the target depth until mid-January and were maintained for shorter periods, likely reflecting a change in dam operations, although the exact rationale remains unclear (Lonergan et al. 2014, Kohli et al. 2017).

Winter drawdowns are commonly used as a management tool to suppress nuisance aquatic vegetation by exposing rooted plants to freezing and desiccation (Cooke et al. 2005, Carmignani and Roy 2017). Achieving effective control depends on multiple abiotic factors, including air temperature, substrate moisture, the depth of water lowering, and the duration of exposure (Carmignani et al. 2021). In addition, biotic factors such as species-specific traits, including propagule type, depth of vegetative buds, and tolerance to desiccation also influence how macrophytes respond to drawdown (Carmignani and Roy 2017). For example, Lonergan et al. (2014) found that roots of Eurasian watermilfoil grown in hydrated sediment were controlled when exposed to temperatures below 0 C for 24 h followed by a slow thaw. In drier sediments, similar control was achieved at temperatures below 4 C. More broadly, Carmignani et al. (2021) demonstrated that sediment freeze-thaw cycles and desiccation are central to effective plant mortality, and that the timing of drawdown initiation relative to winter temperature patterns is critical. However, recent warming trends in the northeastern United States, where winter temperatures have risen by 1.1 C since 1970, may reduce the reliability of these cold periods (U.S. Global Change Research Program 2009, Karmalkar and Horton 2021). Regional climate projections suggest continued warming and variability in winter temperature patterns, which could limit the effectiveness of

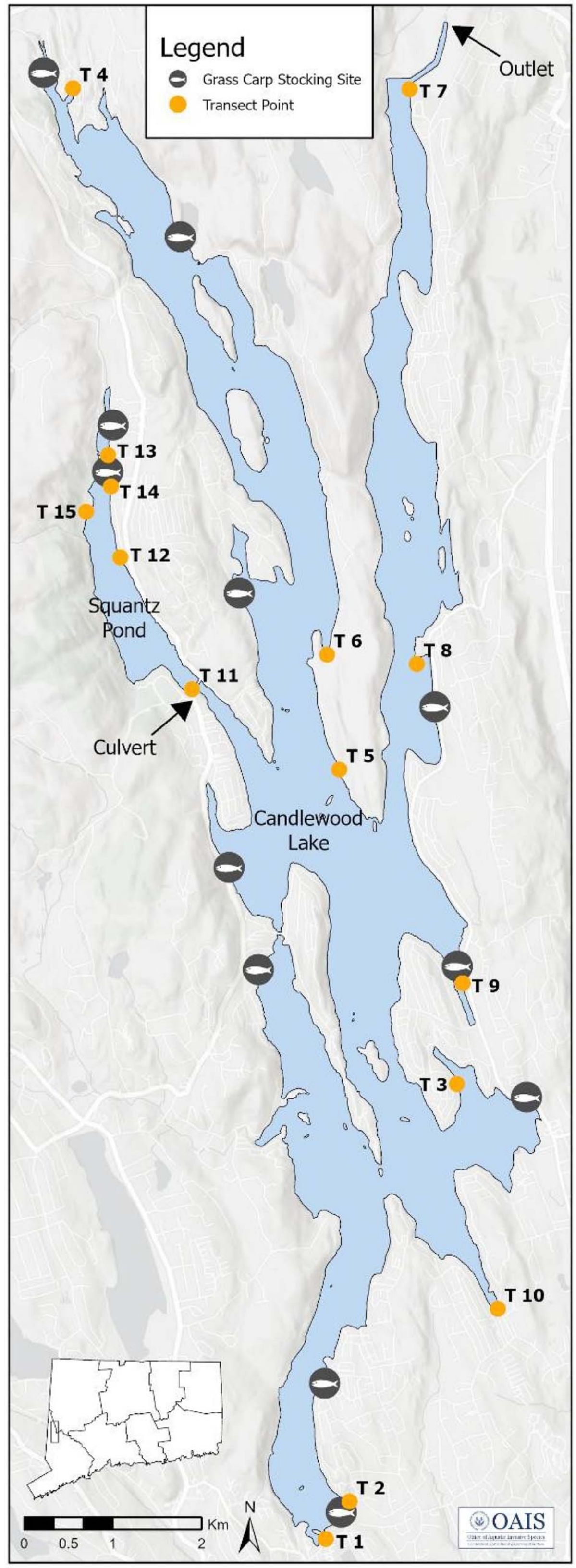


Figure 1. Map of Candlewood Lake and Squantz Pond depicting transect locations, grass carp stocking sites for 2015 and 2017, the culvert between Squantz Pond and Candlewood Lake, and the Candlewood Lake outlet that connects to the Housatonic River.

future drawdowns (Hayhoe et al. 2008). Understanding how drawdown timing intersects with seasonal freeze dynamics is therefore essential for maintaining effective aquatic plant management under changing climate conditions.

Triploid grass carp (*Ctenopharyngodon idella* Val.) have been widely used as a biological control agent for submerged aquatic vegetation (Chilton and Muoneke 1992, Cassani 1996). Triploidy is induced shortly after fertilization using heat, pressure, or chemical treatments to disrupt normal cell division and produce fish with three sets of chromosomes (Cassani and Caton 1986, Thompson et al. 1987). These fish are sterile, ensuring they cannot reproduce and thus eliminating the risk of overpopulation. Grass carp can be considered "selective generalists" and are appealing for managing invasive or nuisance plant species due to their ability to consume large quantities of submerged aquatic vegetation (Kirkagac and Demir 2004, Dibble and Kovalenko 2009). Their herbivorous behavior exhibits preference for certain species when they are available, accessible, and abundant, with Eurasian watermilfoil ranking as a moderately preferred species (Fowler and Robson 1978, Catarino et al. 1997, Dibble and Kovalenko 2009). As preferred vegetation is depleted, grass carp shift to less preferred species. This feeding pattern complicates intermediate control in milfoil-dominated lakes: light stockings tend to reduce preferred species without significantly affecting milfoil, while heavy stockings can lead to the depletion of all aquatic vegetation (Dibble and Kovalenko 2009, Zolfinejad et al. 2017).

Although grass carp have been widely used to manage nuisance aquatic vegetation, their effectiveness depends on several factors, including stocking density, plant community composition, and environmental conditions. In some systems, grass carp have been associated with shifts in plant communities, where preferred native species are eliminated while more resistant or unpalatable species persist or expand (Van Dyke et al. 1984, McKnight and Hepp 1995, Hanlon et al. 2000, Pípalová 2006). Grass carp impacts on water quality vary. Rapid vegetation loss at high grass carp stocking densities has been associated with increased turbidity and altered oxygen dynamics, especially in smaller or more enclosed systems (Cassani et al. 1995, Pípalová 2002). Conversely, gradual vegetation decline under moderate stocking may have fewer negative effects and can even reduce algal abundance in some cases (Leslie et al. 1987, Cassani et al. 1995, Cassani 1996). Over the long term, grass carp–managed lakes have been shown to function similarly to other lakes in the region when herbivory is carefully regulated (Cassani 1996, Hanlon et al. 2000).

The purpose of this study was to examine annual fluctuations in the macrophyte communities of the Candlewood Lake system over 16 yr (2008–2024) of variable drawdown depths and 9 yr (2015–2024) of grass carp presence. Although drawdowns have been a management tool since the 1980s, the combination of fluctuating depths, variability in the timing of drawdown initiation and associated changes in duration, a warming climate that reduces freezing-day exposure, and the introduction of grass carp in recent years presents an opportunity to assess their combined effects on aquatic vegetation dynamics.

MATERIALS AND METHODS

Sites and sampling description

In 2015, 3,868 grass carp, measuring 30.5 to 38.1 cm in length, were released into the Candlewood Lake system to support the management of Eurasian watermilfoil. This initial stocking was based on an estimated 120 ha of milfoil coverage, calculated from an average of prior survey years, and a target stocking rate of 32.4 fish per ha. The 2015 post-stocking aquatic plant survey recorded 179 ha of Eurasian milfoil, indicating that plant coverage was greater than initially estimated. In response, a second stocking occurred in 2017, introducing an additional 5,035 grass carp across both Candlewood Lake and Squantz Pond. This effort was guided by a revised goal of 37.1 fish per ha, using the 204 ha of milfoil observed in 2016. In total, 8,903 grass carp were stocked in 2015 and 2017, resulting in an average stocking density of approximately 27.4 fish per ha across both efforts.

The Candlewood Lake system's Eurasian watermilfoil distribution was documented by outlining patches using GPS. These patch-level data were collected specifically for Eurasian watermilfoil from 2008 to 2020 and again from 2023 to 2024. In contrast, the broader macrophyte community was assessed along 15 transects perpendicular to the shoreline (Figure 1), following the methods of Madsen (1999), with transect data collected annually from 2008 to 2024. Macrophyte observations along transects occurred in mid- to late summer each year. However, curlyleaf pondweed (*Potamogeton crispus* L.), which senesces by midsummer, was recorded only if present during these seasonal surveys. As no additional spring sampling was conducted, its occurrence may be underrepresented.

Patches of Eurasian watermilfoil were mapped with Trimble GeoXT®[1] or R1®[2] GPS with submeter accuracy. Prior to 2014, plant patches were determined by visual sighting and grapple tosses. In 2014 Lowrance® HDS 5 and Hook-5 sonar systems were added to expedite the process. Plant patches were circumnavigated to form georeferenced polygons. Patches covering less than 1 m^2 were recorded as a point and assigned an area of 1 m^2 (8.09371e^{-5} ha). Depth was measured with a rake, drop line, or the sonar system mentioned previously. Plant samples were obtained in shallow water with a rake and in deeper water (< 3 m) with a grapple. Plant abundances were visually accessed using a scale of 0 to 5 (0 = no plants, 1 = single stem; 2 = a few stems; 3 = common; 4 = abundant; 5 = extremely abundant and present at the surface). When field identifications of plants species were questionable, samples were brought back to the lab for review using the taxonomy of Crow and Hellquist (2023). A specimen of each plant species was cataloged in the Connecticut Agricultural Experiment Station Office of Aquatic Invasive Species (CAES OAIS) aquatic plant herbarium for future reference (CAES OAIS 2025). GPS data were postprocessed in Pathfinder® 5.85[3] and then imported into ArcGIS Pro® 3.4.0[4], where it was geocorrected.

The transect dataset for Candlewood Lake was collected from 2008 to 2024. Initially, from 2008 to 2014, data were collected from 10 transects in the main body of

Candlewood Lake. In 2015 the study expanded to include Squantz Pond, increasing the total number of transects to 15: 10 in the main body of Candlewood Lake and five in Squantz Pond (Figure 1). Percent occurrence and abundance data of macrophytes were collected at points along these transects. Transect points were positioned 0.5, 5, 10, 20, 30, 40, 50, 60, 70, and 80 m perpendicular from the shore. However, transect 10 was extended only to 40 m because of the narrowness of the cove where it was located. The total number of sampled transect points for this study was 146: 96 from the 10 transects in the main body of Candlewood Lake and 50 from the five transects in Squantz Pond.

Data processing and analysis

The Candlewood Lake transect dataset was processed to focus on ecologically relevant transect points and address missing depth values. The transect dataset was filtered to retain only those transect points where plants were observed at least once during the study period. Specifically, points were excluded from four transects: six points from Transect 3, three from Transect 7, three from Transect 12, and three from Transect 15. As a result, 87 transect points were retained for 2008 to 2014 and 131 points for 2015 to 2024.

To address missing depth values, we used a modeling approach based on the relationship: water surface elevation = bottom elevation + depth. Since surface elevation was measured daily and bottom elevation was assumed constant for each transect point, we estimated bottom elevation as the median difference between known surface and depth measurements. Missing depths were then imputed by subtracting the estimated bottom elevation from the daily surface elevation.

The processed transect data were analyzed to estimate the percent occurrence of all macrophytes across years using bias-reduced adjusted logistic regression models with year as a categorical predictor (Firth 1993). Firth's method was used to address convergence and small-sample bias issues arising from the extremely low presence of macrophytes in 2022–2024. Pairwise differences among years were evaluated using Tukey's post-hoc tests with a significance threshold of $P < 0.05$ within each species, as well as within three aggregated groups: native species, invasive species, and all species combined. Within each year, permutation tests were used to compare percent occurrence between native and invasive groups, and Holm's method was applied to adjust for multiple comparisons and maintain the familywise error rate at 0.05.

A similar analysis was performed for group richness, defined as the number of macrophyte species present at a transect point, aggregated into three groups: native species, invasive species, and all species combined. Richness across years was modeled using bias-reduced Poisson regression with year as a categorical predictor, followed by Tukey's post-hoc tests at 0.05 level. Within each year, permutation tests were used to compare richness between native and invasive groups, and Holm's method was applied to adjust for multiple comparisons and maintain the familywise error rate at 0.05.

Additional environmental covariates were incorporated into the analysis to provide contextual information. These included winter drawdown data, daily temperature records, and estimated biomass of grass carp in the Candlewood Lake system (defined below).

For this study, the drawdown period was defined as November 1 to April 30. Full lake level occurs at an elevation of approximately 131 m. A data-driven classification system was used to define drawdown intensity, based on the 25, 50, and 75% quantiles of estimated bottom elevations across the 131 retained transect points: 127.9 m, 128.5 m, and 129.5 m, respectively. Shallow drawdowns were defined as elevations between 128.5 m and 129.5 m, intermediate between 127.9 m and 128.5 m, and deep drawdowns as any day below 127.9 m. These classifications align with FERC Article 403, which mandates alternating deep (126.8 m) and shallow (128.6 m) drawdowns. A sign test was used to determine whether an increase or decrease in the annual number of drawdown days classified as at least shallow (including shallow, intermediate, and deep categories) was consistently associated with an opposite change in the surface area of Eurasian watermilfoil in Candlewood Lake the following year. The analysis assessed whether years with more drawdown days tended to have a smaller Eurasian watermilfoil area compared to the previous year, and vice versa. Statistical significance was set at the 0.05 level.

To assess drawdown timing, the first day in each year when lake surface elevation dropped below 129.5 m was identified. This threshold-crossing day was indexed from November 1, with day 1 corresponding to November 1 and day 31 to December 1. Timing data were compared between historical (1984–1993) and current (2007–2024) periods. The average initiation day and standard deviation were calculated for each period, and a two-sample Welch's *t* test was used to assess statistical differences in timing. Additionally, a hypothetical scenario was evaluated in which drawdowns were assumed to begin on day 27 (27 November) in all years. For each year, the number of additional freezing days that would have occurred between day 27 and the actual threshold-crossing day was calculated.

Winter temperatures, specifically freezing conditions, may influence the effectiveness of drawdowns in controlling aquatic vegetation. Daily average temperature data were obtained from the Weather Underground website (https://www.wunderground.com), recorded at Danbury Municipal Airport Station (41.37167°N; 73.48444°W), located approximately 8 km from the nearest shore of the Candlewood Lake system. A freezing day was defined as any day with an average daily temperature below 0 C.

Estimating grass carp density is challenging due to their cryptic behavior, especially in turbid waters with dense vegetation. To address this, we applied the June-Wells et al. (2017) model, which estimates annual grass carp numbers based on stocking, removals, and an assumed 15% annual attrition rate. Reported mortality rates range from 6% to 62% (Clapp et al. 1994, Kirk and Socha 2003), with lower rates observed in northern climates (Gorbach 1961, Kirk and Socha 2003). In temperate systems, wild grass carp have been documented to live more than 20 yr (Gorbach 1961). Longevity in sterile triploids is now better understood, with confirmed ages of 23 yr in Lake Gaston, North Carolina (Caves et al. 2021), demonstrating that multidecade survival is possible under favorable conditions. Thus, a 15% annual attrition rate is a conservative and regionally appropriate modeling choice for lakes in the northeast.

Grass carp removals began in May 2023, with 482 individuals removed by the end of 2024: 244 in 2023 and 238 in 2024. These removals were proportionally attributed to the 2015 and 2017 stocking batches based on the previous year's proportions. Previous research has shown that grass carp biomass is strongly related to aquatic plant abundance, and that the relationship between grass carp weight (W^t, kg) and age (t) is nearly linear, described by the equation $W^t = 1.448 + 1.623t$ (Stich et al. 2013).

To further explore patterns of macrophyte abundance and management influences, a repeated measurement model was developed to account for potential correlations within the data. Transect points within a year were treated as correlated, and measurements at the same transect point across years were also assumed to be correlated, given that the transect points were prespecified. To capture these dependencies, a cumulative link mixed model, specifically designed for analyzing ordinal data (Christensen 2023), was fitted to study the two most common macrophytes: the invasive Eurasian watermilfoil and the native coontail (*Ceratophyllum demersum* L.). The analysis considered the following variables: 1) Macrophyte abundance, the response variable representing the observed macrophyte relative abundance on a scale from 0 to 5 as previously described; 2) Grass carp, the estimated total biomass in thousand kilograms of grass carp in the previous year; 3) Species, a binary variable indicating two macrophytes (Eurasian watermilfoil and coontail); 4) Drawdown, reflecting the number of days in the previous winter's drawdown period when the water level was lower than the depth, coupled with an average daily temperature below 0 C; 5) Depth, measuring the distance in meters from the water surface to the substrate where the plants were found; 6) Waterbody, a binary variable indicating either the main body of Candlewood Lake or Squantz Pond; 7) the interaction between Grass carp and Species; 8) the interaction between Grass carp and Drawdown; 9) the interaction between Grass carp and Depth; 10) the interaction between Grass carp and Waterbody; 11) Transect Point, a random effect for transect points to account for repeated measures at the same transect point across multiple years; and 12) Year, a random effect to account for repeated measures within a year across transect points.

Because the drawdown variable is a composite exposure index integrating elevation, lake-level dynamics, and freezing conditions, additional drawdown interaction terms would be difficult to interpret. To maintain model interpretability and emphasize management-relevant hypotheses, we modeled drawdown primarily through its main effect and its interaction with grass carp biomass.

RESULTS AND DISCUSSION

Overview

From 2008 to 2024, two major system-scale interventions were used to manage Eurasian watermilfoil in the Candlewood Lake system: winter drawdowns and grass carp. Although drawdowns had been employed for decades, their timing and depth varied considerably during the study period (Figures 2 and 3). Grass carp, introduced more recently, were stocked in 2015 and 2017 in response to the continued expansion of Eurasian watermilfoil and its impacts on recreation, habitat structure, and ecosystem function.

Eurasian watermilfoil had long been the dominant macrophyte species in the system, first emerging as a management concern in the 1970s and eventually reaching coverage levels that frequently exceeded approximately 202 ha (Figure 3). From 2008 through 2020, invasive species, particularly Eurasian watermilfoil, strongly shaped the macrophyte community, with high and often cyclical fluctuations in frequency of occurrence across surveyed points (Table 1) and in spatial coverage (Figure 3).

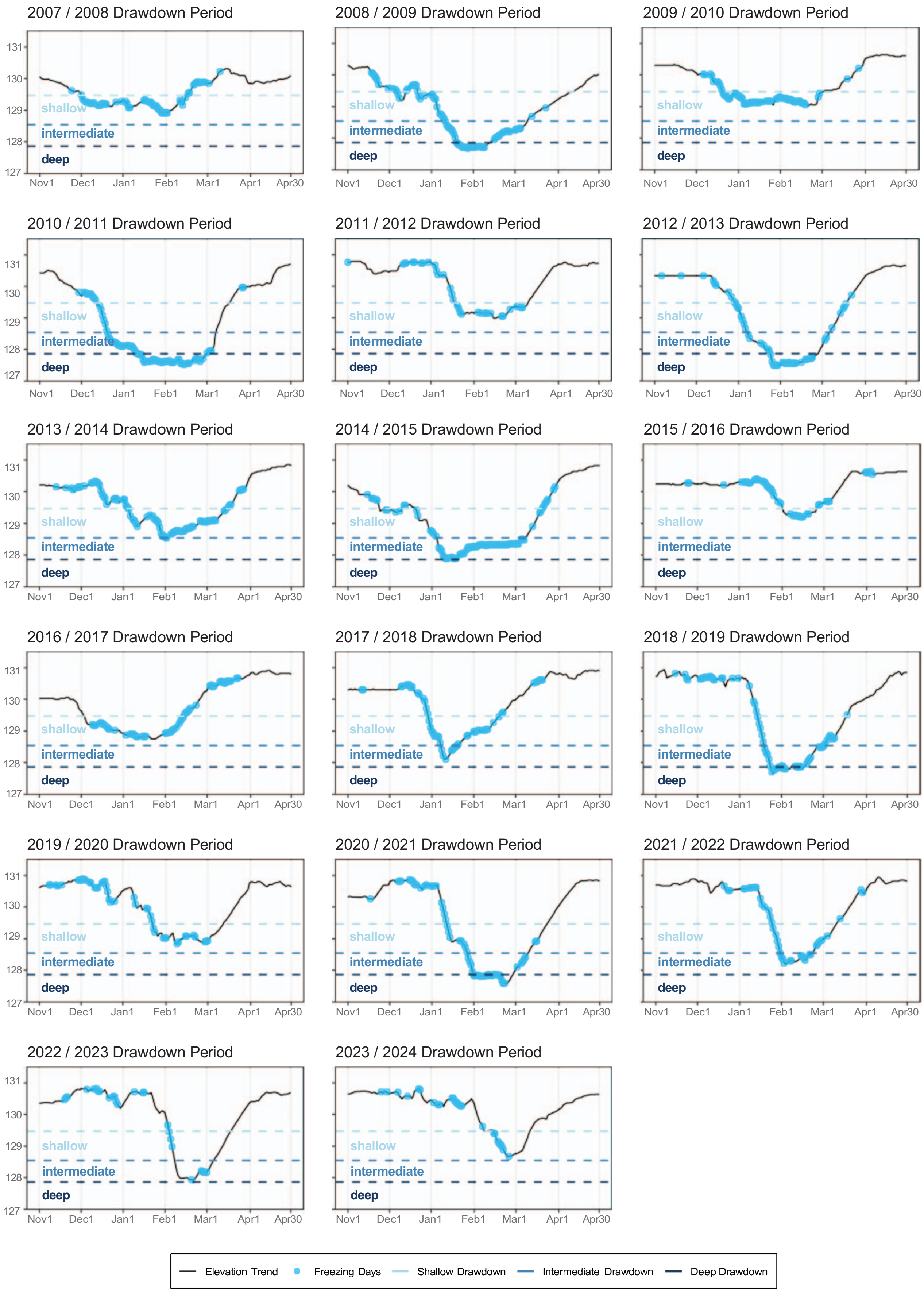
This dynamic began to shift around 2020 and changed dramatically by 2022, as Eurasian watermilfoil declined sharply in frequency of occurrence (Table 1) and the richness of invasive, native, and total species all fell (Table 2). From 2008 to 2020, invasive richness consistently exceeded native richness, but this relationship became inconclusive in 2021–2022 and reversed in 2023–2024. By 2024, plant presence across most transects, including both native and invasive taxa, had reached or were near historically low levels. These changes represent a major turning point in the system's vegetation trajectory and coincide with the delayed but intensifying impacts of grass carp herbivory.

The following sections evaluate the effectiveness of each intervention in detail, beginning with winter drawdowns, followed by grass carp, and concluding with an integrated management perspective.

Impacts of winter drawdowns on macrophyte communities

Percent occurrence data from 2008 to 2024 show that Eurasian watermilfoil initially dominated the macrophyte community but declined sharply in later years following drawdowns and grass carp introduction (Table 1). Mixed-effects modeling results (Table 3) reinforce that winter drawdowns are a significant driver of Eurasian watermilfoil suppression in the Candlewood Lake system. Drawdown duration was a strong negative predictor of Eurasian watermilfoil abundance (estimate $= -0.018$, $P < 0.001$), even after accounting for species, grass carp biomass, depth, and waterbody (Table 3). The interaction between drawdowns and grass carp was not significant ($P = 0.221$), indicating that each contributed additively rather than interactively to vegetation control (Table 3). The results support the conclusion that winter drawdowns independently reduce Eurasian watermilfoil populations and remain an important management tool.

Analysis of drawdown duration and subsequent summer macrophyte coverage from 2007 to 2020 (Table 4) shows that longer drawdowns were often followed by reductions in Eurasian watermilfoil area, though the relationship was not perfectly consistent. A sign test confirmed a significant inverse relationship: when drawdown duration increased from one year to the next (considering at least shallow



2007 / 2008 Drawdown Period
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2021 / 2022 Drawdown Period
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2023 / 2024 Drawdown Period
131
130
129
128
127
shallow
intermediate
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Nov1
Dec1
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Feb1
Mar1
Apr1
Apr30
Elevation Trend
Freezing Days
Shallow Drawdown
Intermediate Drawdown
Deep Drawdown

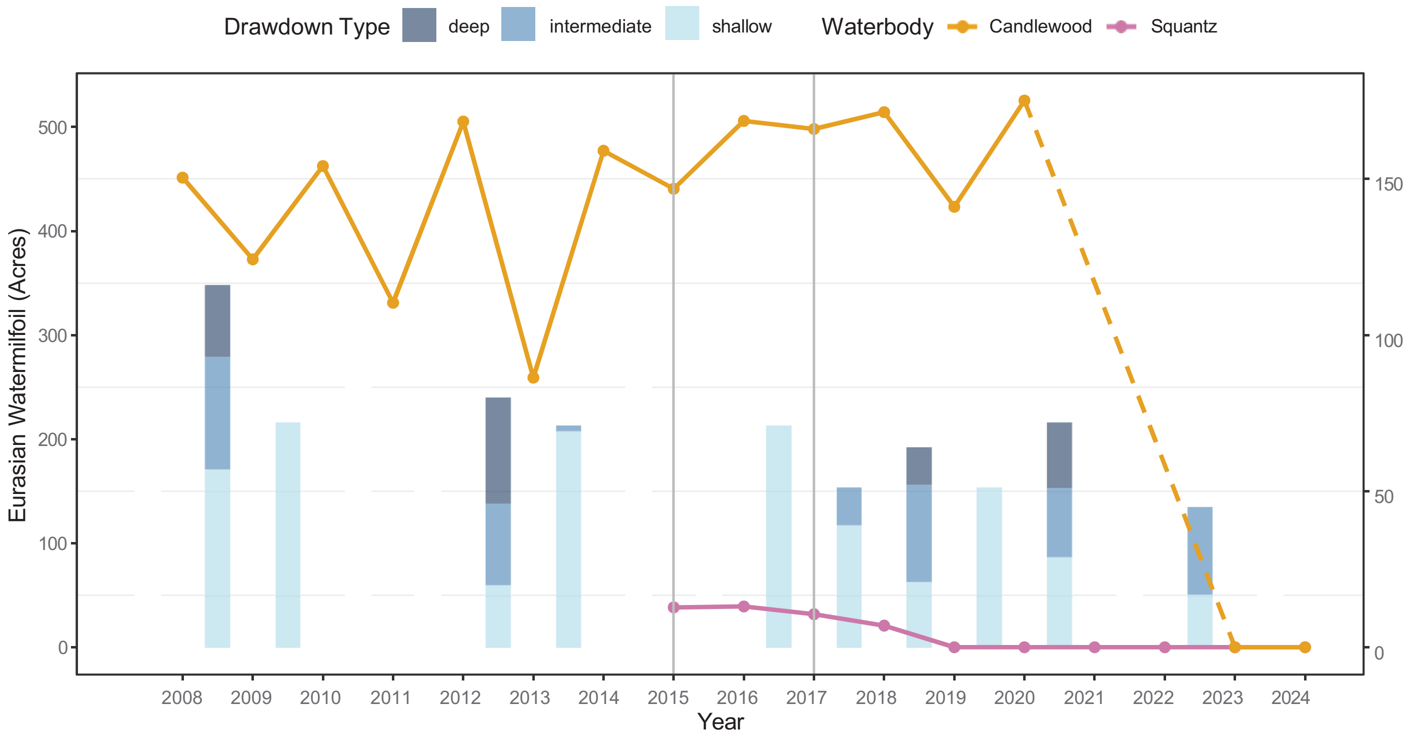

Figure 3. Total area (in hectares) of *Myriophyllum spicatum* from 2008 to 2024 in Candlewood Lake and Squantz Pond. The stacked bars represent the type of drawdown implemented each year: deep (dark blue), intermediate (medium blue), and shallow (light blue). The secondary y-axis shows the number of drawdown days, indicating the duration of drawdowns for each year. Data were offset as drawdown duration (secondary y-axis) corresponds to the winter months of the labeled year (e.g., 2008 represents the 2008/2009 drawdown), while the Eurasian watermilfoil hectares (primary y-axis) reflects vegetation quantified during the following growing season (e.g., summer 2009), showing the temporal relationship between drawdown and vegetation impact.

levels, including shallow, intermediate, and deep drawdowns), Eurasian watermilfoil coverage area typically decreased, and vice versa ($P < 0.001$) (Table 4). Years like 2008/2009 (116 days) and 2012/2013 (80 days) were followed by lower summer coverage (151 and 259 ha, respectively), but this trend did not hold in all cases. For instance, the 24-day drawdown in 2015/2016 was followed by a spike to 205 ha, and the 51-day drawdown in 2019/2020 preceded the highest recorded coverage (213 ha). Conversely, moderately long and deep drawdowns such as 2010/2011 (95 days) were often more effective. These results suggest that duration alone is not sufficient. Instead, the effectiveness of drawdowns likely depends on the combination of timing, depth, and sustained freezing, which can damage overwintering structures such as root crowns and rhizomes.

Since the mid-1990s, regulatory and operational changes have made drawdown timing and duration more variable. After 1995, drawdowns often failed to reach target depths before mid-January and were maintained for shorter periods (Tables 4 and 5; Figure 2). The 2004 FERC license (Article 403) granted FirstLight greater flexibility, establishing alternating deep (~3.3 m, below 127.9 m) and shallow (~1.8 m, 128.5 to 129.5 m) drawdowns in odd and even years, respectively. However, this schedule has not always been followed. In 2017 a shallow drawdown replaced a planned deep one, and 2018 reached only intermediate levels (Figures 2 and 3; Table 4). The 2019 drawdown marked the first sustained deep event in 4 yr, with lake levels below 127.9 m and 12 days of substrate freezing (Table 3). The 2020 shallow drawdown, initiated in mid-December, reached ~128.5 m and held until March. Since 2007, shallow drawdowns have generally met target levels, except in 2018.

Deep drawdowns in 2010/2011, 2012/2013, and 2018/2019 coincided with prolonged substrate exposure and frequent freezing (Figure 2; Table 5), contributing to greater macrophyte suppression (Table 4). In contrast, years with shallower or short-lived drawdowns, such as 2009/2010 and 2015/2016, provided limited exposure and reduced control efficacy (Table 5). These findings are consistent with broader ecological studies showing that deep, sustained drawdowns enhance sediment desiccation and freezing, leading to more effective plant control, while shorter or

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Figure 2. Annual winter water level drawdowns in Candlewood Lake from 2007 to 2024. Each panel represents one drawdown season, spanning November through April. The black line indicates daily lake surface elevation, categorized into three zones based on elevation thresholds: shallow (128.5–129.5 m), intermediate (127.9–128.5 m), and deep (< 127.9 m). These elevation ranges correspond to approximately 1.5–2.5 m, 2.5–3.1 m, and > 3.1 m of drawdown, respectively, from the typical lake level of ~131 m. Horizontal dashed lines mark zone boundaries, while blue dots indicate days when average air temperature was ≤ 0 C. This figure illustrates both the extent of drawdowns and the overlap with freezing conditions critical for effective vegetation control.

Table 1. Macrophyte percent occurrence data for the Candlewood Lake system from 2008 to 2024, presented by individual species and categorized into three groups: All Species, Total Invasive Species, and Total Native Species. Invasive species are marked with asterisks. Percent occurrence reflects the proportion of transects where each macrophyte category was observed. To identify pairwise differences across years, Tukey's post-hoc tests were conducted with a significance threshold of $P < 0.05$. Statistical groupings are indicated by letter codes (e.g., "ab," "abcd").

	Year																
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
Transect points (*n*)	87	87	87	87	87	87	87	131	131	131	131	131	131	131	131	131	131
Bur-reed (*Sparganium* species L.)	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	3.1% a	0.0% a	0.8% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Clasping-leaf pondweed (*Potamogeton perfoliatus* L.)	2.3% a	1.1% a	0.0% a	0.0% a	1.1% a	0.0% a	1.1% a	0.8% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Common duckweed (*Lemna minor* L.)	5.7% a	1.1% a	4.6% a	6.9% a	3.4% a	0.0% a	2.3% a	0.0% a	0.0% a	0.8% a	2.3% a	0.8% a	0.8% a	0.0% a	0.0% a	0.8% a	0.0% a
Coontail (*Ceratophyllum demersum* L.)	36.8% a	12.6% bcd	24.1% abc	32.2% ab	25.3% abc	23.0% abc	25.3% abc	19.8% abc	26.7% abc	32.1% ab	20.6% abc	18.3% abc	11.5% cd	23.7% abc	1.5% d	0.0% bcd	0.0% bcd
Curlyleaf pondweed[1] (*Potamogeton crispus* L.)	1.1% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Eelgrass (*Vallisneria americana* Michx.)	2.3% a	4.6% a	4.6% a	2.3% a	4.6% a	4.6% a	6.9% a	3.1% a	2.3% a	3.1% a	1.5% a	0.8% a	0.0% a	0.8% a	0.8% a	0.0% a	0.0% a
Eurasian watermilfoil[1] (*Myriophyllum spicatum* L.)	86.2% ab	71.3% abcd	78.2% abc	87.4% ab	87.4% ab	46.0% de	86.2% ab	74.8% abc	87.8% a	68.7% bcd	75.6% abc	50.4% de	58.8% cde	43.5% e	3.8% f	0.0% f	0.0% f
Great duckweed (*Spirodela polyrhiza* L. Schleiden)	0.0% a	0.0% a	1.1% a	5.7% a	0.0% a	0.0% a	0.0% a	0.8% a	0.0% a	0.0% a	1.5% a	0.8% a	0.0% a	0.8% a	0.0% a	0.0% a	0.0% a
Horned pondweed (*Zannichellia palustris* L.)	2.3% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Leafy pondweed (*Potamogeton foliosus* Raf.)	0.0% a	0.0% a	0.0% a	2.3% a	0.0% a	5.7% a	1.1% a	0.8% a	0.8% a	0.0% a	1.5% a	0.8% a	2.3% a	0.0% a	0.0% a	0.0% a	0.0% a
Minor naiad[1] (*Najas minor* All.)	5.7% abc	9.2% abcd	12.6% abcd	16.1% abcd	13.8% abcd	21.8% ad	27.6% d	26.7% d	16.0% abcd	16.8% abd	0.8% bc	1.5% c	2.3% bc	0.0% abcd	0.0% abcd	0.0% abcd	0.0% abcd
Pickerelweed (*Pontederia cordata* L.)	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	1.5% a	0.0% a	0.0% a	0.0% a	0.0% a	2.3% a	0.0% a	0.0% a	0.0% a	0.0% a
Primrose-willow (*Ludwigia* species L.)	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	1.5% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Sago pondweed (*Stuckenia pectinata* L. Börner)	1.1% a	0.0% a	4.6% a	0.0% a	3.4% a	1.1% a	2.3% a	0.8% a	3.1% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Slender naiad (*Najas flexilis* Willd. Rostk. & Schmidt)	1.1% a	1.1% a	0.0% a	1.1% a	0.0% a	0.0% a	0.0% a	4.6% a	1.5% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Small pondweed (*Potamogeton pusillus* L.)	1.1% a	0.0% a	0.0% a	0.0% a	1.1% a	0.0% a	0.0% a	1.5% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Snailseed pondweed (*Potamogeton bicupulatus* Fern.)	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	7.6% a	4.6% a	5.3% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Spikerush (*Eleocharis* species L.)	0.0% a	3.4% a	1.1% a	0.0% a	2.3% a	0.0% a	1.1% a	4.6% a	3.1% a	3.1% a	4.6% a	9.9% a	4.6% a	4.6% a	6.1% a	5.3% a	8.4% a
Watermeal (*Wolffia* species Weddell)	0.0% a	0.0% a	0.0% a	0.0% a	3.4% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	2.3% a	0.0% a	0.0% a	0.0% a
Waterwort (*Elatine* species L.)	1.1% a	3.4% a	2.3% a	0.0% a	3.4% a	0.0% a	0.0% a	4.6% a	3.8% a	3.1% a	1.5% a	4.6% a	6.9% a	4.6% a	3.8% a	9.2% a	8.4% a
Western waterweed (*Elodea nuttallii* Planch. St. John)	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	1.5% a	0.8% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
White water lily (*Nymphaea odorata* Aiton)	1.1% a	0.0% a	1.1% a	1.1% a	1.1% a	1.1% a	2.3% a	0.8% a	0.8% a	0.8% a	0.8% a	1.5% a	0.8% a	0.8% a	0.8% a	0.0% a	0.0% a
Yellow water lily (*Nuphar variegata* Engelm. ex Durand)	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	1.1% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a	0.0% a
Total invasive species	86.2% ab	72.4% abcd	78.2% abc	89.7% ab	87.4% ab	54.0% cde	87.4% ab	83.2% abc	90.1% a	72.5% bc	76.3% abc	50.4% de	58.8% cde	43.5% e	3.8% f	0.0% f	0.0% f
Total native species	48.3% a	23.0% abcd	32.2% ab	37.9% ab	33.3% ab	33.3% ab	37.9% ab	33.6% ab	37.4% ab	42.0% a	29.0% abc	26.7% abcd	19.1% bcd	33.6% ab	9.9% d	11.5% cd	12.2% cd
All species	90.8% a	77.0% abcd	79.3% abc	92.0% a	88.5% a	64.4% bcd	89.7% a	87.8% a	90.1% a	87.8% a	83.2% ab	57.3% cd	64.9% bcd	54.2% d	12.2% e	11.5% e	12.2% e

[1]Indicates invasive species.

Table 2. Mean species richness per transect point for invasive, native, and total macrophyte species observed in Candlewood Lake from 2008 to 2024. Richness values represent the average number of species detected per sampling point across surveyed transects. From 2008 to 2014, 87 transect points were surveyed annually, while in 2015 the survey area expanded to 131 transect points, maintaining consistency through 2024. To identify pairwise differences among years, Tukey's post-hoc tests were performed with a significance threshold of $P < 0.05$. Symbols (> and <) in the table denote within-year comparisons between invasive and native richness. For these comparisons, permutation tests were used, and Holm's method was applied to adjust for multiple comparisons and maintain the familywise error rate at 0.05.

	Year																
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
Transect points (n)	87	87	87	87	87	87	87	131	131	131	131	131	131	131	131	131	131
Invasive	0.93 ab	0.82 abcd	0.91 abc	1.03 ab	1.01 ab	0.68 abcd	1.14 a	1.02 a	1.04 a	0.86 abc	0.76 abcd	0.52 cd	0.61 bcd	0.44 de	0.04 f	0 ef	0 ef
	>	>	>	>	>	>	>	>	>	>	>	—	>	—	—	<	<
Native	0.55 a	0.28 abc	0.44 a	0.52 a	0.49 a	0.36 abc	0.44 a	0.51 a	0.48 a	0.53 a	0.34 abc	0.38 ab	0.29 abc	0.38 ab	0.13 c	0.15 bc	0.17 bc
All	1.48 a	1.08 abc	1.35 ab	1.55 a	1.51 a	1.03 abc	1.58 a	1.53 a	1.51 a	1.39 a	1.11 abc	0.90 bc	0.90 bc	0.81 c	0.17 d	0.15 d	0.17 d

less intense drawdowns often fail to produce meaningful suppression (Stich et al. 2013, Carmignani 2021).

The frequency of freezing has also declined over time. From 2008 to 2024, the number of freezing days (≤ 0 C) during exposed periods declined significantly ($\beta = -1.6504$, $SE = 0.5932$, $t = -2.782$, $P = 0.0123$), representing a 53% drop from 55 days in 2007/2008 to 26 in 2023/2024 (Figure 3). This model explains 30% of variation ($R^2 = 0.3007$), indicating a trend toward milder winters. Without sufficient freezing, invasive plants such as Eurasian watermilfoil can readily regrow through root crowns or fragmented stems.

Drawdown timing has also shifted significantly over the past several decades. Historically, drawdowns for the Candlewood Lake system began by late November (Table 6). However, they now often occur in early January or even later (Table 6). Lake elevation records show that the average initiation date shifted from day 26.9 of the water year (approximately November 27) during 1984 to 1993, to day 63.9 (approximately January 3) during 2007 to 2024 (Table 6). This delay represents a significant change, as confirmed by a two-sample Welch's t test ($t = 5.54$, $df = 24.4$, $P < 0.001$). In some recent years, drawdowns did not begin until early February, greatly reducing the likelihood of overlapping with periods of sustained freezing.

A hypothetical model in which drawdowns consistently began on day 27 (November 27) demonstrated substantial potential gains in freezing exposure. In 2015/2016, 2019/2020, and 2023/2024, earlier initiation would have added 22, 25, and 17 freezing days, respectively, representing increases of 200, 179, and 212% compared to actual drawdown initiation (Table 6). Across all years evaluated, improvements ranged from 2 to more than 200% (Table 6). These results highlight the importance of synchronizing both drawdown timing and depth with winter temperature conditions to maximize macrophyte control. Historical evidence supports this conclusion. In 1983 and 1984, early and sustained drawdowns lowered lake levels by 2.0 m and 2.7 m, respectively, and reduced Eurasian watermilfoil biomass by more than 90% in exposed areas (Siver et al. 1986). Based on current classification thresholds, these would be considered shallow and intermediate drawdowns, respectively, though their effectiveness was likely enhanced by earlier timing and longer exposure duration compared to more recent efforts. Notably, both drawdowns began in early November and extended through March, maximizing the likelihood of sediment freezing and desiccation. (Siver et al. 1986, Kohli et al. 2017).

Together, these findings underscore that the effectiveness of winter drawdowns in suppressing Eurasian watermilfoil depends on the combined influence of timing, depth, duration, and freezing conditions. Delays in initiation, milder winters, and inconsistent depth targets have reduced drawdown efficacy over time.

Grass carp impacts on macrophyte communities

Although winter drawdowns have contributed to macrophyte suppression in the Candlewood Lake system, their effectiveness has diminished due to later initiation, reduced freezing, and inconsistent depth targets. As a result, long-term control of Eurasian watermilfoil required an additional

Table 3. Variables used in the cumulative link mixed model to assess macrophyte abundance in the Candlewood Lake system. Species identity (Eurasian watermilfoil vs. coontail) accounts for differences in response. Grass carp biomass represents herbivory pressure, while drawdown reflects plant exposure to freezing. Depth influences growth through light availability. Waterbody (Squantz Pond vs. Candlewood Lake) accounts for location differences. Interaction terms evaluate species-specific herbivory (Grass carp biomass × Species), drawdown-herbivory synthesis (Grass carp biomass × Drawdown), depth-related grazing effects (Grass carp biomass × Depth), and location-based variability (Grass carp biomass × Waterbody).

Variable	Estimate	Std. error	*z* value	*P* value
Species (Eurasian watermilfoil vs Coontail)	2.680	0.112	23.91	< 0.001
Grass carp biomass	−0.059	0.016	−3.70	0.002
Drawdown	−0.018	0.003	−5.37	< 0.001
Depth	−0.446	0.079	−5.64	< 0.001
Waterbody (Squantz Pond vs Candlewood Lake)	0.078	0.267	0.29	0.770
Grass carp biomass × Species	−0.014	0.004	−3.13	0.002
Grass carp biomass × Drawdown	−0.0003	0.0002	−1.23	0.221
Grass carp biomass × Depth	0.007	0.003	2.67	0.008
Grass carp biomass × Waterbody	−0.072	0.008	−8.85	< 0.001

intervention. The introduction of grass carp appears to have enhanced macrophyte management, achieving outcomes that drawdowns alone could not sustain. To highlight baseline conditions before grass carp effects took hold, coverage data from 2008 to 2020 are presented (Table 4), capturing the period prior to and during the 6-yr lag observed before vegetation suppression became evident (Figure 3). Although the first stocking occurred in 2015, Eurasian watermilfoil coverage remained persistently high through 2020, averaging 180 ± 32 ha and ranging from approximately 101 to 213 ha in the main body of Candlewood Lake system.

Following the introduction of grass carp (marked by vertical black lines, Figure 3), Eurasian watermilfoil acreage and percent occurrence (Table 2) began to decline steadily, although the response did not become apparent until six years later. This lag is consistent with patterns observed in other systems, where effective control typically emerges 2–5 yr after stocking because of grass carp dietary preferences and growth limitations early in establishment (Bonar et al. 2002, Edwards 1974, Kirk 1992). In the Candlewood Lake system, 8,903 grass carp were stocked between 2015 and 2017, resulting in an average stocking density of approximately 11.1 fish per acre across both efforts. This density falls within the upper range of typical rates reported for vegetation suppression in other North American systems, which commonly range from 5 to 15 fish per acre depending on plant density and management goals (Fowler and Robson 1978, Kirk 1992, Cassani et al. 1995, Hanlon et al. 2000). Stocking rates above

Table 4. Drawdown duration and corresponding Eurasian watermilfoil hectares in the main body of Candlewood Lake system from 2007/2008 through 2019/2020. The table summarizes winter drawdown lengths and subsequent summer Eurasian watermilfoil area estimates, capturing variation in plant response prior to the emergence of grass carp impacts. Arrows indicate the direction of year-to-year change in drawdown duration and plant coverage.

Year	Season	Drawdown days	Area (ha)	Change in days	Change in area (ha)
2007/2008	Winter	75			
2008	Summer		183		
2008/2009	Winter	116		↑	
2009	Summer		151		↓
2009/2010	Winter	72		↓	
2010	Summer		187		↑
2010/2011	Winter	95		↑	
2011	Summer		134		↓
2011/2012	Winter	53		↓	
2012	Summer		205		↑
2012/2013	Winter	80		↑	
2013	Summer		105		↓
2013/2014	Winter	71		↓	
2014	Summer		193		↑
2014/2015	Winter	106		↑	
2015	Summer		178		↓
2015/2016	Winter	24		↓	
2016	Summer		205		↑
2016/2017	Winter	71		↑	
2017	Summer		201		↓
2017/2018	Winter	51		↓	
2018	Summer		208		↑
2018/2019	Winter	64		↑	
2019	Summer		171		↓
2019/2020	Winter	51		↓	
2020	Summer		213		↑

Table 5. Year Drawdown extent Total Days; Frozen (≤ 0 C); Cumulative Total Days and Cumulative Frozen Days reflect the cumulative duration of drawdown and freezing days, respectively.

Year	Drawdown extent	Total days	Frozen days	Cumulative	
				Total days	Frozen days
2007/2008	Insufficiently lowered	106	14	181	55
	Shallow	75	41	75	41
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2008/2009	Insufficiently lowered	65	17	181	76
	Shallow	57	16	116	59
	Intermediate	36	24	59	43
	Deep	23	19	23	19
2009/2010	Insufficiently lowered	109	11	181	65
	Shallow	72	54	72	54
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2010/2011	Insufficiently lowered	86	12	181	80
	Shallow	17	6	95	68
	Intermediate	30	24	78	62
	Deep	48	38	48	38
2011/2012	Insufficiently lowered	129	16	182	31
	Shallow	53	15	53	15
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2012/2013	Insufficiently lowered	101	10	181	52
	Shallow	20	12	80	42
	Intermediate	26	8	60	30
	Deep	34	22	34	22
2013/2014	Insufficiently lowered	110	35	181	85
	Shallow	69	49	71	50
	Intermediate	2	1	2	1
	Deep	0	0	0	0
2014/2015	Insufficiently lowered	75	14	181	84
	Shallow	43	13	106	70
	Intermediate	63	57	63	57
	Deep	0	0	0	0
2015/2016	Insufficiently lowered	158	34	182	45
	Shallow	24	11	24	11
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2016/2017	Insufficiently lowered	110	21	181	53
	Shallow	71	32	71	32
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2017/2018	Insufficiently lowered	130	23	181	53
	Shallow	39	22	51	30
	Intermediate	12	8	12	8
	Deep	0	0	0	0
2018/2019	Insufficiently lowered	117	24	181	63
	Shallow	21	12	64	39
	Intermediate	31	21	43	27
	Deep	12	6	12	6
2019/2020	Insufficiently lowered	131	30	182	44
	Shallow	51	14	51	14
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2020/2021	Insufficiently lowered	109	20	181	59
	Shallow	29	10	72	39
	Intermediate	22	15	43	29
	Deep	21	14	21	14
2021/2022	Insufficiently lowered	135	19	181	40
	Shallow	23	10	46	21
	Intermediate	23	11	23	11
	Deep	0	0	0	0
2022/2023	Insufficiently lowered	136	17	181	25
	Shallow	17	3	45	8
	Intermediate	28	5	28	5
	Deep	0	0	0	0
2023/2024	Insufficiently lowered	155	18	182	26
	Shallow	27	8	27	8
	Intermediate	0	0	0	0
	Deep	0	0	0	0
2024/2025	Insufficiently lowered	33	0	33	0
	Shallow	0	0	0	0
	Intermediate	0	0	0	0
	Deep	0	0	0	0

Table 6. Combined comparison of historical (1984–1993) and recent (2007–2024) drawdown initiation dates and associated freezing-day exposure in the Candlewood Lake system. Columns include period, winter season, initiation day (indexed from 1 November), and initiation date when lake elevation first dropped below 129.5 m. For recent years, the table also lists actual freezing days, additional freezing days if drawdowns had started earlier on 27 November, and the resulting percent increase. Historical freezing-day data are unavailable and shown as blank, as drawdowns in that period already began earlier and a hypothetical earlier initiation scenario was not applied. On average, historical drawdowns began on Day 27 (27 November) compared to Day 64 (3 January) in the recent period, reducing overlap with freezing conditions critical for macrophyte control.

Period	Year	Drawdown initiation day	Drawdown initiation date	Actual freezing days[1]	Additional freezing days if initiated earlier[1]	Percent increase in freezing days[1]
Historical	1984/1985	31	1 December 1984	—	—	—
Historical	1985/1986	37	7 December 1985	—	—	—
Historical	1986/1987	20	20 November 1986	—	—	—
Historical	1987/1988	33	3 December 1987	—	—	—
Historical	1988/1989	35	5 December 1988	—	—	—
Historical	1989/1990	31	1 December 1989	—	—	—
Historical	1990/1991	28	28 November 1990	—	—	—
Historical	1991/1992	17	17 November 1991	—	—	—
Historical	1992/1993	10	10 November 1992	—	—	—
Recent	2007/2008	32	2 December 2007	41	1	2%
Recent	2008/2009	37	7 December 2008	59	4	7%
Recent	2009/2010	50	20 December 2009	54	9	17%
Recent	2010/2011	42	12 December 2010	68	10	15%
Recent	2011/2012	78	17 January 2012	15	15	100%
Recent	2012/2013	59	29 December 2012	42	7	17%
Recent	2013/2014	65	14 January 2014	50	24	48%
Recent	2014/2015	24	24 November 2014	70	0	0%
Recent	2015/2016	93	1 February 2016	11	22	200%
Recent	2016/2017	34	4 December 2016	32	0	0%
Recent	2017/2018	59	29 December 2017	30	13	43%
Recent	2018/2019	74	13 January 2019	39	19	49%
Recent	2019/2020	83	22 January 2020	14	25	179%
Recent	2020/2021	72	11 January 2021	39	19	49%
Recent	2021/2022	85	24 January 2022	21	16	76%
Recent	2022/2023	94	2 February 2023	8	14	175%
Recent	2023/2024	106	14 February 2024	8	17	212%

[1]Indicates values not calculated.

approximately 10 fish per acre have frequently been associated with substantial or complete removal of submersed vegetation within a few years (Van Dyke et al. 1984, Hanlon et al. 2000). These comparisons suggest that the delayed Eurasian watermilfoil decline in Candlewood Lake reflects typical grass carp establishment dynamics under similar ecological and management conditions.

Mixed-effects modeling results (Table 3) support these observations. Grass carp biomass had a significant negative effect on macrophyte abundance (estimate $= -0.059$, $P = 0.002$). This effect was stronger on Eurasian watermilfoil than on coontail, as indicated by a significant interaction term (estimate $= -0.014$, $P = 0.002$). The suppressive effect of grass carp also varied by depth, with a weaker impact at greater depths (interaction estimate $= 0.007$, $P = 0.008$). This is consistent with known carp behavior reported in other systems, where 75% of grass carp locations were observed at depths of 3 m or less (Hessler et al. 2023). A significant interaction between grass carp biomass and waterbody (estimate $= -0.072$, $P < 0.001$) revealed stronger impacts in Squantz Pond, where macrophyte community collapse occurred earlier (Table 3; Figure 3). This difference may reflect environmental and behavioral factors. Grass carp are known to prefer quieter, less-disturbed environments, and Squantz Pond has lower boat traffic and a simpler shoreline than the main body of Candlewood Lake, potentially enabling more efficient foraging (Bugbee and Stebbins 2021, Hessler et al. 2023). Although the interaction terms revealed depth- and waterbody-specific patterns, the main effect of waterbody was not significant (estimate $= 0.078$, $P = 0.770$), indicating that differences in overall macrophyte abundance between Squantz Pond and the main body of Candlewood Lake were primarily driven by grass carp biomass and its interactions rather than location alone.

The temporal trends in grass carp populations in the Candlewood Lake system from 2015 to 2024 reveal distinct patterns in both estimated abundance and biomass, reflecting the dynamics of herbivory pressure over time. Following initial stocking events in 2015 and 2017, marked by vertical red dotted lines in Figure 4, the estimated number of grass carp (Figure 4: blue line) increased sharply, reaching a peak of approximately 7,900 in 2017. However, post-2017, the estimated number of grass carp declined steadily due to natural attrition (assumed at 15% annually) and the onset of active removal efforts beginning in 2023. By 2024, the estimated number of grass carp had dropped to approximately 2,317 individuals, representing a 71% decline from peak levels (Figure 4).

In contrast, estimated biomass (Figure 4: green line) exhibited a delayed peak, reflecting continued growth of individual fish even as overall numbers decline. Biomass increased rapidly after 2015 and reached its maximum (~46,569 kg) in 2021, approximately 4 yr after the population size peaked. This lag highlights the growing ecological impact of the

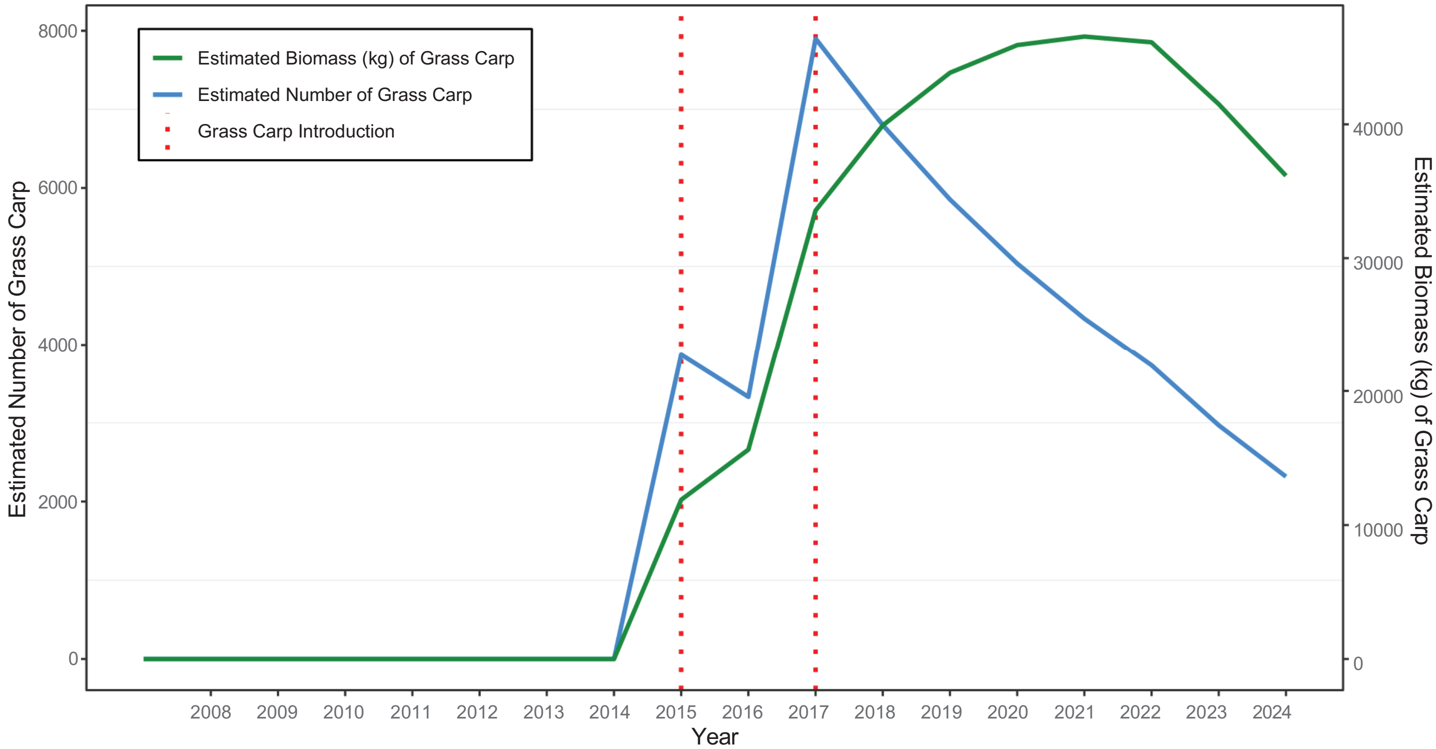

Figure 4. Temporal trends in the estimated number and biomass of grass carp in the Candlewood Lake system from 2008 to 2024. The left vertical axis represents the estimated number of grass carp (blue line), which increased sharply following introductions in 2015 and 2017 (marked by red dashed vertical lines). The population peaked in 2017 before gradually declining in subsequent years. The right vertical axis represents the estimated biomass of grass carp (green line), which steadily increased following the initial introduction in 2015, reaching a plateau around 2021.

carp population even as numbers declined (Pípalová 2006, Stich et al. 2013). Notably, between 2017 and 2021, the system experienced both high carp numbers and rapidly increasing biomass, representing the period of greatest herbivory pressure on the macrophyte community (Figure 4).

After 2021, the estimated fish biomass began to decline gradually, due to aging fish and the effects of recent removal efforts. These trends emphasize that biomass, not just fish abundance, is a critical metric for evaluating the ecological impact of grass carp. Even with declining numbers, large-bodied individuals likely continued to exert substantial grazing pressure. Grass carp exhibit approximately linear growth with age (Stich et al. 2013), requiring continued intake beyond maintenance levels. As such, older fish likely maintain a meaningful role in vegetation suppression. These findings reinforce the need to monitor not just fish abundance, but also biomass and age structure, to accurately assess herbivory pressure and inform long-term management decisions.

Based on current model projections (Figure 4), peak grass carp biomass was approximately 46,569 kg in 2021. If no further removals occur, this biomass is expected to decline to around 23,874 kg by 2030, with the two stocking cohorts reaching ages 14 and 16. These projections suggest that additional removal of grass carp may be warranted if recovery of the native aquatic plant community is a management priority. However, reducing grass carp biomass, and by extension, herbivory pressure, could inadvertently allow invasive macrophytes such as Eurasian watermilfoil to rebound. To avoid this outcome, recovery strategies should integrate complementary control measures, including selective herbicide use, manually removal, continued monitoring, and targeted native plantings within carp exclusion frames to encourage native species resilience and suppress invasive regrowth.

Integrated management implications and recommendations

As we continue to examine the Candlewood Lake system, local lake managers and stakeholders have begun efforts to support the recovery of the aquatic plant community. Primarily, this involves the continued removal of grass carp from the system. As these removals progress, we expect both the native and invasive plant communities to begin to rebound once herbivore pressure drops below the threshold necessary for sustained plant growth. Continued surveys are crucial during this period.

As the aquatic plant community begins to rebound, shifts in species composition may occur, influenced by regrowth dynamics, ongoing winter drawdowns, and the herbivory preferences and pressure of grass carp. If vegetation growth rates eventually exceed consumption rates, selective grazing may alter the balance between native and invasive species. Although the grass carp population is aging, individuals remain large and capable of sustained consumption, particularly in shallow habitats. As such, future declines in grazing pressure are likely to depend more on continued removal or long-term attrition than on age-related changes in feeding alone. These conditions may gradually create space for macrophyte recovery, especially under management strategies that reduce localized herbivory.

In addition, the analysis presented here suggests that not only grass carp pressure, but also the timing of winter drawdowns plays a critical role in long-term vegetation control. The documented shift in drawdown initiation, from historical late-November timing to mid-January in recent decades, has reduced the overlap between water level reductions and freezing conditions. Analysis indicates this shift has likely contributed to diminished drawdown efficacy, with several years potentially missing 100–200% more freezing-day exposure compared to a scenario in which drawdowns began in late November. As climate change continues to reduce overall freezing-day frequency, restoring earlier drawdown initiation could serve as an important complementary strategy to grass carp removal. This dual approach, reducing herbivory pressure while maximizing exposure to effective freezing conditions, may help delay or limit the resurgence of Eurasian watermilfoil and bolster efforts to reestablish a more resilient native aquatic plant community. A strong native community is also critical for resisting future invasions, as systems with low vegetation cover can be especially vulnerable to emerging threats.

Hydrilla verticillata (L.f.) Royle poses a growing threat to the Candlewood Lake system, especially as northern hydrilla (*H. verticillata* subsp. *lithuanica*) spreads beyond the Connecticut River into new waterbodies in Connecticut and Massachusetts (Foley et al. 2024). Most new infestations are linked to public or private boat ramps, implicating boating as a key vector. Candlewood's high trailer traffic, low aquatic plant biomass, and reduced vegetation following grass carp introduction may increase its vulnerability to hydrilla establishment. In fact, hydrilla fragments have already been intercepted on a vessel at a boat ramp on Candlewood Lake, and similar transfers and findings have occurred in other regions like Lake Champlain and Lake George. These findings highlight the urgent need for robust boat inspection and decontamination protocols to protect Candlewood from hydrilla invasion.

Based on the findings presented here, we support the continuation of an integrated management strategy to promote the recovery of native aquatic vegetation while minimizing the resurgence of Eurasian watermilfoil in the Candlewood Lake system. This strategy includes 1) continued removal of grass carp to reduce herbivory pressure, 2) restoration of earlier winter drawdown initiation to enhance cold exposure and sediment desiccation, with the goal of achieving biennial deep drawdowns more consistently, and 3) sustained aquatic vegetation monitoring to track regrowth, new invasions, and inform adaptive management. Together, these coordinated actions can help restore ecological balance, limit the resurgence of Eurasian watermilfoil, and promote the resilience of native macrophyte communities.

SOURCES OF MATERIALS

[1]GeoXT®, Trimble Inc., 935 Stewart Dr., Sunnyvale, CA 94085.
[2]R1 GNSS®, Trimble Inc., 935 Stewart Dr., Sunnyvale, CA 94085.
[3]Pathfinder® 5.85, Trimble Inc., 935 Stewart Dr., Sunnyvale, CA 94085.
[4]ArcGIS Pro® 3.4.0, ESRI Corp., 380 New York St., Redlands, CA 92373.

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LITERATURE CITED

Blanchette D, Schaffner R. 2017. Understanding the vulnerability of Maine lakes to invasive aquatic plants. Maine Department of Environmental Protection. https://www.maine.gov/dep/water/invasives/vulnerability.html. Accessed February 7, 2025.

Bonar SA, Bolding B, Divens M. 2002. Effects of triploid grass carp on aquatic plants, water quality, and public satisfaction in Washington State. N. Am. J. Fish. Manag. 22:96–105.

Bugbee GJ, Stebbins S. 2021. Invasive aquatic plant monitoring report for Candlewood Lake and Squantz Pond: 2020. Bulletin No. 1071. Connecticut Agricultural Experiment Station, New Haven, CT. 91 pp.

[CAES OAIS] Connecticut Agricultural Experiment Station Office of Aquatic Invasive Species. 2025. Connecticut Agricultural Experiment Station Office of Aquatic Invasive Species. http://www.portal.ct.gov/caes-oais. Accessed February 6, 2025.

Carmignani JR, Roy AH. 2017. Ecological impacts of winter water level drawdowns on lake littoral zones: A review. Aquat. Sci. 79(4):803–824.

Carmignani JR, Roy AH, Stolarski JT, Richards T. 2021. Hydrology of annual winter water level drawdown regimes in recreational lakes of Massachusetts, United States. Lake Reserv. Manage. 37(1):1–21.

Cassani JR. 1996. Managing aquatic vegetation with grass carp, a guide for resource managers. American Fisheries Society, Bethesda, MD. 196 pp.

Cassani JR, Caton WE. 1986. Efficient production of triploid grass carp (*Ctenopharyngodon idella*) utilizing hydrostatic pressure. Aquaculture 55(1):43–50.

Cassani JR, de la Vega EL, Allaire H. 1995. An assessment of triploid grass carp stocking rates in small warm water impoundments. N. Amer. J. Fish. Manage. 15:400–407.

Catarino LF, Ferreira MT, Moreira IS. 1997. Preferences of grass carp for macrophytes in Iberian drainage channels. J. Aquat Plant Manage. 35(4):79–83.

Caves S, Baumann JR, Stitch DS. 2021. Density-dependent changes in grass carp growth and mortality in long-term aquatic plant management. N. Am. J. Fish. Manag. 41(2):355–365.

Chilton EW, Muoneke MI. 1992. Biology and management of grass carp (*Ctenopharyngodon idella*, Cyprinidae) for vegetation control: A North American perspective. Rev. Fish. Biol. Fish. 2:283–320.

Christensen RHB. 2023. ordinal: Regression models for ordinal data (version 2023.12-4.1) [R package]. Retrieved from https://CRAN.R-project.org/package=ordinal. Accessed August 20, 2025.

Clapp DF, Hestand RS, III, Thompson BZ. 1994. Hauling and post-stocking mortality of triploid grass carp. J. Aquat. Plant Manage. 32:41–43.

Cooke GD, Welch EB, Peterson SA, Nichols SA. 2005. Restoration and management of lakes and reservoirs. 3rd ed. CRC Press, Boca Raton, FL. 616 p.

Crow GE, Hellquist CB. 2023. Aquatic and wetland plants of northeastern North America. University of Wisconsin Press, Madison.

Dibble ED, Kovalenko K. 2009. Ecological impact of grass carp: A review of the available data. J. Aquat. Plant Manag. 47(1):1–15.

Edwards DJ. 1974. Weed preference and growth of young grass carp in New Zealand. New Zealand. Aust. J. Mar. Freshw. Res. 8(2):341–350.

Eiswerth ME, Donaldson SG, Johnson WS. 2017. Potential environmental impacts and economic damages of Eurasian watermilfoil (*Myriophyllum spicatum*) in western Nevada and northeastern California. Weed Technol. 14(3):511–518.

Fantle-Lepczyk JE, Haubrock PJ, Kramer AM, Cuthbert RN, Turbelin AJ, Crystal-Ornelas R, Diagne C, Courchamp F. 2022. Economic costs of biological invasions in the United States. Sci. Total Environ. 806:151318.

Firth D. 1993. Bias reduction of maximum likelihood estimates. Biometrika 80(1):27–38.

Fishman KJ, Leonard RL, Shah FA. 1998. Economic evaluation of Connecticut lakes with alternative water quality levels. University of Connecticut, Storrs. 64 pp.

Foley JR, Stebbins SE, Doherty R, Tippery NP, Bugbee GJ. 2024. Northern hydrilla (*Hydrilla verticillata* ssp. *lithuanica*): Discovery and establishment outside the Connecticut River. Inv. Plant Sci. Manage. 17:55–59.

Fowler MC, Robson TO. 1978. The effects of the food preferences and stocking rates of grass carp (*Ctenopharyngodon idella* Val.) on mixed plant communities. Aquat. Bot. 5:261–276.

Gorbach EI. 1961. Age composition, growth, and age of onset of sexual maturity of the white *Ctenopharyngodon idella* (Val.) and the black *Mylophryngodon piceus* (Rich.) in the Amur River basin. Vop. Ikhtiol. 1(18):119–126.

Hanlon SG, Hoyer MV, Cichra CE, Canfield DE. 2000. Evaluation of macrophyte control in 38 Florida lakes using triploid grass carp. J. Aquat. Plant Manage. 38:48–54.

Hartleb CF, Madsen JD, Boylen CW. 1993. Environmental factors affecting seed germination in *Myriophyllum spicatum* L. Aquat. Bot. 45(1):15–25.

Hayhoe K, Wake CP, Liang X-Z, Maurer EP, Zhu J, Bradbury J, DeGaetano A, Anderson B, Wuebbles D. 2008. Regional climate change projections for the Northeast U.S. Mitig. Adapt. Strateg. Glob. Change 13(5–6):425–436.

Hessler TM, Chapman DC, Paukert CP, Jolley JC, Byrne ME. 2023. Winter habitat selection and efficacy of telemetry to aid grass carp removal efforts in a large reservoir. N. Am. J. Fish Manage. 43(1):189–202.

Jacobs RP, O'Donnell EB. 2002. A fisheries guide to lakes and ponds of Connecticut. Including the Connecticut River and its coves. Bulletin 35. Connecticut Department of Environmental Protection.

June-Wells M, Simpkins T, Coleman MA, Henley W, Jacobs R, Aarrestad P, Buck G, Stevens C, Benson G. 2017. Seventeen years of grass carp: An examination of vegetation management and collateral impacts in Ball Pond, New Fairfield, Connecticut. Lake Reserv. Manage. 33:84–100.

Karmalkar AV, Horton RM. 2021. Drivers of exceptional coastal warming in the northeastern United States. Nat. Clim. Change 11(10):854–860.

Kimbel JC. 1982. Factors influencing potential intralake colonization by *Myriophyllum spicatum* L. Aquat. Bot. 14:295–307.

Kirk JP. 1992. Efficacy of triploid grass carp in controlling nuisance aquatic vegetation in South Carolina farm ponds N. Am. J. Fish Manage. 12(3):581–584.

Kirk JP, Socha RC. 2003. Longevity and persistence of triploid grass carp stocked into the Santee Cooper reservoirs of South Carolina. J. Aquat. Plant Manage. 41:90–92.

Kirkagac MU, Demir N. 2004. The effects of grass carp on aquatic plants, plankton and benthos in ponds. J. Aquat. Plant Manage. 42:32–39.

Kohli P, Siver PA, Marsicano LJ, Hamer JS, Coffin AM. 2017. Assessment of long-term trends for management of Candlewood Lake, Connecticut, USA. Lake Reserv. Manag. 33:280–300.

Leslie AJ, Van Dyke JM, Hestand RS, Thompson BZ. 1987. Management of aquatic plants in multi-use lakes with grass carp (*Ctenopharyngodon idella*). Lake Reserv. Manage. 3:266–276.

Lonergan T, Marsicano L, Wagner M. 2014. A laboratory examination of the effectiveness of seasonal lake drawdown to control invasive Eurasian watermilfoil (*Myriophyllum spicatum*). Lake Reserv. Manage. 30:381–392.

Madsen JD. 1998. Predicting invasion success of Eurasian watermilfoil. J. Aquat. Plant Manage. 36: 28–32.

Madsen, JD. 1999. Point intercept and line intercept methods for aquatic plant management. U.S. Army Corps of Engineers Aquatic Plant Management Note MI-02. 11 pp.

Madsen JD, Eichler LW, Boylen CW. 1988. Vegetative spread of Eurasian watermilfoil in Lake George, New York. J. Aquat. Plant Manage. 26:47–50.

Madsen JD, Smart MR, Dick GO, Honnell DR. 1994. The influence of an exotic submersed aquatic plant. *Myriophyllum spicatum*, on water quality, vegetation and fish populations in Kirk Pond, Oregon. pp. 30–34. In: Proceedings, 29th Annual Meeting, Aquatic Plant Control Research Program.

McKnight SK, Hepp GR. 1995. Potential effect of grass carp herbivory on waterfowl foods. J. Wildl. Manag. 59(4):720–727.

Murphy S, Smolen G. 2005. Images of America: Candlewood Lake. Arcadia Publishing, Charleston, SC, 128 pp.

Pípalová I. 2002. Initial impact of low stocking density of grass carp on aquatic macrophytes. Aquat. Bot. 73:9–18.

Pípalová I. 2006. A review of grass carp use for aquatic weed control and its impact on waterbodies. J. Aquat. Plant Manage. 44:1–12.

Siver PA, Coleman AM, Benson GA, Simpson JT. 1986. The effects of winter drawdown on macrophytes in Lake Candlewood, Connecticut. Lake Reserv. Manage. 2:69–73.

Smith CG, Barko JW. 1990. Ecology of Eurasian watermilfoil. J. Aquat. Plant Manage. 28:55–64.

Stich DS, Dicenzo V, Frimpong EA, Jiao Y, Murphy BR. 2013. Growth and population size of grass carp incrementally stocked for Hydrilla control. N. Am. J. Fish. Manag. 33(1):14–25.

Thompson BZ, Wattendorf RJ, Hestand RS, Underwood JL. 1987. Triploid grass carp production. Prog. Fish Cult. 49(3):213–217.

[USDA-NRCS] U.S. Department of Agriculture–Natural Resources Conservation Service. 2025. Plants database. https://plants.usda.gov/plant-profile/MYSP2. Accessed February 6, 2025.

U.S. Global Change Research Program. 2009. Global climate change impacts in the United States. U.S. Global Change Research Program, Washington, DC. 188 p. https://nca2009.globalchange.gov/. Accessed February 20, 2025.

Van Dyke JM, Leslie AJ, Jr., Nall LE. 1984. The effects of the grass carp on the aquatic macrophytes of four Florida lakes. J. Aquat. Plant Manage. 22:87–95.

Zolfinejad K, Khara H, Filizadeh, Y. 2017. Food preference and growth of grass carp, *Ctenopharyngodon idella* (Cuvier and Valenciennes, 1844) fed some aquatic and terrestrial plants. Iran. J. Fish. Sci. 16(4):1278–1286.