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INVESTIGATING THE EFFECTS OF WINTER DRAWDOWNS ON THE ECOLOGICAL CHARACTER OF LITTORAL ZONES IN MASSACHUSETTS LAKES

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INVESTIGATING THE EFFECTS OF WINTER DRAWDOWNS ON THE ECOLOGICAL CHARACTER OF LITTORAL ZONES IN MASSACHUSETTS LAKES

A Dissertation Presented

by

JASON R. CARMIGNANI

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University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Organismic and Evolutionary Biology

INVESTIGATING THE EFFECTS OF WINTER DRAWDOWNS ON THE ECOLOGICAL CHARACTER OF LITTORAL ZONES IN MASSACHUSETTS LAKES

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DEDICATION

To my parents, the scuds, and the exploration of freshwater ecosystems

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ABSTRACT

INVESTIGATING THE EFFECTS OF WINTER DRAWDOWNS ON THE ECOLOGICAL CHARACTER OF LITTORAL ZONES IN MASSACHUSETTS LAKES

FEBRUARY 2020

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Anthropogenic alteration of water levels in lakes is a major stressor to the ecological integrity of littoral zones, which provide critical heterogenous resources that support diverse biological communities. Annual winter drawdowns have been practiced in Massachusetts (MA) for several decades; however, few studies have estimated impacts to littoral zone habitat and biological communities, particularly at relatively mild magnitudes (i.e., <2 m) and in lakes that co-occur with other anthropogenic pressures (e.g., lakeshore development) as seen in MA lakes. My dissertation reviewed the winter drawdown literature and collected empirical data in MA lakes to characterize winter drawdown hydrological regimes and estimate responses of physical habitat (macrophytes, sediment texture, coarse wood), macroinvertebrate assemblages, and mussel assemblages to variable levels of drawdown magnitude. Through a stratified random selection approach, I selected 21 MA lakes (18 drawdown, 3 non-drawdown) based on drawdown information from an email survey to local conservation commissions and lake and pond associations. I continuously monitored water levels for 3–4 years within these lakes that represented a drawdown magnitude gradient. Drawdown regimes displayed considerable inter- and intra-lake variability in the timing and duration of annual drawdown events. The majority of winter drawdown events were incongruous to MA state issued timing guidelines, particularly for April 1st refill dates. In the same set of lakes, I found increased drawdown magnitude was correlated with coarser substrates and reduced silt, reductions in macrophyte biomass and biovolume, and proportional increases of macrophyte taxa with annual longevity strategy and amphibious growth form. During normal water levels, I found markedly lower freshwater mussel densities at drawdown-exposed depths compared to the same depths in non-drawdown lakes. I also found drawdown magnitude significantly structured macroinvertebrate taxonomic and functional composition with evidence that suggests several drawdown-sensitive taxa (e.g., *Amnicola*) and traits (e.g., semivoltinism). To minimize losses to lake ecological integrity, winter drawdown management should consider the extent of lakebed and littoral zone area exposed during drawdowns, incorporate depth-specific monitoring efforts for susceptible biota (e.g., mussels), and anticipate water level responses to climate change.

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CHAPTER 1

INTRODUCTION

Lake water level fluctuations are a natural disturbance regime that creates spatial and temporal heterogeneity of abiotic and biotic components of littoral zones (Gasith and Gafny 1990; Strayer and Findlay 2010) that influence whole-lake ecosystem patterns (Coops and Hosper 2002). Anthropogenic alteration of water level fluctuation regimes to achieve human derived goals (e.g., hydropower, recreation, flooding, habitat management) pose a significant threat to lake ecological integrity when regulated water levels exceed the hydrological variability of natural water level fluctuations (Zohary and Ostrovsky 2011). Elucidating the potential impacts of altered water level regimes on littoral zone ecological patterns requires focused investigation on specific water level management practices such as annual winter drawdowns.

Annual wintertime water level drawdown is a multi-purpose management technique used in impounded freshwater systems of boreal and temperate climates. Winter drawdowns are conducted to reduce nuisance densities of macrophytes, prevent ice damage to shoreline structures (e.g., docks, retaining walls, impoundments), access shoreline property for maintenance, meet hydropower demand, provide flood storage, consolidate loose sediments, and reclaim fish populations (Ploskey 1983; Hellsten 1997; Mattson et al. 2004). In Northeastern U.S.A. recreational lakes with residential shoreline development, winter drawdowns are regularly conducted to control aquatic macrophytes and protect shoreline properties (Mattson et al. 2004).

In the state of Massachusetts (MA), annual winter drawdowns have been implemented and practiced from the early and mid-20th century through the present day. Many MA recreational lakes were the result of industrialization in southern New England to provide water power and outfitted with outflow control structures to manipulate water levels (Steinberg 1991). Over time, the construction of impoundments, increased watershed nutrient loads, lakeshore development, and accessibility for recreational activities (e.g., boating) likely enabled the proliferation of invasive macrophytes (e.g., *Myriophyllum spicatum*) across the landscape (Johnson et al. 2008). In efforts to manage macrophytes and continuously maintain recreational value, lake management strategies often include winter drawdown because it is among the cheapest macrophyte control techniques to perform and does not have a negative environmental stigma like chemical treatment (Cooke et al. 2005).

In MA, winter drawdowns are regulated under the Wetland Protection Act (Massachusetts General Laws (MGL) Chapter 131, Section 40) by local conservation commissions and overseen by the MA Department of Environmental Protection (MADEP). Drawdown project proponents are required to file a Notice of Intent (i.e., detailed project proposal) with the community's conservation commission, which reviews and issues an Order of Conditions that approves or rejects the proposed drawdown. An appeal to the issued Order of Conditions can be made to the MADEP by the applicant, abutters, a group of $\geq$10 citizens, or MADEP. If the drawdown overlaps with estimated or priority habitat for rare species, the Natural Heritage and Endangered Species Program within the MA Division of Fisheries and Wildlife (MassWildlife) also has regulatory authority. To help develop and evaluate Notices of Intent, the MA Eutrophication and

Plant Management Final Generic Environmental Impact Report (Mattson et al. 2004) and its accompanying document (Langley et al. 2004) provide examples of potential impacts to non-target organisms, and detailed implementation and monitoring guidance. In addition, MassWildlife has developed performance standards that help protect and limit potential impacts to fish and wildlife resources, while still allowing to meet management goals. The performance standards recommend limits on the magnitude, timing, in-lake recession rate, and outflow discharge of winter drawdowns (MassWildlife 2002; see Chapter 2 for specific standards). Furthermore, if drawdowns are >3 ft, MassWildlife must be contacted to evaluate potential site-specific impacts to fish and wildlife resources. Although these documents provide valuable guidance for winter drawdown practice, it remains uncertain how winter drawdowns are actually performed in terms of their magnitude, timing, duration, and water level rates in MA lakes. Moreover, few empirical studies have examined impacts of winter drawdowns associated with recreational purposes (such as those conducted in MA) on lake littoral habitats.

The damming of streams and shallow wetlands to create lake systems (i.e., reservoirs) changes fundamental physical, chemical, and biological processes. Increased water residency time from lotic to lentic conditions changes water temperature (e.g., seasonal stratification) and sediment regimes (e.g., increased sedimentation), energy (e.g., increased autochthony and detrital inputs) and nutrient flow (Baxter 1977, Friedl and Wüest 2002) in turn structuring the biological community and ecosystem functioning (Vanni et al. 2005, Furey et al. 2006). Furthermore, water residency time is dependent on lake morphometry (e.g., surface area, depth profile) and a lake's hydrologic position in the landscape, all of which influence the operation of lake water levels (Kennedy 2005).

Regulation of water levels after impoundment construction often accompanies lake/reservoir system creation, which further modifies lake biogeochemical patterns (Black et al. 2003, Furey et al. 2004, Haxton and Findlay 2009). Additionally, these hydrogeomorphic features can mediate watershed and lakeshore land use (e.g., agriculture, impervious cover) nutrient and energy inputs in turn influencing lake biological community dynamics (Bremigan et al. 2008). Therefore, the effects of damming, watershed and lakeshore land use development and change, and the regulation of water levels as winter drawdowns variably contribute to the current ecological condition of Massachusetts lakes. However, we lack a general understanding of the relative influence of winter water level drawdown on lake ecological condition.

Although winter drawdowns are likely implemented widely across MA, a centralized database of historical and current winter drawdowns does not exist. Therefore, to facilitate selection of study lakes for the current and future projects, I generated an email survey to collect winter drawdown information throughout MA (Appendix A). In 2013 and 2014, I emailed MA town conservation commissions and lake and pond associations on 2074 waterbodies for information about the history of winter drawdowns in the waterbodies they manage. I received responses for 403 waterbodies (19.4% response rate by waterbody) and found that 99 of 403 waterbodies (24.6%) had a history of winter drawdowns (Appendix B). Reported drawdown magnitudes ranged from 0.3–2.24 m with a median of 0.76 m (n = 37 waterbodies), although 62 waterbodies did not provide information on drawdown magnitude (Appendix B). Only 26 waterbodies had information on the number of years of annual drawdown, with ongoing annual winter drawdowns for 10–154 years (median = 40 years). This survey suggests that winter drawdowns are commonly used across Massachusetts and over several decades.

My dissertation includes a literature review (Chapter 2) and four empirical research projects (Chapters 3–6). In Chapter 2, I review the winter drawdown literature summarizing winter drawdown effects on littoral zone ecology and highlight knowledge gaps to direct future research. This comprehensive review helps inform my research focus for subsequent data chapters (3–6). The data chapters assess the relative impact of annual winter drawdown regimes on abiotic properties and biotic assemblages of littoral zones from a representative set of lakes in Massachusetts. Generally, I anticipate winter drawdowns regimes to significantly structure littoral zone abiotic and biotic patterns as a function of drawdown magnitude or drawdown exposure. Chapter 3 quantifies the spatiotemporal variability of winter drawdown hydrology metrics (e.g., magnitude, timing, duration, rate) and compares these metrics to performance standards issued by MassWildlife. Hydrological metrics generated from Chapter 3 (e.g., magnitude, recession rate) are used to explain variability of ecological responses in Chapters 4–6. In Chapter 4, I investigate the relative effect of winter drawdown magnitude on physical habitat components (e.g., sediment, coarse wood) and macrophyte assemblages of shallow waters in the presence of covarying environmental factors (e.g., alkalinity, water transparency) and cooccurring anthropogenic pressures (e.g., lakeshore development, herbicides) across 21 lakes (18 drawdown, 3 non-drawdown). Chapter 4 also considers winter drawdowns as an effective macrophyte management tool. Within a subset of these lakes, I use a comparative approach in Chapter 5 to estimate the effect of winter drawdown presence on mussel densities using 6 drawdown and 3 non-drawdown lakes and estimate drawdown-related mortality in exposure zones at 9 drawdown lakes. Mussels are particularly sensitive to water level fluctuations, and this chapter aims to determine if mussel distributions are limited to depths deeper than drawdown magnitudes between annual drawdown events (i.e., summer). In Chapter 6, I estimate the relative importance of winter drawdown magnitude in explaining macroinvertebrate abundance, and taxonomic, and functional trait composition across 14 lakes representing a drawdown magnitude gradient. Although previous work has estimated the effect of magnitude on abundance (Trottier et al. 2019) and composition (Aroviita and Hämäläinen 2008; White et al. 2011), this chapter examines macroinvertebrates from three different mesohabitats (cobble, macrophytes, soft-substrate), which may have diverging responses to drawdowns. Since annual winter drawdowns have been conducted for several decades in the sampled drawdown lakes, the empirical data chapters (Chapters 3–6) are essentially measuring the cumulative effects of consecutive annual drawdown events. Furthermore, by sampling most response variables in the summer during full-pool levels, I focus not on the acute effects (except with mussels, Chapter 5), but on chronic effects that carry over from wintertime disturbance (e.g., desiccation, freezing, erosion). Lastly, I provide general conclusions from my results and make recommendations for lake management to improve the implementation and practice of winter drawdowns in Chapter 7. Overall, this dissertation will help to determine the relative influence of winter drawdown regimes on littoral zone ecological conditions. Results will help MA state agencies, local conservation commissions, and lake managers refine the implementation and practice of winter drawdowns to limit impacts on vulnerable biota while still maintaining recreational value.

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CHAPTER 2

ECOLOGICAL IMPACTS OF WINTER WATER LEVEL DRAWDOWNS ON LAKE LITTORAL ZONES: A REVIEW

Introduction

In lentic ecosystems, water level fluctuations create a natural disturbance regime that helps to structure the littoral zone (Gasith and Gafny 1990; Wantzen et al. 2008; Strayer and Findlay 2010*)*. Seasonal and inter-annual water level fluctuations influence the survival of numerous flora and fauna in the littoral zone (Hill et al. 1998; Riis and Hawes 2002; White et al. 2008). High flows and flooding release nutrients from riparian areas (Baldwin and Mitchell 2000) and provide spawning habitat for numerous fish species (Kahl et al. 2008; Gertzen et al. 2012). Sediment dewatering and subsequent desiccation stimulates macrophyte species propagation and enhances nutrient cycling (Keddy and Reznicek 1986; Hill et al. 1998; Baldwin and Mitchell 2000). Through the interplay of direct (e.g., physiological stress) and indirect (e.g., habitat alteration) mechanisms, water level fluctuations create temporal and spatial heterogeneity that structures littoral zone communities (Hofman et al. 2008).

Although natural water level fluctuations are critical for ecosystem structure and function, hydrologic alterations in impounded lakes and river reservoirs (hereafter referred to as lakes) that exceed natural variability may be detrimental to lake ecosystems (Winfield 2004; Peters and Lodge 2009; Strayer and Findlay 2010). Hydrologic modification and concomitant habitat loss threaten ecosystem functioning and biodiversity in lakes (Stendera et al. 2012). Altered water level regimes include frequent, extreme fluctuations and water level stabilization, both that create novel environments (Boschilia et al. 2012).

In temperate and boreal regions, annual fall and winter water level drawdowns (hereafter: winter drawdowns) and subsequent spring refills (Figure 2.1) are a common lake and reservoir management practice to achieve a variety of human goals. Increased energy demand lowers water levels in hydroelectric reservoirs during winter months (Aroviita and Hämäläinen 2008) and further provides storage in anticipation for seasonal spring flooding (Hellsten 1997). In recreational lakes throughout North America, annual winter drawdowns serve as a preventative measure to protect docks and retaining walls from ice scour damage, permit shoreline cleanup, and reduce nuisance levels of aquatic vegetation (Cooke et al. 2005). Historically, fishery managers used drawdowns to stimulate piscivorous sport fish populations by reducing prey refuge habitat, concentrating prey populations (Hulsey 1957; Lantz et al. 1967; Groen and Schroeder 1978), and promoting macrophyte growth for spawning and rearing refuge for these species (Fox et al. 1977). In addition, managers use drawdowns to attempt to eradicate undesired fish species (e.g., common carp) to promote clear water conditions (Verrill and Berry Jr. 1995).

Although the goals of winter drawdowns vary, comparison of responses of abiotic conditions and biotic assemblages to drawdowns across study systems can be useful in advancing the understanding of lake alteration. Despite an increase in research on water level fluctuations since the early 1990s, research on winter drawdowns remains limited and needs an updated synthesis. Recent review papers focus on the influence of regulated water level fluctuations on shallow lakes and wetlands (Coops et al. 2003), stratified lakes (Zohary and Ostrovsky 2011), lakes in general (Leira and Cantonati 2008), and alpine hydropower reservoirs (Hirsch et al. 2017). Previous reviews specific to winter drawdowns include Cooke (1980), Ploskey (1983), Wilcox and Meeker (1992), and most recently by Cooke et al. (2005) and Abrahams (2006) with a specific focus on macrophyte management. A comprehensive synthesis of winter drawdowns has not happened in the last 25 years.

Given the widespread use of winter drawdowns as a management tool, a current review is needed to update and centralize knowledge on impacts of drawdowns. Here, we synthesize the effects of winter water level drawdowns and subsequent spring refills on multiple components of the lake ecosystem. We describe responses of the physicochemical environment, macrophytes, algae, invertebrates, and fish, emphasizing the potential bottom-up cascading impacts. Lastly, we identify knowledge gaps and propose future research to advance the understanding of abiotic and biotic dynamics in response to winter drawdowns across a gradient of environmental conditions.

Physicochemical Changes

Sediment & Ice

Littoral sediment patterns (i.e., grain size, soil water content, bulk density) are a function of wind/wave energy modified by lake morphometric measures including depth, slope, shoreline exposure, and fetch (Rowan et al. 1992; Blais and Kalff 1995; Hellsten 1997; Cyr 1998). In many deep lakes with steep shorelines, waves suspend fine sediment from littoral areas and deposit sediments into deeper areas (Håkanson 1977; Hellsten 1997; Cyr 1998). Drawdown can accelerate this sediment focusing process (Lukon and Bezold 2000), whereby sediment coarsening occurs in the upper littoral zone and fine sediment deposition increases in the sublittoral and the profundal zones (Figure 2.2**,** Hellsten and Riihimäki 1996; Wagner and Falter 2002; Effler and Matthews 2004; Furey et al. 2004), potentially leading to shallower lake profiles (Beklioglu et al. 2006). Sediment desiccation and erosion from precipitation and wind/wave action consolidate sediment in the drawdown exposure zone (Tarver et al. 1980; Wagner and Falter 2002; Furey et al. 2004) and increase sediment bulk density (Gottgens 1994). Conversely, a reduction in drawdown amplitude in an annual drawdown system can promote the deposition of fine sediment back into previously exposed littoral area (Benson and Hudson 1975).

The rate of refill and shoreline slope influence shoreline erosion and sedimentation during spring refills (Alasaarela et al. 1989). Rapid refills can enhance shoreline erosion in deeper depths (Furey et al. 2004) and resuspend fine sediment into the water column, increasing turbidity especially in shallow areas (Hestand and Carter 1974). Strong winds and waves during refill can exacerbate the rate of erosion (Luettich et al. 1990; Coops and Hosper 2002). Thus, a relatively low rate of water drawdown and refill may enhance erosion of shallow littoral areas by increasing the exposure time to wind/wave energy (Lorang et al. 1993). Shallow, gently sloping lakes show a less distinct sedimentation response to drawdowns (Hellsten 1997) because fine sediment is more susceptible to entrainment in these lakes (Havens et al. 2004; Shantz et al. 2004).

Winter drawdowns also increase the area of lake sediment exposed to desiccation, freezing, and snow cover (Hellsten et al. 1997). In the absence of groundwater seepage and inlets, water depth is inversely related to desiccation potential and further modified by physical sediment characteristics (e.g., porosity, grain size). Compared to finer sediments (e.g., clay, silt), coarse sediments (e.g., sand, gravel) possess lower water content (Håkanson 1977) and retain less water under drying conditions (i.e., drawdown phase).

The extent of scour from ice in drawdown lakes is determined by climate and weather patterns, winter drawdown regimes, substrate size distributions, and surface and groundwater seepages, among other factors (Erixon 1981; Rørslett 1988; Hellsten 1997). Generally, the level of ice disturbance on submerged sediments is higher in drawdown lakes compared to unregulated lakes (Rørslett 1984, 1988; Renman 1989; Palomäki and Koskenniemi 1993; Pugh and Davenport 1997; Hall et al. 1999). Where descending ice penetrates the sediment, needle ice can form causing frost heave (Renman 1989). Needle ice can also form on the surface of fine-grained sediment, particularly when sediment is moist (Renman 1993). In the deeper, non-frozen sediment zone, ice exerts mechanical pressure on the sediment surface (Hellsten 1997). In a hydroelectric lake in Finland, Hellsten (1997) found deeper ice-sediment penetration, larger area of ice, and longer durations of sediment-penetrating and non-penetrating ice zones compared to an unregulated lake. Under zero to low snow cover, frozen sediment under drawdown is vulnerable to upheaval and subsequent transport to other areas of the lake upon refill (Mattson et al. 2004). However, snow cover can also insulate sediment, preventing freezing conditions and ice scour (Siver et al. 1986; Mattson et al. 2004). Furthermore, substrate composition modifies freezing patterns with sandy substrates most susceptible to freezing compared to finer and organic matter-rich substrates (Palomäki and Koskenniemi 1993, Hellsten 1997).

The timing of winter drawdowns relative to ice cover affects the location and extent of ice disturbance in lakes. Most studies on the distribution and cover of ice derive from Scandinavian countries, where ice cover can last for 5-8 months (e.g., Rørslett 1988; Renman 1993; Hellsten and Riihimaki 1996; Hellsten 1997). There, ice-on typically occurs before drawdown initiation, resulting in heavy ice scour at full pool levels and low drawdown water levels (Rørslett 1984, 1988). In contrast, ice-related disturbance in temperate climates likely result in ice scour in one location in the lake since drawdowns are initiated before ice-on and may not reach low drawdown water level before freezing conditions. Sediment desiccation is likely a more important stressor in temperate lakes.

Nutrient Dynamics

Nutrient dynamics are altered in drawdown lakes compared to non-drawdown lakes based largely on the effect of drawdowns on sediment. Sediment coarsening and increased bulk density reduces the nutrient storage capacity (Barko and Smart 1986) and can further limit sediment-water nutrient flux via sediment burial in deeper areas (Figure 2.2, Hall et al. 1999). The redistribution of organic and inorganic matter from littoral to deeper locations can result in a shift from autochthonous to allochthonous carbon (Gottgens 1994; Furey et al. 2004; McEwen and Butler 2010), likely resulting in changes to the composition, distribution, and densities of primary producers (e.g., benthic algae).

Regulated drawdowns may enhance the release of nitrogen and phosphorous from previously exposed sediment upon rewetting (Cooke 1980). In mesocosm experiments, nutrient release rates in dried and rewetted sediment can exceed the release rates under oxygenated submerged conditions for ammonium (Peverly and Kopka 1991; Qiu and

McComb 1996; McGowan et al. 2005) and soluble reactive phosphorous (Qiu and McComb 1994; Steinman et al. 2012). Consequently, the nutrient pulse from reflooded sediments can temporarily increase nitrification (i.e., microbial activity) in aerobic conditions (Qiu and McComb 1996; Baldwin and Mitchell 2000; Corstanje and Reddy 2004). Upon reinundation, sediments located closest to the water-air interface (i.e., driest sediment) show the highest release of nutrients compared to deeper littoral depths (de Vicente et al. 2010; Steinman et al. 2012). Additionally, phosphorous can increase in both porewater and in the water column (Peverely and Kopka 1991). The main mechanisms of nutrient release include: (i) a reduced binding capacity of oxidized and desiccated mineral (e.g., iron, calcium, aluminum, manganese) phases (Qiu and McComb 1994; Baldwin 1996; Olilia et al. 1997; Watts 2000; Song et al. 2007; de Vicente 2011; Steinman et al. 2012); (ii) increased mineralization of organic phosphate and nitrogen (Qiu and McComb 1994; Olilia et al. 1997; James et al. 2001; Song et al. 2007; Steinman et al. 2009); (iii) and microbial cell lysis (Qui and McComb 1995; Olilia et al. 1997; Mitchell and Baldwin 1998; Klotz and Linn 2001; Wilson and Baldwin 2008). Though system specific, these mechanisms of nutrient release depend on factors such as the size of the mineral resource pool (Jensen and Andersen 1992), the composition and desiccation tolerance of the microbial community (Baldwin and Mitchell 2000), the frequency and timing of drawdown and refill (Song et al. 2007; Wilson and Baldwin 2008), and the duration of drying (Olila et al. 1997).

The duration of sediment desiccation alters the chemical structure of phosphate-adsorbing minerals (e.g., iron). The initial phosphate adsorption capacity of oxidized sediment minerals is higher than submerged sediment (Baldwin 1996). However, with time (e.g., months), increasing oxidation and desiccation replaces high phosphate affinity amorphous mineral structures with low phosphate affinity crystalline structures, resulting in phosphate desorption (Baldwin 1996). After 0.5-1 years of lake sediment exposure, James et al (2001) recorded a notable increase in phosphate-sediment release coincident with refill. Mineralization during sediment oxidation and desiccation contributes to nutrient pool availability for release upon inundation (James et al. 2001). Repeated cycles of sediment desiccation and rewetting also show higher phosphate release rates via mineralization and mineral desorption of phosphate compared to submerged conditions (Song et al. 2007).

Few studies have examined the effect of winter drawdowns on changes of element and ion concentrations in water (Turner et al. 2005) and sediments (Peverly and Kopka 1991). Increases in calcium concentration is evident upon re-wetted conditions, as seen in soft-water lakes (Peverly and Kopka 1991; Turner et al. 2005). Other ions that show increases include silica (Tuner et al. 2005) and potassium (Peverly and Kopka 1991), which in turn increase water alkalinity, conductivity, and pH levels.

Dissolved Oxygen & Temperature

Winter drawdowns also impact water-column dissolved oxygen (DO) levels. DO is naturally low in the winter via reduced photosynthesis, lower respiration demand, and lower atmosphere-water oxygen exchange (i.e., reduced wave action) due to snow and ice cover. Water volume loss with drawdowns also lowers DO concentrations during the winter months (Gaboury and Patalas 1984; Mills et al. 2002; Cott et al. 2008). In small (<30 ha) and shallow lakes (maximum depth <8m) of the Northwest territories, the DO during drawdown with low snow cover and ice thickness resemble DO under no drawdown with relatively thick snow and ice cover (Cott et al. 2008). DO will be higher in lakes with continuous groundwater or surface water inputs over lakes without continuous DO sources (Gaboury and Patalas 1984).

The effects of winter drawdown on water temperature vary with the regional climate and lake morphometry. Water temperature during winter drawdown can be within the natural variability in small boreal lakes (Cott et al. 2008). However, littoral zone depths that become relatively shallow during a winter drawdown can experience cooler than normal water temperatures. During an abnormally low winter water event in Lake Constance, Germany, Werner and Rothhaupt (2008) recorded sustained low water temperatures at depths rarely exposed to such low temperatures.

Primary Producer Responses

Macrophytes typically receive the most attention in studies that examine the effects of general water level fluctuation on the littoral zone (Leira and Cantonati 2008). In contrast, winter drawdown studies more equally cover macrophytes, invertebrates, and fishes (Figure 2.3, Appendix C). Patterns of macrophyte distribution, community composition, and abundance are primarily determined by abiotic factors such as organic matter content (Koch 2001), wind/wave exposure (Riis and Hawes 2003), temperature, light, sediment characteristics (i.e. texture, cohesion, stability, moisture content), and nutrient levels (Bornette and Puijalon 2011). Drawdowns modify these abiotic conditions, indirectly regulating macrophyte assemblages (Hill et al. 1998; Bornette and Puijalon 2011). Sediment desiccation and freezing exert direct mechanical disturbance and physiological stress on vegetative root structures (Siver 1986). Subsequent spring refills can erode frozen sediment and displace plants (Beard et al. 1973; Mattson et al. 2004). In soft-water systems drawdowns can stifle species growth by increasing acidity and cations (zinc, manganese) to toxic concentrations (Peverly and Kopka 1991). In contrast, the potential release of limiting nutrients upon refill may enhance primary production at least temporarily (Cooke 1980). Over time, annual winter drawdowns coarsen sediment texture and remove nutrients in the exposure zone often rendering it unsuitable for macrophyte colonization and growth, especially in more steep-sided basins (Hellsten 1997). Depths beyond the exposure zone are enriched with organic matter and sediment-adsorbed nutrients potentially inhibiting plant growth (Hellsten and Rhiihimaki 1996). Macrophyte responses to winter drawdown further depends on species' tolerance, life-history strategy, and growth plasticity, as described in more detail below.

Macrophyte Density and Biomass

Studies have documented reduced macrophyte density, biomass, and % cover in the drawdown exposure zone compared to reference systems or previous non-drawdown conditions (Figure 2.3, Tarver 1980; Wagner and Falter 2002; Turner et al. 2005; Beklioglu et al. 2006; Sutela et al. 2013). Annual drawdowns of relatively large amplitude (e.g. >2-3m) significantly reduce density and biomass (Rorslett 1989; Turner et al. 2005**;** Keto et al. 2006 Sutela et al. 2013). Relatively mild drawdowns show less impact on macrophyte density, but decreases are apparent (Keto et al. 2006). Shallow and exposed water depths typically experience the strongest density declines due to atmospheric exposure and sediment desiccation (Thomaz et al. 2006). After a novel winter drawdown (1.2-m amplitude) in a Vermont lake/deep marsh system that exposed 13% of the sediment, 18 of 30 submergent and emergent macrophyte species in the deep marsh and 7 species in the lake portion showed significant decreases in cover and stem density (Crosson 1990). Moreover, average surface plant cover and submerged plant cover decreased by 80% in the marsh and 46% in the lake (Crosson 1990). Generally, macrophyte colonization and growth occurs in areas that remain wet year-round. Olson et al. (2012) found that winter drawdown amplitude corresponds with the shallow depth distribution of the invasive *Myriophyllum spicatum* (Eurasian water milfoil), and increased abundance with water depth. Similarly, McGowan et al. (2005) demonstrated higher biomass at depths greater than the drawdown amplitude. The extent of macrophyte biomass below the drawdown exposure zone depends on species-dependent thresholds of light and physicochemical sediment properties (Wagner and Falter 2002).

Re-colonization of the drawdown exposure zone from deep residing individuals can occur during the growing season if suitable growing conditions exist (Crosson 1990; Turner et al. 2005; Thomaz et al. 2006; Olson et al. 2012). Species persistence in the exposure zone ultimately depends on the drawdown frequency and the species response to desiccation, freezing, and accelerated erosion. Reductions in winter drawdown amplitude can increase macrophyte biomass in newly submerged depths. For example, after a reduction in the amplitude of an annual drawdown regime, Wagner and Falter (2002) documented an increase in mean macrophyte biomass at depths shallower than the historical drawdown amplitude.

Macrophyte Richness and Composition

Assemblage composition is a function of the hydrological components of the drawdown regime (e.g., frequency, duration, and amplitude), competitive interactions, and the species-level tolerance to drawdown-related disturbance (e.g., desiccation, low temperatures, erosional forces). Seasonal water level fluctuations and inter-annual fluctuations together structure spatio-temporal assemblage composition and richness (Hill et al. 1998; Casanova and Brock 2000). As a result, macrophyte composition across winter drawdown lakes varies by depth with dissimilarities most pronounced in the eulittoral (Rørslett 1989; Hall et al. 1999; Turner et al. 2005) or sublittoral zone (Wilcox and Meeker 1991; Hellsten and Rhiihimaki 1996).

In annual winter drawdown systems, distinct assemblage compositions develop relative to reference systems (Wilcox and Meeker 1991; Sutela et al. 2013). Large amplitude drawdowns decrease species richness (Wilcox and Meeker 1991; Hellsten and Riihimaki 1996) with the potential loss of entire macrophyte assemblages if amplitudes are extreme (Rørslett 1989). In contrast, relatively intermediate amplitudes facilitate high macrophyte richness (Wilcox and Meeker 1991; Van Geest et al. 2005; Mjelde et al. 2012). For example, in numerous floodplain lakes of the lower Rhine River, Van Geest et al. (2005) recorded higher submergent species richness in lakes with drawdowns of 0.4-0.6 m compared to amplitudes of <0.2 m. Similarly, Mjelde et al. (2012), found a positive correlation of species richness and drawdown amplitude in Scandinavian lakes with water level amplitudes <1.5 m.

The annual frequency of winter drawdowns can establish a drawdown-tolerant assemblage (Nichols 1975). Even after 2-3 annual winter drawdowns, tolerant species can become the dominant species throughout the drawdown exposure zone (Beard et al. 1973; Turner et al. 2005). Annual deep (e.g., > 2-3 m) winter drawdowns support the development of macrophyte assemblages mainly composed of species with ruderal or semi-ruderal (e.g., stress-ruderal, competitive-ruderal) life history strategies and species that are polymorphic, amphiphytic, and/or free-floating (Table 2.1, Rørslett 1989;

Hellsten 2002; Turner et al. 2005; Mjelde 2012). Ruderal species, characterized as fast growing with early reproduction and a high annual seed production (Grime 1977; Rørslett 1989), tend to have multiple propagating strategies to increase the likelihood of individual persistence and population viability (Tazik et al. 1982; Siver et al. 1986). For example, winter buds or turions removed by erosion or thwarted by physiological stress can propagate from resistant seed banks or unspecialized vegetative fragments (Combroux and Bornette 2004). The viability of seed banks can last for multiple years until suitable germination conditions arise (Howard and Wells 2009). Generally, sediment desiccation stimulates seed germination (Keddy and Reznicek 1986) and facilitates propagation in the drawdown exposure zone (McGowan et al. 2005). Rising water temperatures and concomitant ice-off in the spring promote rapid growth and establishment of ruderal species, limiting growth of other macrophyte species (Wagner and Falter 2002). With increasing lake bed desiccation intensity and frequency, species that produce sexual diaspores or seeds (e.g., *Najas minor*, *Potamogeton pectinatus*) are expected to dominate assemblages (Bornette and Puijalon 2011; Arthaud et al. 2012). Species that are polymorphic or amphiphytic (e.g., *Eleocharis acicularis*, *Ranunculus reptans*) can tolerate erosion and sediment dewatering, enabling them to persist in drawdown lakes (Wilcox and Meeker 1992; Mjelde et al. 2012). Further, the likelihood of persistence for drawdown-tolerant taxa increases because of reduced competition (i.e., for nutrients, light, space) with reduced or extirpated drawdown sensitive species (Hellsten 2000; Boschilia et al. 2012).

While drawdown favors ruderal and polymorphic species, other macrophyte species are restricted to low densities or are extirpated (Table 2.1). Taxa most vulnerable in the drawdown exposure zone include perennial species (e.g., many *Potamogeton* spp.) that rely heavily on rhizomic structures (e.g., thallus) for propagation (Siver et al. 1986), obligate-submergent species (Thomaz et al. 2006; Boschilia et al. 2012), and species sensitive to ice scour (Hellsten 2002) For example, large isoetids (e.g., *Isoetes lacustris*, *Lobelia dortmanna*), highly sensitivity to freezing and ice-scour, show consistent declines and low abundances in boreal winter drawdown lakes (Hellsten 2002; Mjelde 2012).

Phytoplankton and Alternative Stable States

Studies on the effects of winter drawdowns on phytoplankton not only are few, but also show contrasting results. Limited evidence supports the prediction that phytoplankton blooms would increase upon sediment re-flooding because of potential nutrient pulses (Cooke 1980). Under a novel drawdown, seasonal climate more likely controlled phytoplankton densities and assemblage composition over water level variation (McGowan et al., 2005). Similarly, Turner et al. (2005) found no differences in phytoplankton biomass and photosynthetic rates after a series of drawdowns compared to reference lakes; but did find a small reduction in taxonomic diversity in the drawdown lake potentially due to a large lake bed exposure area. In a hydroelectric reservoir in Finland, Vuorio et al. (2015) found a positive correlation between the biomass and presence of the diatom *Aulacoseira islandica* on stationary fishing nets and above average drawdown amplitude and associated water release. Stronger currents generated by higher amplitudes and water release are likely responsible for increased diatom suspension in the water column even under ice cover. Little is known about the effect of winter drawdown on harmful cyanobacteria blooms (Bakker and Hilt 2015). Nõges and Nõges (1999) found that low winter and summer water levels enhanced light conditions and increased susceptibility to phosphorous via sediment resuspension, enabling cyanobacteria proliferation, but no studies have shown blooms with just winter drawdowns.

Seasonal drawdowns can transform shallow, eutrophic ecosystems from a clear-water, macrophyte-rich state to a turbid, phytoplankton-dominated state (Blindow 1992). However, little study exists on the influence of winter drawdowns on clear- and turbid-water states. A rapid refill can increase turbidity, reduce light penetration, and decrease macrophyte survival, growth, and recruitment (Hestand and Carter 1974). Macrophyte cover loss can increase sediment resuspension, reducing water clarity, which further inhibits macrophyte growth. A significant loss of submerged macrophyte cover from a winter drawdown, in combination with a pulse of limiting nutrients into the water column upon refill, can stimulate phytoplankton and cyanobacteria growth resulting in spring and summer blooms (Cooke 1980). High phytoplankton concentrations reduce light attenuation and favor macrophyte species tolerant to low-light conditions, such as free-floating or rooted floating species (Hestand and Carter 1974; Arthaud et al. 2012). In floodplain lake systems, shallow drawdowns (0.4-0.6 m) enhanced the development of transient submerged macrophyte assemblages before ultimately returning to a stable turbid state (Van Geest et al. 2007). The magnitude, frequency, and timing of drawdowns may influence whether a shallow, eutrophic lake will shift from a clear to turbid state.

Benthic Algae

The depth gradient and associated substrate and light environment in part drive benthic algal assemblages (Cantonati and Lowe 2014), with water level fluctuations as a primary disturbance that can select for desiccation-tolerant benthic algae and cyanobacteria in littoral zones (Cantonati et al. 2009, 2014). Despite their central role in littoral zones and lake ecosystems, benthic algae are understudied in response to winter drawdowns and, where studied, periphyton show mixed responses. Turner et al. (2005) found no significant effect of three consecutive winter drawdowns on periphyton biomass, composition, and metabolism. The lack of periphyton response may be explained by rapid algal turnover rates and increases in algae associated with nutrient pulses offsetting potential reductions from substrate losses. Furthermore, frequent water level fluctuations can favor mobile benthic algae (Evtimova and Donohue 2016), with the potential to adapt to annual winter drawdowns systems (Turner et al. 2005). Sediment desiccation and freezing can promote taxa with spores resistant to these stresses. For example, species from the macroalgal genus *Chara* can proliferate via desiccation and freezing resistant oospore sediment banks (Havens et al. 2004), dominating the drawdown exposure zone during spring and summer months (Wagner and Falter 2002). Benthic algae grow on a variety of substrates that include macrophytes, wood, and a range of sediment textures (Vadeboncoeur and Steinman 2002), which differ in substrate-specific algal productivity (Vadeboncoeur et al. 2006). Where winter drawdowns decrease macrophytes and fine sediment, it is possible that epiphytic, epipelic, and episammatic algae will be reduced. In contrast, epilithic and epixylic algal species may benefit from sediment coarsening associated with drawdowns. The potential for periphyton assemblages to shift to less palatable taxa is unknown, and requires more study to detect cascading impacts in lake trophic structures.

Benthic Invertebrate Responses

Benthic invertebrate taxa distribution and abundance are largely determined by the spatio-temporal hierarchy of habitat and resource heterogeneity of the littoral zone (Heino 2008; Tolonen and Hämäläinen 2010). Significant environmental factors that influence littoral zone invertebrate distribution and abundance include lake morphometry (Palomaki and Hellsten 1996; Scheifhacken et al. 2007), benthic algae distribution and availability (Devlin et al. 2013), macrophyte density/biomass, substrate physical characteristics (e.g., texture, stability, physical complexity), and organic matter (Weatherhead and James 2001; Brauns et al. 2008; Free et al. 2009). Winter drawdowns interact with these lake-wide and local environmental parameters to indirectly structure benthic invertebrate assemblages (Scheifhacken et al. 2007; White et al. 2008; White et al. 2010; Evtimova and Donohue 2016). For example, the coarsening of exposed substrates and associated declines in macrophyte biomass and changes in macrophyte composition can respectively decrease and alter benthic and phytophilous invertebrate density and composition (Wilcox and Meeker 1992). Winter drawdowns directly influence benthic invertebrates in the drawdown exposure zone via stranding (Benson 1973) and increased exposure to desiccation and freezing above and within the sediment (Grimås 1961; Grimås 1965; Paterson and Fernando 1967; Palomaki and Koskenniemi 1993; Scheifhacken et al. 2007; Haxton and Findlay 2008). Winter drawdowns also directly intensify physiological stress, particularly for relatively immobile taxa (e.g., bivalves) by exposing invertebrates to cooler water temperatures (Werner and Rothhaupt 2008).

Density

Winter drawdowns tend to reduce benthic invertebrate density in the exposure zone. In an analysis of 10 studies, Haxton and Findlay (2008) found a large negative effect size of reservoir dewatering on littoral zone macroinvertebrate density. Other studies also found that biomass and density are often lowest in lakes with large (e.g. >3 m) drawdown amplitudes (Grimås 1965). However, at relatively low amplitudes, impacts of drawdowns on invertebrate density may be limited. For example, Delong and Mundahl (1995) found significant reductions in invertebrate densities in littoral zones after a 4.6 m drawdown; however, in the same lake 16 years later, Swanson (2010) found no significant density reductions at 0.6 and 1.5 m depths shortly after a 0.9 m winter drawdown. Under these amplitudes, other environmental factors (e.g., lake morphometry, local-habitat features, water quality) may better explain variation of assemblage level character (McAfee 1980; White et al. 2011). Despite the level of drawdown amplitude, invertebrate densities can remain similar across winter drawdown lakes at exposed and unexposed depths (Aroviita and Hämäläinen 2008). Invertebrate mortality from exposure can differ between substrates, with higher mortality on sand substrates compared to silt and organic substrates (Palomäki and Koskenniemi 1993; Koskenniemi 1994) and leaf litter potentially serving as refuge (Delong and Mundahl 1995). By late summer (i.e., several months after refill) most invertebrates have fully recolonized and exhibit similar densities between drawdown and non-drawdown lakes in the exposure zone (Aroviita and Hämäläinen 2008; Swanson 2010), with lag time inversely related to depth (Kraft 1988). In fact, after heavy assemblage mortality from desiccation and freezing, the survival or addition of opportunistic and tolerant species (e.g., *Glyptotendipes barbipes*) can produce a higher standing crop of invertebrates than the pre-drawdown level in the subsequent growing season (Paterson and Fernando 1969; Fiske 1989).

Richness and Composition

Annual winter drawdowns that exceed natural water level fluctuations tend to reduce benthic invertebrate richness and alter composition relative to unregulated lakes (Kraft 1988; Aroviita and Hämäläinen 2008; White et al. 2011). For example, in the Boreal Shield Ecozone where natural water level fluctuations are <2 m, White et al. (2011) found invertebrate taxa richness reduced at ~2 m, assemblage composition altered at 2-3 m, and functional composition shifts at amplitudes >3 m. Benthic invertebrate richness and assemblage composition in lakes with relatively moderate drawdown amplitudes (e.g., 1.5-3 m) show varying responses compared to naturally fluctuating or semi-regulated lakes (Aroviita and Hämäläinen 2008 versus White et al. 2011). Also, taxa richness may recover in late summer (e.g., August) at exposed drawdown depths before the next annual drawdown (Kraft 1988).

Species' resilience and sensitivity to winter drawdowns is related to their life history strategies, functional traits (e.g., swimming ability, feeding), and habitat preferences (Table 2.1). Generally, annual drawdown conditions impact invertebrates with longer generation times more than those with shorter life cycles (Koskenniemi 1994; McEwen and Butler 2010). Semi-voltine taxa (e.g., *Hexagonia* spp., *Oulimnius tuberculatus, Ephemera vulgata, Limnius volckmari, Sialis* spp.) are found in low numbers in winter drawdown lakes, presumably because larval stages experience the disturbance and stress of multiple drawdown events (Benson and Hudson 1975; Aroviita and Hämäläinen 2008).

Annual drawdowns of moderate to high amplitude (e.g., 2-3m) promote opportunistic species with r-selected life history strategies (Benson and Hudson 1975; Kaster and Jacobi 1978; Septhton and Paterson 1986). Rapid growth and reproduction upon inundation of the exposure zone are highly advantageous traits in frequently disturbed conditions. For example, chironomids possess short generation times with multiple generations per year, enabling these invertebrates to avoid inhospitable conditions associated with drawdown (Fillion 1967; Koskenniemi 1994; McEwen and Butler 2010). Other taxa characteristic of annual drawdown regimes includes amphipods (Smagula and Connor 2008), oligochaetes (Grimås 1965; Kaster and Jacobi 1978), and ceratopogonids (Benson and Hudson 1975; McEwen and Butler 2010). These invertebrates can physiologically tolerate freezing and burrow in sediment to inhabit relatively unaffected substrates (Grimås 1965; Patterson and Fernando 1967; Kaster and Jacobi 1978). These taxa tend to dominate the biomass in heavily regulated annual systems (Grimås 1965; McEwen and Butler 2010), particularly in shallow reservoirs with unstable sediments (Sephton and Paterson 1986).

Receding water levels during a drawdown favor fast-swimming invertebrate taxa (White et al. 2011). Consequently, relatively immobile taxa are most susceptible to experiencing drying and freezing conditions. White et al. (2011) found significantly fewer crawlers (e.g., Elmidae with moderate mobility) and bivalves (e.g., clams with low mobility) in reservoirs with relatively high drawdown amplitudes (>3m) compared to more mobile taxa (e.g., Talitridae, Dyticidae, Corixidae). Bivalve and gastropod populations are particularly vulnerable to drawdowns because of their slow and sometimes undirected movement (Samad and Stanley 1986) and slow re-colonization rates (Fiske 1989). Samad and Stanley (1986) showed the mussel species *Elliptio complanata* and *Lampsilis radiata* moved randomly before burrowing in response to receding water levels in a Maine lake, and Kaster and Jacobi (1978) observed many *Lasmigona complanata* mussels moving landward during water recession. Bivalves burrow to lessen the effects of exposure; however, weeks to months of dry and freezing conditions likely lead to mortality (Samad and Stanley 1986; Werner and Rothhaupt 2008). A single winter drawdown of sufficient amplitude with a long exposure time can result in mass mortality (Samad and Stanley 1986; Werner and Rothhaupt 2008). The impact on these sensitive species will vary with drawdown amplitude (i.e., exposure zone) relative to species distribution in the littoral zone.

Distribution

Water level fluctuations can strongly determine benthic invertebrate zonation (Gathman and Burton 2011) by influencing habitat availability and condition (Baumgärtner et al. 2008). Under natural water level fluctuations, the benthic invertebrate density generally decreases with depth, with the highest densities in shallow depths found in the upper littoral zone(Grimås 1991; Kaster and Jacobi 1978). Invertebrate species limited to the upper littoral are most vulnerable to wintertime low water events (Brauns et al. 2008). The maximum benthic invertebrate density or biomass in spring and summer months shift to depths below the exposure zone (Grimås 1961; Fillion 1967; Benson and Hudson 1975; Kaster and Jacobi 1978; Kraft 1988; Palomäki and Koskenniemi 1993; Palomäki and Hellsten 1996; Furey et al. 2006; Sheifhacken et al. 2007). The shift corresponds to the distribution of food resources (e.g., and organic matter), suitable habitat, and mortality (Fillion 1967; Palomäki 1994; Palomäki and Hellsten 1996; Furey et al. 2006). However, invertebrates resistant to freezing (e.g., *Chironomus*, *Glyptotendipes*) can withstand exposed conditions and reemerge in the spring from recently exposed substrates in high abundance, showing comparable depth distributions as in naturally fluctuating lakes (Koskenniemi 1994; Delong and Mundahl 1995). Similarly, Aroviita and Hämäläinen (2008) did not find any taxa indicative of winter drawdown lakes at upper and lower littoral zones across a gradient of amplitudes.

Fish Responses

The littoral zone provides spawning habitat, young of year (YOY) refuge habitat (Winfield 2004), rich benthic algae and invertebrate food resources (e.g., Vadeboncoeur et al. 2002; Vander Zanden et al. 2011), and physically complex habitat (e.g. macrophytes, coarse woody debris) that mediates competition and predation (Diehl 1988; Savino and Stein 1989; Beauchamp et al. 1994; Lewin et al. 2004). For example, macrophyte assemblages offer a variety of meso- and microhabitats including transient heterogeneous DO and temperature refugia (Miranda et al. 2000) that can harbor distinct fish size-classes (Chick and McIvor 1994; Yamanaka 2013), high fish densities (Keast et al. 1978; Barwick 2004; Randall et al. 2012), and high species richness (Keast et al. 1978; Pratt and Smokorowski 2003; Barwick 2004) compared to other littoral mesohabitats. Declines in fish diet, growth rate, biomass, and abundance correlate with reduced littoral physical habitat complexity (Bettoli et al. 1993; Sass et al. 2006). Anthropogenic regulation of water level regimes is a primary threat to fish species that use the littoral zone for all or part of their lives (Winfield 2004; Miranda et al. 2010; Strayer and Findlay 2010). Annual winter drawdowns can reduce the availability and suitability of spawning habitat, limit the availability of winter habitat refuge from lethal DO concentrations (Cott et al. 2008) and predation, decrease and alter food supplies, and alter the levels of predator-prey and competitive interactions via macrophyte structural and taxonomical composition alteration and density reduction (Wilcox and Meeker 1992).

Feeding Trait Composition and Growth

Altered and reduced benthic invertebrate assemblages in annual winter drawdown systems negatively affect insectivorous fish species (Haxton and Findlay 2009; Sutela et al. 2011; Sutela et al. 2013). Insectivores (e.g., *Acipenser fulvescens*, *Ameiurus nebulosus*, *Ictalurus punctatus*, *Lepomis gibbosus*) show lower abundances in winter drawdown lakes compared to natural systems (Haxton and Findlay 2009). Furthermore, the density and biomass of insectivorous species tend to decline with increasing drawdown amplitude (Sutela et al. 2011). Sutela et al. (2013) found a positive correlation between abundance of fish insectivores and macroinvertebrate composition (e.g., proportion of sensitive Ephemeroptera, Plecoptera, and Trichoptera taxa) suggesting a potential bottom-up trophic control for insectivores. Reduced littoral habitat structure, such as macrophyte biomass, can shorten food chain length in small lakes (Ziegler et al. 2015, 2017) that can destabilize food web dynamics (McCann et al. 2005). Despite predictions of whole food web structure changes, winter drawdowns show negligible cascading food web impacts (McGowan et al. 2005, Turner et al. 2005), unless amplitudes are extreme for a given lake by severely limiting littoral habitat for consumers and associated productivity (e.g., Black et al. 2003). In extreme annual winter drawdowns (e.g., >10m), fish generally incorporate more pelagic-derived carbon because of diminished littoral-benthic production (Black et al. 2003).

Habitat generalists, feeding generalists, and species that primarily reside in the pelagic and profundal zones are largely unaffected by annual winter drawdowns (Table 2.1). For example, Dupont (1994) showed higher catch rates for habitat generalists (e.g., *Catostomus macrocheilus*) and species that utilize the pelagic zone in a winter drawdown reservoir relative to a natural system. Feeding generalists (e.g., *Catostomus commersonii*) also maintain high abundances in winter drawdown lakes (McAfee 1980), suggesting resilience to an impoverished littoral macroinvertebrate food supply (Haxton and Findlay 2009). Piscivores with pelagic juvenile stages (e.g., *Sander vitreus*, *S. canadensis*) are more abundant in annual winter drawdown lakes, compared to unregulated lakes. Some species (e.g., *Notemigonus crysoleucas*) show resilience despite heavy predation from *Micropterus salmoides* (largemouth bass) during a single drawdown event (Wegener and Williams 1975). However, drawdowns constrain available winter habitat, and, where it results in insufficient shelter (e.g., macrophytes, wood, and boulders), can expose fish to increased predation. Increased predation exposure is particularly a problem for small species and YOY (Lantz et al. 1967; Dupont 1994; Paller 1997; Smagula and Connor 2008; Haxton and Findlay 2009). For example, *M. salmoides* YOY were absent from samples following a relatively deep drawdown (~1.8m) in a New Hampshire lake, and it was suggested that this was related to high winter predation levels (Smagula and Connor 2008).

Only a few recent studies on the effects of annual winter drawdowns include fish growth. McDowell (2012) observed slower mean daily growth rates of YOY bluegill in winter drawdown lakes compared to an unregulated lake. Although the mechanisms for slower growth rate are uncertain, benthic invertebrate supply may be limiting (McDowell 2012). Insufficient YOY growth from a reduced benthic invertebrate food supply may explain high winter mortality rates for YOY (Sutela et al. 2013). Predatory piscivores generally benefit from drawdowns because of the increased concentration and exposure to prey relative to pre-drawdown conditions (Henman et al. 1969; Alexander 1988; Haxton and Findlay 2009). Consequently, growth rates, biomass and relative condition of piscivores increase during- and post-drawdown (Wegener and Williams 1975; Alexander 1988).

Growth rates are highly dependent on local factors (e.g., fish density, food resources, temperature) and several studies report no effect of drawdowns on fish growth. Despite reduced densities of cladocerans and higher numbers of less nutritious rotatorians in a Finland regulated drawdown lake, planktivorous vendace larvae growth rates were comparable to an unregulated system (Sutela and Huusko 1995). Vendace larvae potentially compensate for a low energy diet by increasing consumption when cladoceran densities are low. Shallow systems, although most susceptible to littoral exposure, warm quickly following refill, possibly negating effects of cold winter water temperatures on fish growth (McDowell 2012). Similarly, mild drawdown amplitudes (e.g. <2 m) may not affect YOY growth rates of species that spawn in spring and summer (after refill), including *M. salmoides*, *P. flavascens*, and *L. macrochirus* (McDowell 2012).

Spawning and Recruitment

A winter drawdown-spring refill event can impact littoral spawning species by disturbing spawning and rearing activity, limiting access to spawning habitat, and producing physiological stressful conditions. Impacts are most extreme when regulated water levels are unnaturally low before and during spawning (Ozen and Noble 2002; Ozen and Noble 2005; Kahl et al. 2008), and during YOY hatching, such that there is limited habitat availability and suitability (Gafny et al 1992; Wilcox and Meeker 1992), strongly impacting recruitment and year-class strength (Kohler 1993; Neal et al. 2001; Ozen and Noble 2005). Regulated water level fluctuations (e.g., rises and recessions) during spawning can negatively affect juvenile fish densities (Miranda and Lowery 2007), partly due to the loss of physical structural complexity (Neal et al. 2001). For species that spawn in littoral areas in late autumn, winter, and early spring (Table 2.1), low water levels during the spawning period reduce year class sizes (Kallemeyn 1987a; Sutela et al. 2002). A delay in spring flood peak relative to natural variation limits recruitment for early spring spawning species because of inaccessibility to littoral spawning habitat (Gaboury and Patalas 1984; Kallemeyn 1987a, b; Wilcox and Meeker 1992). For example, *Esox niger* (chain pickerel), a spring phytophilous spawning species, has experienced population declines in winter drawdown lakes likely because of recruitment failure due to insufficient spawning habitat (Wegener and Williams 1975; McDowell 2012). If water levels are low during the spring, *S. vitreus* (walleye) are unable to find suitable upper littoral habitat for spawning (e.g., stony bottom), with documented negative effects on recruitment (Kallemeyn 1987a). In the same annual winter drawdown system, Larson et al. (2016) found increases in age-0 abundance of *S. vitreus* and *P. flavascens* in a year after a drawdown amplitude reduction. Although not examined, a winter or spring drought in combination with a regulated drawdown may exacerbate impacts on early spring littoral spawning species (McDowell 2012). Spring refills completed in April at drawdown amplitudes of <2 m show negligible effects on spawning timing and frequency for spring and summer spawning species (e.g. *Lepomis macrochirus*, *Perca flavascens*, *M. salmoides*) in multiple Connecticut water bodies (McDowell 2012). Similarly, intra- and inter-annual water level fluctuations did not directly account for annual age-0 abundances of *S. viterus* and *P. flavascens* potentially because of secondary effects of water level change on aquatic vegetation cover and/or benthic invertebrate food resources (Larson et al. 2016). Winter drawdowns can also affect littoral spawning species if eggs are exposed to desiccation (Gaboury and Patalas 1984; Mills et al. 2002) and low DO concentrations (Sutela et al. 2002). McAfee (1980) recorded significantly lower abundances of *Salvelinus fontinalis* (brook trout) in winter drawdown lakes potentially due to temporal overlap of water level lowering and their spawning period. Drawdowns and subsequent refills can also benefit recruitment for some fish species. For example, rising water winter levels create newly inundated stones absent of algae, which are necessary for the cyprinid *Mirogrex terraesanctae* to allow egg adherence and prevent egg mortality (Gafny et al. 1992).

Movement and Habitat Use

Winter drawdowns or extremely low winter water levels can induce species-specific sub-lethal responses such as changes in fish movement. The loss of vegetated littoral habitat and/or the increased availability of prey during winter drawdown can cause increased daily movement of largemouth bass (Rogers and Bergersen 1995), which are normally quiescent during the winter (Shuter et al. 2012). In contrast, reduced winter water levels show negligible effects on movement behavior in *Esox lucius* (northern pike), an active winter species (Rogers and Bergersen 1995). Low winter water levels can also alter life history strategies as seen in *Lota lota* (burbot). *L. lota* require suitable daytime shelter to maintain an optimal metabolic rate to ensure somatic growth (Fischer and Öhl 2005). Lowering winter water levels creates high competition for littoral daytime shelters and accelerates their ontogenetic migration from the littoral to the profundal zone (Fischer et al. 2004; Fischer and Öhl 2005).

For phytophilous species, loss of macrophytes or cooler water temperatures in shallow water during winter drawdown limit access to macrophyte stands in deeper, warmer water, if present (Dupont 1994; Karchesky and Bennet 2004). Dupont (1994) recorded lower abundances of pumpkinseed, largemouth bass, and black crappie in the littoral zone and in deeper areas during a winter drawdown compared to a reference lake. Reduced littoral habitat during the drawdown particularly affected the YOY by increasing exposure to higher flows in this run-of-river reservoir (Dupont 1994). Low spring water levels can also impede movement to littoral refuge habitat. Relative to a reference system, Sutela and Huusko (1995) show low vendace fry densities in nearshore habitats during a winter drawdown, because those areas are prone to sediment entrainment during heavy wind/wave action. Annual winter drawdowns can also decrease the macrophyte structural heterogeneity in the exposure zone (Figure 2.2, Wilcox and Meeker 1991), which can alte predator-prey interactions and reduce refuge availability for YOY fish, small fish species, and invertebrates (Wilcox and Meeker 1992).

Winterkill

Winterkill is a relatively frequent natural disturbance in small boreal and north temperate lakes that structure fish composition and population dynamics (Danylchuck and Tonn 2003, 2006). Winter drawdowns increase the likelihood of fishkills by reducing seasonally low winter DO concentrations (Gaboury and Patalas 1984; Mills et al. 2002; Cott et al. 2008). For example, Mills et al. (2002) recorded extreme abundance decline (~80%) of lake whitefish during novel winter drawdowns in a shallow reservoir, associated with low DO concentrations. Stressful conditions (e.g., predator avoidance, low water temperatures) can reduce the tolerance of fish to low DO concentrations (Cott et al. 2008). Species or age classes that seek shallow areas for winter spawning or refuge with relatively low DO replenishment (i.e, a basin with no direct inflows) are most susceptible to fishkills via drawdown (Gaboury and Patalas 1984; Dupont 1994, Mills et al. 2002). Additionally, larger fish (e.g., *Esox lucius*) are generally more susceptible to low DO levels (see Gaboury and Patalas 1984; Cott et al. 2008).

Research Needs

Despite the numerous studies that investigated the effects of winter lake drawdowns on lake physicochemistry, macrophytes, invertebrates, and fishes, there remain several research gaps. These gaps arise from the limited scope of most drawdown studies, which typically only include a small number of lakes, limited years, and limited response variables. Here, we identify 8 key research needs; several of these are aligned with a recent review by Hirsch et al. (2017) on water level fluctuation impacts in hydropower reservoirs. Given that lake ecosystems are increasingly stressed by humans and winter drawdowns are one of the few tools available to address nuisance macrophytes (and other tools such as herbicides and mechanical harvesting have different potential impacts on lakes), increased understanding of impacts of lake drawdowns is critical to compare ecosystem consequences of different management approaches.

1. Design more studies to expand inferential scope and mechanistic understanding

Most studies use a before-after study design in a single lake or a reference-experimental approach that typically consist of 2 to 5 lakes (Figure 2.4a). Relatively few studies have used a before-after-control-impact (BACI) design, which provides a more suitable control to address interannual variation than before-after designs. Moreover, very few studies include a gradient or reference-experimental approach with >5 lakes (Figure 2.4a), although these designs have been more common in recent years (Figure 2.4b, Appendix C). Studies that include several lakes (>10) are necessary to understand how responses vary among different types of drawdown (i.e., different frequencies, rates, amplitudes, etc.) in different lakes, allowing inference for a broader geographical areas or environmental contexts (e.g., Aroviita and Hämäläinen 2008, White et al. 2011, Mjelde et al. 2012). Further, controlled mesocosm designs can help to isolate causal links between responses and drawdowns by removing confounding factors typically found in observational studies (e.g., Evtimova and Donohue 2014). We advocate, where logistically feasible, for more studies employing gradient and BACI designs at multiple sites, more mesocosm studies, and ultimately more meta-analyses comparing study responses to increase broad understanding of winter drawdown responses.

2. Develop novel metrics for quantifying drawdown extent based on habitat loss

Most studies use drawdown amplitude as a measure of the magnitude of drawdown disturbance. While amplitude has been identified as a good predictor of hydrological status and littoral assemblages in regulated Finnish lakes (Keto et al. 2008), lake shape is needed to translate amplitude into water volume and littoral habitat loss.

Shallow lakes and littoral zone areas with gentle slopes are more sensitive to water level fluctuations than steeper slope lakes (Coops et al. 2003), with the potential to expose a high proportion of the lake bottom during a relatively moderate low water event (e.g., Beklioglu et al. 2006). The extent or proportion of exposed lake bed relative to the whole lake or littoral zone area can help to predict disturbance in addition to drawdown amplitude. Bathymetric maps and habitat assessments can be used to develop measures of habitat loss associated with drawdowns to better quantify drawdown magnitude and extent, allow more accurate comparisons across lakes, and identify areas particularly susceptible to drawdown.

3. Quantify multiple characteristics of drawdowns (e.g., duration, timing, frequency, rate)

Factors other than drawdown amplitude or area of lakebed exposure can predict ecosystem and population-level effects. Water level fluctuation can be described by several additional variables, including duration, timing, frequency, rate of change, and timing of fluctuations (Wantzen et al. 2008). Drawdown duration (i.e., time from drawdown initiation to full refill) in the northeastern US is typically 4-5 months from November through March (Table 2.1), but shorter or longer drawdown periods may have different ecosystem responses, particularly if the timing avoids critical species life history stages (see Larson et al. 2016). Furthermore, drawdown rate can affect responses; if water levels drop fast, less mobile taxa like bivalves (Werner and Rothhaupt 2008) or even small fish (Nagrodoski et al. 2012) can become stranded. Differences in frequency of drawdown (e.g. annual, biannual) are rarely investigated; the drawdown history of a lake is critical in assessing current physicochemical and biotic patterns (McDowell 2012) because of potential legacy effects from past water level disturbance (Hall et al. 1999).

By incorporating these water level metrics into predictive models, we identify mechanistic links between drawdowns and responses and determine how drawdowns can be managed to minimize impacts.

4. Measure responses over long time periods (e.g., decades)

As typical in most ecological studies, studies of winter drawdowns are short in duration with most studies <5 y and few studies exceeding 10 y (Figure 2.4a). Only a few studies monitor changes in littoral communities across two to three annual drawdowns (Siver et al. 1986; Mills et al. 2002; Turner et al. 2005), and only a few lakes have been studied over long time periods to monitor responses variables after winter drawdown regime change (e.g., Namakan Reservoir: Kraft 1988; McEwen and Butler 2010, Lake Wissota: Delong and Mundahl 1995; Swanson 2010). Water level fluctuations can be highly variable among lakes and across years (White et al. 2008) due to inter-annual differences in drawdown management and precipitation. Differences in precipitation (and therefore drawdown "success") may mask the ability to detect responses in short-term studies. Moreover, responses to drawdown disturbances may change over time as ecosystems evolve to the new abiotic environment. Long term studies (e.g., >10 y) and studies that compare lakes that differ in the number of successive years of drawdown will help to elucidate abiotic and biotic responses to drawdown frequency. Studies incorporating long-term water level records would also provide more water level disturbance context in past years that could explain current littoral biotic patterns (Palomäki 1994) and increase predictive ability of new winter drawdown regimes.

5. Study lakes with a broad range of natural abiotic factors

As mentioned previously (#2) lake morphometry (e.g., area, depth, slope) will affect habitat loss associated with drawdown. Additional abiotic factors may alter the extent of effects of drawdowns, including geology (bed texture, chemistry), climate (e.g., precipitation and ice cover), lake trophic status, and time since reservoir creation (see Hirsch et al. 2017). For example, mesotrophic and eutrophic shallow lakes may be more susceptible to changes in ecosystem states (clear-water to turbid) with drawdowns, whereas effects on deep, stratified lakes may be limited to littoral zones except with deeper drawdowns. Lakes with restricted littoral zones (e.g., deep, steep-sided oligotrophic lakes) could be particularly susceptible to changes in littoral zone community dynamics, including benthic algal production (Vadeboncoeur et al. 2008). Shoreline slope influences the extent of ice-sediment penetration, affecting benthic invertebrate mortality levels (Palomäki and Koskenniemi 1993). Studies across a gradient of environmental conditions will help to parse natural abiotic variation from drawdown effects and better predict drawdown outcomes at a local scale where management typically takes place.

6. Simultaneously examine multiple sources of anthropogenic stress

Given that lake drawdowns are frequently conducted to meet human needs, lakes that undergo drawdowns often also have other anthropogenic stressors, such as watershed land use, lakeshore development, herbicides, and ongoing climate change. Studies have shown that land use, and particularly development along lake shorelines, can alter littoral habitat and biotic assemblages (Christensen et al. 1996; Francis and Schindler 2009; Brauns et al. 2011; Kovalenko et al. 2014), and thus lakeshore development may mask the effects of drawdowns. Furthermore, herbicides and winter drawdowns share the same goal by attempting to control and diminish aquatic vegetation, and are sometimes used simultaneously in the same lake, making it challenging to separate effects of each management practice. Additionally, climate change will likely increase the variability of water level fluctuation extent, duration, and frequency (Wantzen et al. 2008) and reduce ice cover periods (Magnuson et al. 2000). Climate change could also lengthen drawdown periods from winter to summer months, thus increasing lakebed exposure time, with associated consequences to littoral zone communities. Determining the relative importance and potential interaction of winter drawdowns and other threats is critical to predict biotic variation and resilience under changing water level management and climate, and inform lake front owners and managers about how different management approaches interact.

7. Focus on understudied response variables

As highlighted in this synthesis, most research on winter drawdowns has been on macrophytes, macroinvertebrates, and fishes (Figure 2.3). In contrast, little is known about the influence of winter drawdowns on benthic algal composition; the relative importance of epiphytic, epixylon, and epipelon; and benthic algal productivity. Similarly, the effects of winter drawdowns on phytoplankton composition and biomass are covered in few studies (e.g., Vuorio et al. 2015), but also show mixed effects. Further, it is relatively unknown if winter drawdowns promote harmful phytoplankton taxa, as seen only in one study (Nõges and Nõges 1999). Future study on phytoplankton would help determine the role of winter drawdowns in alternative stable state shifts because of the decline of macrophyte assemblages. While there have been some studies on growth of sport fishes and trust species, relatively little is known about fish assemblage responses to drawdown (e.g., Sutela et al. 2011, 2013) and food web interactions (e.g., Black et al. 2003). Semi-aquatic organisms that partially rely on aquatic environments for food resources or refugia (e.g., frogs, turtles, beavers, muskrats, waterbirds) are likely to experience increased risk and stress associated with finding resources (e.g., Smith and Peterson 1991), yet research on potential winter drawdown effects on these taxa are limited.

8. Scale up studies to include whole-lake ecosystem modeling, functioning, & terrestrial-aquatic linkages

Winter drawdowns are whole-lake phenomena. As with most lake studies, sampling takes place in parts of the lake, and the responses are assumed to be representative of the entire lake. This assumption may be flawed especially in lakes with highly diverse habitats. Furthermore, whole-lake assessments of ecosystem functioning, such as energy fluxes and nutrient dynamics do not exist in winter drawdown lakes, and these may constitute important responses to lake drawdowns. There is limited study on the release of limiting nutrients upon spring inundation and the corresponding effect on primary production and consumers. Given winter drawdowns are used in part to reduce macrophytes, understanding the role of littoral refuge reduction for consumers in winter drawdown lakes will help to predict stability of predator-prey dynamics and whole lake ecosystem functioning. Additionally, the lake-wide extent of organic matter redistribution to deeper depths and the concurrent changes of sediment stoichiometry has only been shown in few studies (e.g., Furey et al. 2004). If shorelines are not heavily developed, potential declines in benthic autochthonous primary production and increases in allochthonous organic matter in the drawdown exposure zone (Furey et al. 2004) could increase energetic connectivity between riparian-lake environments. More studies are needed to determine the relative influence and interaction of human stressors on the strength of riparian-lake energetic linkages in winter drawdown lakes.

Conclusion

As described in this review, many studies have documented the numerous and varied effects of winter water level drawdowns on littoral zone communities. Given that each lake has unique environmental characteristics and lakes are typically managed individually, research that encompasses a gradient of lake conditions and identifies factors influencing varied responses are critical to apply research to inform lake management. Further, incorporating depth gradients in monitoring plans will increase accuracy and prediction of winter drawdown responses at shoreline and lake-level scales (Evtimova and Donohue 2016). Also, incorporating anticipated climate change effects on water level fluctuations will help lake managers in drawdown systems to mitigate potential extreme fluctuations within lake-specific thresholds, particularly in lakes with current moderate drawdown amplitudes (Abrahams 2008).

Increasing human populations are demanding more services (e.g., energy, recreation, food) from lakes, putting added stress on lake ecosystems. Most lake management plans aim to simultaneously meet both human and ecosystem needs. Since annual winter drawdowns are conducted to achieve various human purposes (e.g., hydroelectric power, aquatic vegetation and fish management), understanding the nuances of purpose-specific drawdown regimes and its ecological impacts can provide a more holistic management decision-making process. Research designs with direct application to management (e.g., adaptive management) will further our understanding of lake ecological responses and facilitate effective restoration among a growing and interacting array of anthropogenic pressure.

Tables

Table 2.1. Ecological trait relation to winter drawdown.

Macrophyte, macroinvertebrate, and fish traits that are sensitive (unshaded) or tolerant (shaded) to winter drawdowns. Traits include functions, life history characteristics, and habitat preferences. Example taxa and key literature sources are included.

Assemblage		Trait	Taxa Examples	Source
Macrophytes	Sensitive	Submergent species that propagate mostly by rhizomes (perennials); low propagation via seeds	*Potamogeton robbinsii*	Beard et al. 1973; Crosson 1990; Wilcox and Meeker 1991
			Myriophyllum spicatum	Siver et al. 1986; Olson et al. 2012
			Nuphar lutea	Beard et al. 1973; Crosson 1990; Hellsten 2000; Mjelde et al. 2012
		Sensitive to ice scour	*Isoetes lacustris* (i.e., large Isoetids)	Rorslett 1984; Turner et al. 2005; Keto et al. 2006; Mjelde et al. 2012
	Tolerant	High seed/oospore production	*Najas flexilis*	Turner et al. 2005
			Chara sp.	Wagner and Falter 2002
		Amphiphytic & polymorphic growth forms	*Eleocharis acicularis*	Wilcox and Meeker 1992; Hellsten 2000; Mjelde et al. 2012
		Fast growth	*Elodea* sp.	Wagner and Falter 2002
		Multiple viable propagation strategies	*Potamogeton spirillus, P. epihydrus*	Turner et al. 2005

Assemblage		Trait	Taxa Examples	Source
Macroinvertebrates	Sensitive	Semivoltine	*Hexagonia* sp., *Oulimnius tuberculatus, Sialis* sp.	Aroviita and Hämäläinen 2008
		Low to moderate mobility (i.e., clams and crawlers)	Elmidae, Hydrobiidae, Psephenidae *Asellus* sp.	White et al. 2011 Grimås 1961; Kraft 1988
		Fine-sediment burrowers	*Caenis* sp., *Hexagonia* sp., *Sialis* sp. *Ephemera vulgata*	Benson and Hudson 1975; Kraft 1988; McEwen and Butler 2010 Aroviita and Hämäläinen 2008
	Tolerant	Moderate to fast mobility (i.e., swimmers)	Talitridae, Dyticidae, Corixidae	White et al. 2011
		Multivoltine to univoltine	Chironomidae, Amphipoda	Kraft 1988
		Fully aquatic life cycle	Amphipoda	McEwen & Butler 2010
		Physiological tolerance to freezing	*Chironomus*, *Glyptotendipes*	Grimäs 1965; Paterson and Fernando 1969; Koskenniemi 1994
Fish	Sensitive	Littoral spawning in the fall	*Coregonus*	Gaboury and Patalas 1984; Sutela et al. 2002; Mills et al. 2002
		Littoral spawning in the spring	*Esox* spp.	Wegener and Williams 1975; Kallemeyn 1987b; McDowell 2012
		Littoral juvenile life stage	*Lota lota*	Fischer and Öhl 2005; Sutela et al. 2011

Assemblage	**Trait**	**Taxa Examples**	**Source**
	Insectivorous	*Ameiurus nebulosus* *Lepomis gibbosus*	Haxton and Findlay 2009
		Cottus poecilopus	Sutela et al. 2011
Tolerant	Opportunistic feeders	*Catostomus commersonii*	McAfee 1980; Haxton and Findlay 2009
	Pelagic feeders	*Sander vitreus* (juveniles)	Haxton and Findlay 2009
	Habitat generalists	*Catostomus commersonii*	Haxton and Findlay 2009

Figures

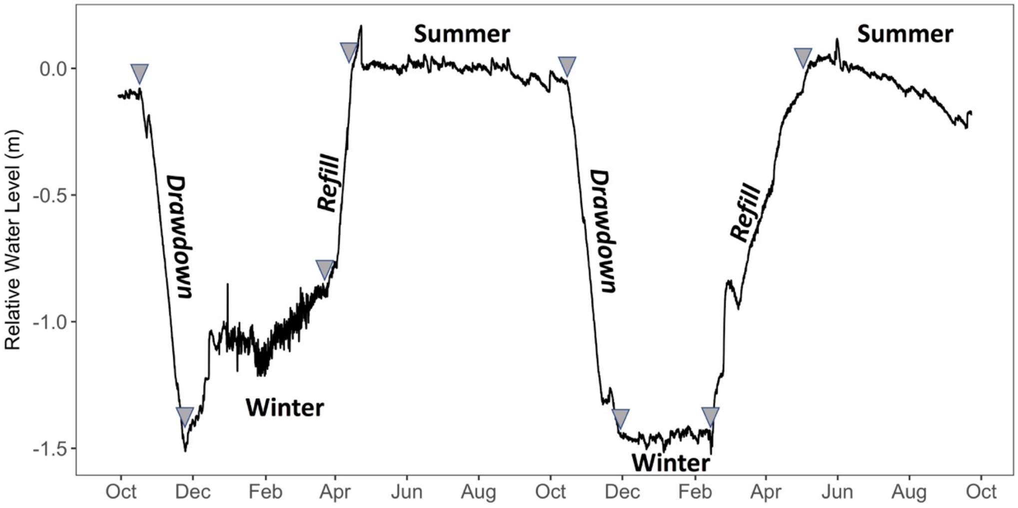

Figure 2.1. Water level time series.
Water level time series of an annual winter drawdown lake (Goose Pond, Tyringham, Massachusetts) over two drawdown periods (2014-2016). Water level is expressed relative to median summer water levels. Grey triangles indicate initiation and cease of drawdown and refill phases.

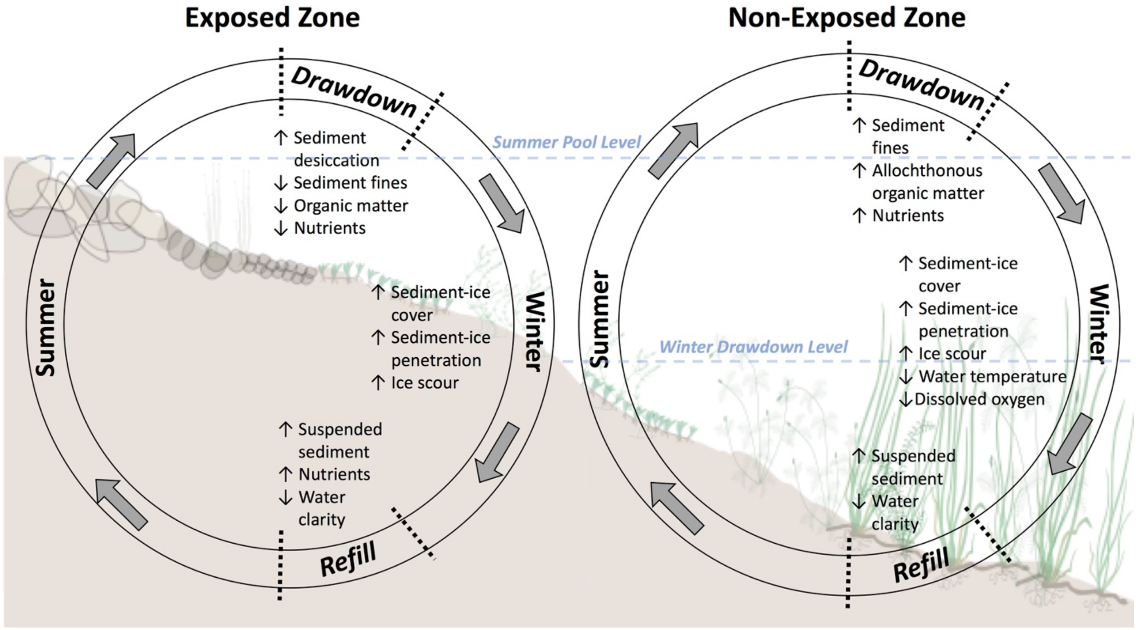

Figure 2.2. Littoral zone profile of an annual winter drawdown lake.
Conceptual littoral zone profile of an annual winter drawdown lake. Circles represent abiotic patterns through time corresponding to water level drawdown, low winter water levels, and subsequent refill in exposed (left circle) and non-exposed areas (right circle) of the littoral zone. Background littoral zone represents theoretical depth-specific sediment and macrophyte character during summer given the summer pool and winter drawdown water levels (dashed lines). Macrophytes are generally reduced to low-growing (e.g., *Elatine*, *Sagittaria*) and seed-bearing species (e.g., *Najas*) in the exposure zone and sensitive species shift to deeper depths. Note that the level of erosion and macrophyte biomass loss is modified by littoral slope, photozone depth, and shoreline exposure to wind-wave action

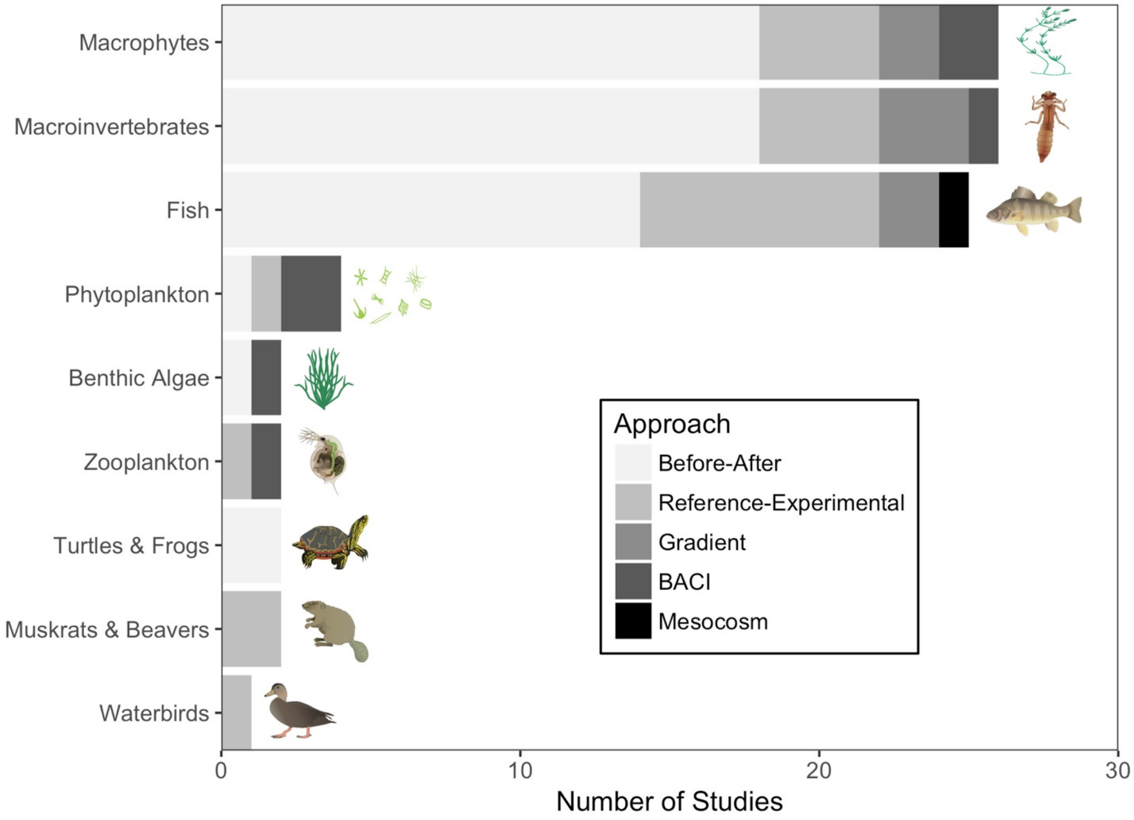

Figure 2.3. Winter drawdown study approaches.
Biotic responses variables from 73 winter drawdown studies color-coded by study approach.

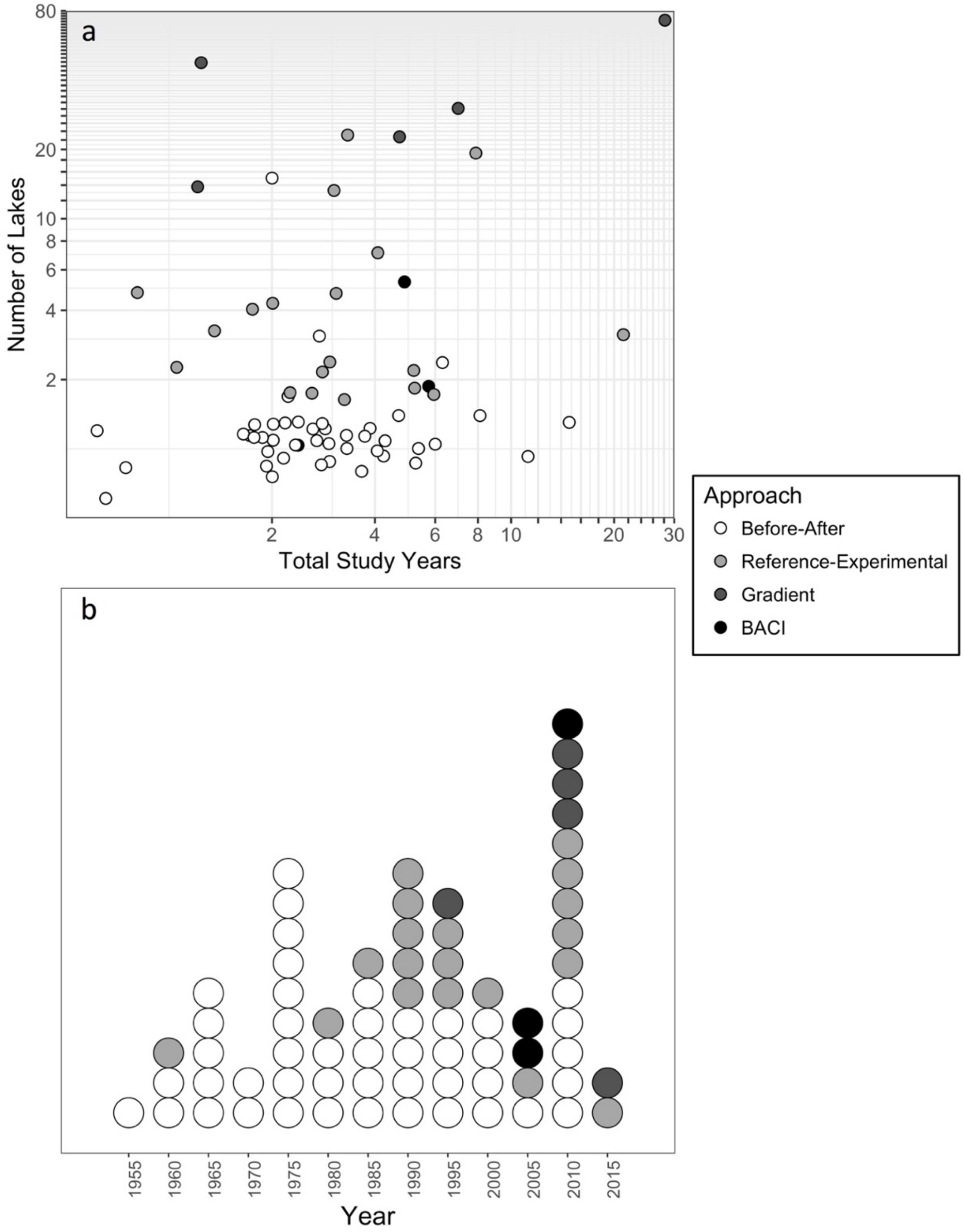

Figure 2.4. Winter drawdown study summary.
Winter drawdown studies before 2016 plotted by (a) total study years against number of lakes per study on a log-scale and with points jittered to remove overlap; and by (b) year of publication aggregated in 5-year bins. Each point represents one study (n=72) and color-coded by study approach (Before-After=45, Reference-Experimental=19, Gradient=5, BACI=3).

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CHAPTER 3

HYDROLOGY OF ANNUAL WINTER WATER LEVEL DRAWDOWN REGIMES IN RECREATIONAL LAKES OF MASSACHUSETTS, U.S.A.

Introduction

Freshwater reservoirs are unique lentic habitats often characterized by altered water level regimes in comparison to natural lakes (Kennedy 2005). Regulated water level regimes can alter the magnitude, timing, duration, rate, and frequency of wet and dry periods relative to natural water level regimes, thereby serving as a major stressor to lake ecosystem dynamics (Wantzen et al. 2008, Miranda et al. 2010, Zohary and Ostrovsky 2011). The direction and strength of various ecological responses to altered lake water levels depends on the specific hydrologic metrics and biota. Therefore, reliable prediction of ecological responses requires accurate quantification of water level fluctuations.

Annual winter drawdowns (WD) are an example of a regulated water level regime that is regularly performed in temperate and boreal lakes to maximize wintertime power demand in hydroelectric reservoirs or to provide spring flood storage (Hellsten 1997). In recreational lakes of Massachusetts (MA) and other states in the Northeastern USA, WD are purportedly used to improve recreational value (e.g., boating, swimming) by reducing nuisance densities of macrophytes and protecting shoreline structures (e.g., docks, retaining walls) from ice damage (Mattson et al. 2004). WD events are initiated in autumn, reach target drawdown levels in winter, and are refilled in the spring (e.g., Mjelde et al. 2012, Carmignani and Roy 2017). Previous studies, primarily from hydroelectric and storage reservoirs, have characterized WD hydrology to explain patterns in littoral zone communities predominantly as a function of WD magnitude or annual amplitude (e.g., White et al. 2011, Mjelde et al. 2012). For example, Sutela et al. (2013) quantified WD intensity as the 20-y mean of the difference between the highest and lowest water level per winter in 16 regulated lakes, which correlated with ecological quality indices of littoral assemblages. In contrast, the spatiotemporal variability of WD regimes in Northeastern USA recreational lakes have not been quantified despite its widespread and historical prevalence. Furthermore, few studies have decomposed WD regimes into hydrological components other than magnitude— timing of WD events, duration, water level recession and refill rates, and degree and duration of exposure, which may be more important than magnitude for predicting ecological responses (Carmignani and Roy 2017, Hirsch et al. 2017).

To better understand the hydrology of annual winter drawdowns in recreational lakes in MA, we monitored water levels in 18 WD lakes and 3 non-drawdown lakes continuously for 3-4 years. We assessed the inter-lake and interannual variability of WD metrics (i.e., timing, magnitude, rate, and duration). Lastly, we evaluated the correspondence of empirical WD metrics with the general performance standards issued by the MA Division of Fisheries and Wildlife for WD events (MassWildlife 2002) and restated in the MA Generic Environmental Impact Report on Eutrophication and Aquatic Plant Management (Mattson et al. 2004). Mattson et al. (2004) provides general guidance to implement and perform WD's in Massachusetts to minimize impacts to in-lake and downstream non-target organisms (e.g., molluscs, amphibians, reptiles, spawning fish species, mammals) and water-supply availability (i.e., wells), while managing macrophytes. Hydrologic data collected in this study will guide future WD management in Northeastern USA recreational lakes to help balance ecological sustainability and recreational value, and to help guide realistic WD implementation in the face of climate change.

Methods

Lake Selection & Study Area

We selected 18 lakes with current WD regimes (Table 3.1) and 3 lakes (Quacumquasit, Congamond, Leverett) with no history of annual winter drawdowns (Figure 3.1) using a stratified random approach to primarily capture a WD magnitude gradient (see Appendix I for details). Lakes were located in central and western MA in the Housatonic, Connecticut, Thames, Merrimack, and Blackstone River watersheds (Figure 3.1). Inland Massachusetts has a continental temperate climate with four seasons. Mean minimum/maximum July and January temperatures for ecoregions in the western MA tend to be 1–3°C degrees lower than in central MA (Griffith et al. 2009). Winter precipitation averages 21.6–25.4 cm (1981–2010) across western and central MA (National Oceanic and Atmospheric Administration 2018). Watersheds of study lakes have mixed land use with variable urban development ranging from 2–40% (median = 9%) with a general increase from west to east, and relatively small proportions of pasture (0-15%) and agriculture (0-8%). Concomitantly, total watershed forest cover ranged from 20–83% (median = 64%) among lakes. Forests are primarily composed of mixed deciduous and conifer stands including northern, central, and transition hardwoods.

Watersheds are underlaid by various geologies across the study area. Lakes located in the Northeast Highlands are characterized by coarse-loamy to loamy soils and metamorphic bedrock or limestone derived coarse-loamy soils and calcareous bedrock (Griffith et al. 2009). In central MA or the Northeast Coastal Zone, lakes are underlain with sedimentary bedrock and alluvium soils, metamorphic bedrock with coarse-loamy soils, or coarse-loamy and sandy soils (Griffith et al. 2009).

Water Level Monitoring & Quality Control

Water levels were continuously monitored from fall 2014 to fall 2018 at 18 drawdown and 3 non-drawdown lakes. We deployed paired non-vented pressure transducers (Onset HOBO U20L-01, Bourne, MA, USA) in 14 lakes in September–October 2014 and in 6 lakes in September–November 2015 (Table 3.1). Water level data for Otis was provided by the MA Department of Conservation and Recreation where data started in March 2012 up to May 2018. Water level data collection ceased in May – November 2018 resulting in 3-4 years of winter water levels per lake (6 for Otis). We generally followed methods from Stamp et al. (2014) for pressure transducer (i.e., logger) installation and monitoring. In each lake we installed paired transducers adjacent to the point of outflow (i.e., near or on the dam) underwater and above water on shore. If access was limited, we installed underwater loggers adjacent to access points (e.g., bridges, culverts) in other parts of the lake. All loggers were sheltered in PVC housing. Underwater loggers were fixed to dam or bridge abutments and suspended on non-stretch cable within a PVC pipe. If we could not attach an underwater logger to a fixed structure, loggers were fixed to a wood stake or metal pipe that was anchored into the lake bed. All loggers were set to record at 2-h intervals. We downloaded loggers at least twice per year (pre- and post-drawdown event) and recorded relative elevation from a secondary fixed location (e.g., staff gauge, spillway, dam abutment) to help identify unintentional logger movement (e.g., from ice formation/melt) and instrument accuracy drift.

Paired pressure measurements were converted to water levels using HOBOWarePro software (version 3.7.8, Onset Computer Corporation, Bourne, MA, USA) and imported into R software. We used the ContDataQC package (Leppo et al. 2017, version 2.0.2.9001) in R (R Core Team, 2017, version 3.4.2) to identify potential inaccurate water level records based on water level change and minimum and maximum records. We flagged records with an absolute change ≥ 3 cm and adjusted preceding data to account for apparent transducer movement or drift derived from discrete water elevation measurements from secondary locations. We removed water level records with negative values and within transducer accuracy (i.e., values < 1 cm) relative to zero. Additionally, we examined coupled water temperature data to help identify inaccurate water level records, such that records with water temperatures < 0°C were flagged for inspection. To compensate for lost barometric air pressure readings at Wyola (6/19/17–11/2/18) and hence estimate water levels, we used predicted air pressure records generated from Leverett (7.2 km from Wyola).

Water Level Metrics

We defined two general water level time periods to calculate water level metrics: the WD period or event and the summer or the non-drawdown period. We further split the WD period into three timeframes or phases: water level decline (recession phase), drawn down water levels (drawdown phase), and the period of refill to pre-defined normal pool levels (refill phase, Figure 3.2). Using bi-hourly records, we first isolated

WD periods by visually identifying the recession initiation date as the first record of consistent water level decline in the fall (i.e., October–November) with no clear water level increase, and the refill phase end date as the first record reaching pre-defined summer pool levels in winter-spring (i.e., drawdown end in January–June). Summer or normal pool water levels (i.e., drawdown refill target) were defined as the median water level from non-drawdown phases in 2015 (n=15) or from spillway elevations (n=6). Within the WD period, the end of water level recession (i.e., start of drawdown phase) was marked by stable (i.e., no visually evident increase in near future records) or visually increasing water levels in the hydrograph. The start of the refill phase (i.e., end of drawdown phase) was marked by a consistent visual water level increase in the hydrograph with no clear water level decline before reaching reference water levels. These definitions allowed for the inclusion of precipitation or melting events to influence recession and refill phases. For non-drawdown lakes, we divided water level records into spring/summer and fall/winter period that covered 4/2–9/30 and 10/1–4/1 respectively to generally correspond to summer and WD periods in drawdown lakes. For the summer period and each of the WD period phases (e.g., recession, drawdown, refill), we calculated basic statistics using bihourly records including duration, minimum, maximum, mean, median, SD, CV, and selected quantiles.

For each WD event, we quantified drawdown magnitude, drawdown and refill rates, and drawdown duration, and identified the timing of each WD phase (Figure 3.2). We calculated magnitude as the difference between reference pool level and the 1) maximum (i.e., lowest) water level recorded during the entire WD period, and 2) mean water level during the drawdown phase. Rates of recession and refill were calculated using consecutive bihourly records and summarized into mean, median, minimum, and maximum values, and scaled from cm/hr to cm/day for ease of interpretation. Durations were determined in days for the entire WD period (i.e., recession start to refill end) and for each drawdown phase. Further, we estimated duration of exposure/emersion for 0.25–2.0-m depth contours at 0.25-m depth intervals relative to reference water levels. All drawdown metrics were calculated using bihourly records except for daily water level data at Otis between 10/2015–5/2018. Results are reported using mean drawdown metric values averaged across winter years (e.g., 2014-2015 winter) and also expressed by the interannual variation per lake.

Bathymetry Collection & Analysis

We sampled depths for all lakes in April–June 2015 or 2016 when water levels were at or above normal pool levels. Following a cross-hatched pattern over the lake surface, depths were estimated using a Garmin GPSMAP®431s with 1,309–48,803 sample points per lake depending on surface area. We used empirical Bayesian kriging in ArcGIS 10.3 (Krivoruchko 2012) to interpolate unsampled depths from empirical depths (see Appendix J for details).

We estimated the maximum depth of macrophyte colonization as a surrogate of littoral zone boundaries to determine lake-wide littoral zone area. We established 4–21 transects based on lake area to sample the presence of macrophytes from 8/29 – 9/9 in 2017. We sampled macrophytes along transects perpendicular to contours at 1-m depth intervals using a double-headed rake. The rake was dragged approximately 0.5–1 m along the bottom at each sampling point and then inspected for macrophyte or macroalgae presence. Maximum depth values per transect were averaged for each lake and incorporated into littoral area exposure calculations for given WD events.

We coupled interpolated depths with water level records by connecting water levels at the time of depth sampling to contemporaneous water level records. We further determined water level differences between depth sampling and reference levels to apply calculated magnitudes. If the difference in water levels was greater than the accuracy of the pressure transducers (1 cm), we applied the difference to magnitudes to more accurately estimate drawdown exposure area metrics. We calculated area of lakebed and littoral area exposure as the number of 1-m^2 depth cells for lake and littoral areas less than the maximum magnitude for a given WD event. Areas exposed were relativized by whole lake and littoral areas and converted to percent exposure to compare across lakes.

Comparison to State Guidelines

We compared observed water levels to the magnitude, timing, and recession rate guidelines of MassWildlife (2002) and Mattson et al. (2004). We identified the number and proportion of drawdown events > 3 feet (0.914 m) because additional state guidance is needed for drawdowns > 0.914 m. For timing, drawdown initiation is recommended to start after November 1st, achieve the target drawdown level by December 1st, and to refill to normal pool levels by April 1st. Therefore, we identified the percentage of drawdown phases that did and did not meet corresponding timing guidelines. For recession rates, we determined cumulative water level rates over a 24-hour moving window to compare against the recommended ≤ 3 inches/d (i.e., 7.62 cm/d) of water level decline. We determined the percentage of cumulative daily recession rates ≤ 7.62 cm/d per recession event and the number of recession events whereby all cumulative recession rates were ≤ 7.62 cm/d.

For a given lake, municipal conservation commissions can permit special drawdown performance conditions that deviate from state issued guidelines in MassWildlife (2002). For example, several lakes are permitted to initiate drawdowns by October 1st (Boon), October 15th (Goose, Otis, Wickaboag, Watatic), or sometime after Columbus Day (Hamilton) before the November 1st state recommendation. Additionally, several lakes are permitted to perform drawdowns with magnitudes > 0.914m (e.g., Otis, Goose, Onota, Garfield). Although several lakes possess special drawdown performance conditions that differentiate from state guidelines, we did not assess if lake-specific permit conditions were met. Rather, we used state recommendations because they are grounded in minimizing negative ecological impacts and for ease of interlake comparison.

Results

We captured 2–4 complete WD events per drawdown lake and 3–4 years of water level data for non-drawdown lakes. Overall, we collected water level data on 69 complete WD events across 18 lakes. Due to the timing of logger installation and logger failure, we did not capture complete phase durations for 2014–2015 recessions at Brookhaven and Silver, 2015–2016 recessions at Hamilton, Wickaboag, and Wyola, and drawdown and refill phases at Cranberry Meadow for the 2015–2016 WD event.

Drawdown vs. Non-drawdown Lakes

Overall, hydrology of WD lakes differed from non-drawdown lakes, particularly during winter months (Figure 3.3). Relative to reference pool levels, median water levels in non-drawdown lakes during winter months (e.g., 10/1–4/1) ranged from −13.2 cm (Congamond) to 62.4 cm (Quacumquasit) with an overall mean of 10.3 cm. The lowest winter water levels ranged from −5.7 to −31.6 cm, with the extreme lowest water levels occurring in the 2016–2017 winter across all non-drawdown lakes. In comparison, median water levels in WD lakes across WD periods ranged from −202.4–0.1cm with an overall mean of −54.3 cm. Winter water level ranges for each lake was similar among years across WD (ranges: min. =11–22.2 cm, max. = 201.1– 268.7 cm) and non-drawdown lakes (ranges: min. =22.1–38.6 cm, max. = 80–115.6 cm), but ranges were larger and more variable in WD lakes (mean ± SD = 84.0 ± 61.3 cm) compared to non-drawdown lakes (mean ± SD = 53.1 ± 32.6 cm). Median summer water levels varied across years with the lowest water levels in 2016, but were similar across WD and non-drawdown lakes (ranges: 2015, WD = −0.1–11.2 cm, non-drawdown = 0.5–3.4 cm; 2016, WD = −21.8–7 cm, non-drawdown = −17.7- −12.4 cm; 2017, WD = −5.2–7.4 cm, non-drawdown = −4.6–36.8 cm; 2018, WD = −2.9–19.2 cm, non-drawdown = −4–8.6 cm).

Metric intercorrelations

We found correlations among several WD metrics (Appendix H). Generally, duration metrics were positively correlated with magnitude metrics. WD event duration and recession and refill phase durations had positive correlations with magnitude metrics (*r* = 0.41–0.89) and weaker positive correlations with percent areas exposed (*r* = 0.23–0.65). Magnitude metric correlations with depth exposure durations displayed a unimodal relationship with the lowest correlations at 0.25 m and 2 m (*r* = 0.55–0.65), and with the highest correlations at 0.75-m and 1-m depths (*r* = 0.86–0.92). Littoral area exposed had stronger correlations with magnitude metrics (*r* = 0.74–0.80) compared to lake area exposed (*r* = 0.56–0.65). Lastly, duration and magnitude metrics rates exhibited weak correlations with recession (*r* = -0.46–0.43) and refill rates (*r* = -0.45–0.41).

Magnitude

We captured a magnitude gradient with interannual means of drawdown phase water levels ranging from 0.001–2.16 m with an average of 0.66 m across lakes (Table 3.2.1, Figure 3.4). Average maximum magnitudes (i.e., lowest water levels below reference levels) ranged from 0.09–2.24 m with the lowest maximum magnitude of 0.13 m at Silver and the highest at 2.66 m at Onota (Figure 3.4). Mean water levels during drawdown phases were consistent among years for most lakes, varying < 0.10 m for 9 lakes and < 0.20 m for 14 lakes among years. Onota showed the highest interannual variability in maximum magnitude (1.67 m) because of a regime with two shallow drawdowns followed by one deep drawdown every third year. Stockbridge (0.64 m), Wyman (0.54 m), and Wyola (0.53 m) also had relatively high interannual variability. Maximum magnitudes were > 0.914 m than the guideline recommended by Mattson et al. (2004) in 6 of 18 WD lakes and 20 of 74 WD periods (27%) consistently (e.g., Otis, Onota, Garfield, Goose) or variably (e.g., Stockbridge-3 of 4, Wyola-1 of 3) among years. Mean drawdown phase water levels for 5 lakes also variably exceeded this guideline among years (e.g., Otis, Onota, Garfield, Goose, Stockbridge).

Area Exposed

Interannual mean lake exposure ranged from 1.3% (Watatic) to 35.3% (Garfield) across lakes (Table 3.1). Mean littoral exposure ranged from 9.3% (Greenwater) to 66.8% (Garfield) across lakes (Table 3.1). Lake area and littoral area exposed was largely consistent (within 10% exposure difference) among years for most lakes (Figure 3.5), with the exception of Onota, Stockbridge, Wyola, and Wyman. Onota displayed the highest interannual variability in lake and littoral percent exposure (Figures 3.5 & 3.6). The highest maximum magnitudes typically equated to the highest littoral and lake area exposed (e.g., Otis, Garfield, Onota, Figure 3.5). However, relatively small magnitudes at a few lakes resulted in relatively high percent littoral and lake area exposed (Silver, Watatic, Figure 3.5). Conversely, several lakes with moderate to high magnitude had relatively low percent exposures (e.g., Goose, Richmond, Figure 3.5).

Durations

WD period durations ranged from 5–246 days with an overall mean of 161 days (Table 3.2). Otis exhibited the longest mean duration at 230 days and Wyman the shortest at 22 days. WD duration varied interannually within lakes from 2 (Wyola) to 117 (Silver) days with a mean of 52 days. Proportionally the recession phase composed 20.8%, the drawdown phase 59.6%, and the refill phase 19.6% for an average WD period (Appendix E). WD phases also exhibited wide variability (Figure 3.7). The recession phase varied from 3 days (Silver, 2016–2017) to 70 days (Otis, 2016–2017) and mean duration averaged 28 days across lakes (Table 3.2). The drawdown phase overall ranged from 0 days (Wyman) to 215 days (Wickaboag) with a mean of 106 days. Lastly, the refill phase varied from 0 (Buel) to 139 days (Otis) across lakes with a mean of 27 days.

Along the drawdown magnitude gradient, depth contours were variably exposed across lakes and this exposure varied interannually within lakes (Figure 3.8). The 0.25-m depth contour was exposed in 16 of the 18 WD lakes, 0.5-m contour in 13 lakes, 1-m contour in 6 lakes, 1.5-m contour in 4 lakes, and 2-m contour in 2 lakes (Figure 3.8). Within lakes that exposed the 0.25-contour, mean duration exposure varied from 8–183 days with overall range of 1–229 days across years. Mean duration exposed at the 0.5-m contour varied from 1–165 days with an overall range of 1–217 days. The 1-m depth was exposed on average varied from 3–135 days and ranged from 3–169 days. Lastly, the 2-m contour was exposed on average for 1 day (Onota) or 77 days (Otis) and overall was exposed for 1–127 days.

Timing

WD events were initiated between October 1st and December 1st (Figure 3.9), excluding late drawdown events from Wyman that occurred in February – April. On average, drawdowns were initiated on October 22nd across all lakes, and means varied between 10/7 and 11/9 within lakes. Recessions ceased (i.e., drawdown phases started) on average on 11/23 and ranged from 10/7–1/9 (Figure 3.9). Drawdown phases ended and refills started on 3/13 on average and ranged from 1/4–6/5. WD periods ended (i.e., refill end) between Jan. 13th and Jun. 26th and on average reached reference levels on Apr 11th. There was variability in timing across years. The median recession start dates varied from 10/21 (2014–2015) to 10/29 (2016–2017) and end dates varied from 11/16 (2014–2015) to 12/01 (2017–2018) (Appendix F). The median refill start dates varied from 2/27 (2015–2016) to 3/23 (2014–2015) and end dates varied from 4/4 (2016–2017) to 4/23 (2014–2015) (Appendix F). In Wyman, 2–3 WD events were conducted per winter-year that includes 1 WD event in the fall and 2 events in the late winter and spring. Fall WD events were initiated between 10/23 – 10/27 and ended between 11/4 – 11/12. The two late winter spring WD events started between 2/22 – 3/13, and 3/18 – 4/17 and ended between 2/27 – 3/30 and 3/26 – 4/27 respectively.

Relative to the Mattson et al (2004) drawdown timing guidelines, 83.1% of WD events were initiated before 11/1, with 8 distinct WD periods that occurred in Wyman in February to April. Target drawdown water levels were reached (i.e., recession end) before 12/1 for 63.6% of WD events. Lastly, 70.6 % of WD periods did not reach reference water levels by 4/1 (Figure 3.9).

Rates

Sequential recession and refill rates varied across lakes and years (Appendix G). Overall mean recession rates varied from 0.81–5.4 cm/d with an average of 2.9 cm/d across lakes (Table 3.1). The highest mean rate occurred at Wyman (8.5 cm/d) and the lowest at Greenwater (0.4 cm/d) with interannual variation ranging from 0.02–5.9 cm/d across all lakes. Overall the highest recorded recession rates occurred at Onota with 188.4 cm/d followed by 73.2 cm/d at Wickaboag, and 71.7 cm/d at Otis. During recession phases, water levels also increased, most notably during 2017–2018 when a relatively large precipitation event occurred during the recession phase.

Mean refill rates varied from 1.2–12.3 cm/d with a mean of 4.0 cm/d across lakes. Mean refill rates ranged across years from 0.7–36.1 cm/d with the highest mean rate occurring at Richmond (37.9 cm/d) and the lowest at Silver (0.44 cm/d). The highest overall refill rates occurred Stockbridge (315.6 cm/d), Garfield (126 cm/d), and Greenwater (98.4 cm/d). Similar to recession rates, declines in water level occurred during refill phases. Several lakes reached reference pool level after a strong precipitation/melting event in January 2018 and did not attempt water level recession again.

Of the 71 recession periods, 39 (55%) possessed cumulative daily recession rates that exceeded the -7.62 cm/d rate standard (MassWildlife 2002, Appendix G). Several lakes exceeded the -7.62 cm/d standard consistently across WD periods, including Watatic (5.1– 30.2% of time), Otis (4.5–27.8% of time), Garfield (8.3–17.1% of time), Brookhaven (1.3– 30.1% of time), Wyola (2.2–34.8 % of time), and Hamilton (1.8–27.0% of time). Other lakes also exceeded this threshold but not consistently across WD periods (e.g., Onota, Ashmere, Stockbridge) and few lakes did not exceed this threshold overall (Silver, Goose, Boon, Buel). There were 2 recession events where median cumulative recession rates exceeded 7.62 cm/d (both in Wyman).

Discussion

Our results indicate that WD hydrology varies among MA recreational lakes and interannually across WD events. Most lakes had drawdown magnitudes < 0.914 m (i.e., the trigger for additional state guidelines) which remained consistent across years; however, differences in lake bathymetry and water quality (i.e., transparency) translated to variable lake and littoral zone exposure. Timing and duration of WD refill phases varied widely across years suggesting the importance of seasonal-specific precipitation and temperature events. The majority of WD events did not adhere to MA timing and recession rate performance standards, which may have severe ecological impacts (e.g., limited fish spawning habitat, mollusk stranding). Understanding the timing, duration, and rates of WD events in addition to drawdown magnitude will be critical for predicting WD impacts on lake ecosystems and managing WD's under future climate change.

Potential drivers and ecological implications of WD regimes

WD management context is likely an important driver for magnitude decisions. Most magnitudes were less than 0.91 m (0.001 – 2.16 m, mean = 0.66 m) in our study lakes, in contrast to Canadian and northern New England hydroelectric reservoirs, reporting magnitudes of 0.3–7.2 m (n =15, mean = 3.0 m, Trottier et al. 2019) and 0.8–10 m (n = 24, White et al. 2011). Many WD regimes are implemented in recreational lakes to dewater shoreline structures (e.g., docks, retaining walls, dam) before ice-on to prevent damage from ice erosion, to reduce nuisance densities of macrophytes that may impede recreational activities (Clayton 1996), or to prevent the spread of nonnative invasive species (Hussner et al. 2017). Thus, most magnitudes are relatively mild to correspond to shallow depths of shoreline infrastructure, but deeper magnitudes may be conducted to maintain dam integrity (e.g., Otis) or expose a significant portion of a nonnative invasive species like *Myriophyllum spicatum* (e.g., Garfield, Mattson et al. 2004).

These relatively small WD magnitudes can have significant ecological impacts. For example, within a subset of the current study lakes, Carmignani et al. (2019) found annual winter drawdown regimes with <1m magnitudes limited freshwater mussel distributions below drawdown water levels presumably due to their low mobility and susceptibility to desiccation. Also, relatively low water levels over short time period that exceed mean magnitudes and high recession rates as seen in this study may expose high mussel densities on shallow benthic shelves (e.g., Onota). Although rare, these extreme events may have severe ecological consequences to non-target biota via disturbance legacies (Richardson et al. 2002).

Although WD water level magnitude was moderately correlated with littoral and lake exposure, these relationships were not strong, emphasizing the importance of morphometry and water transparency in determining exposure. In shallow lakes or lakes with expansive shallow benthic shelves, relatively small to moderate magnitudes can expose a significant proportion of lakebeds (e.g., Silver). In contrast, lakes predominantly composed of steep-sided basin slopes show small whole-lake exposure even at high magnitudes observed in this study (e.g., Goose). Furthermore, nutrient availability and factors that influence water transparency including phytoplankton and non-algal suspended solids (Brezonik et al. 2019), will affect littoral zone depth boundaries (i.e., macrophyte colonization) and hence the relative exposure given a WD magnitude. Given littoral zones can provide disproportionately high energy and habitat resources for a diversity of consumers across lake morphometries (Vander Zanden et al. 2011), it is important to estimate littoral zone exposure. Although deep and steep-sided lake morphometries may be less sensitive to overall lake area exposure, valuable benthic-littoral resources (e.g., habitat, energy) are naturally constrained to relatively small areas (Vadeboncoeur et al. 2008) and hence are particularly susceptible to regulated water levels (Eloranta et al. 2018). Even at WD magnitudes of <0.91m in the current study large proportions of littoral zone habitat were exposed. Accurate estimation of lake and littoral exposure areas will require fine-scaled bathymetry data to generate area exposed and volume lost and will require depth estimations of littoral zone boundaries during summer months.

Typically, WD periods lasted >120 days where water levels were receding, refilling, or in drawdown for the majority of non-summer months (e.g., Oct. to Apr-Jun). Magnitude had a strong positive correlation with recession and refill phase durations, indicating that more time is needed to reach target water levels as drawdown magnitudes increase. Consequently, drawdown phase water levels are maintained for shorter durations with increasing magnitudes. Similarly, duration of exposure for depth-contours was a function of magnitude, with longer exposure times with increasing magnitudes. Despite these relationships, entire WD period duration and magnitude were weakly correlated suggesting event durations are relatively similar along the magnitude gradient. This lack of correlation could be attributed to variable interlake WD management decisions to maintain drawdown water levels up to different dates and owes to interlake differences in water budget components (i.e., inflows, outflows, residence time) in response to precipitation events.

The timing of WD phases resulted in timing incongruous with the recommendations of the MassWildlife (2002) standards. The majority of WD events were initiated before November 1st guideline and reached reference pool levels after April 1st. In contrast, the majority of WD recessions ended by the beginning of December per state recommendation and might be the result of relatively early WD initiation dates. Consistent recession initiation before November 1st across lakes and years is likely the result of permitted special conditions that allow for drawdowns to start in October. The timing of recession initiation was relatively consistent across years which suggests lake managers largely dictate and control recession starts. In comparison, the higher interannual variability for the timing of recession end, and refill start and end dates implies less water level control and more influence of external factors such as precipitation and ice melt. For example, sustained cold winter temperatures into late March and April of the 2014–2015 winter, synchronously delayed refill phases into mid–April to May across many of our study lakes. In contrast, the timing of refill phases in 2017–2018 was highly variable across lakes, which demonstrates the heterogenous water level responses likely because of differences in WD management and hydrological budgets.

Since the MassWildlife (2002) guidelines are to help minimize ecological impacts, the general incongruity with timing standards may have ongoing negative ecological effects. In particular, the April 1st refill guideline is in part to ensure access to critical shallow-water spawning habitat for spring spawning species (MassWildlife 2002), such as yellow perch (*Perca flavascens*), chain pickerel (*Esox niger*), and northern pike (*E. lucius*). Impacts to annual recruitment will depend on the amount of spawning habitat available below drawdown water levels and the disturbance to eggs from fluctuating water levels and wave action (Larson et al. 2016). More investigation is needed to assess the availability of spawning habitat (e.g., water temperature, substrate) under different refill scenarios (Papenfuss et al. 2018) and for different fish species that require different spawning substrates. The November 1st recession start guideline is to help prevent fish kills downstream because of relatively low-oxygenated and high temperature surface water that may dominate downstream flow during water level recession phases. Also, the start date may help to prevent fish kills within shallow, macrophyte-dominated lakes because of the predominance of low-oxygenated water (MassWildlife 2002). Future research to estimate the probability of fish kills across a range of bathymetries, winter weather conditions (e.g., ice and snow depth, duration), and winter drawdown metrics (e.g., magnitude, duration) will help prevent major fish die offs. In contrast, recession initiation dates before November 1st may benefit benthic species susceptible to exposure. Warmer water temperatures in mid-October could allow for more efficient movement of benthic organisms (e.g., mussels, Schwalb and Pusch 2007) if recession rates are not extreme. Lake management will need to consider and balance these potential impacts given their downstream and lake community composition.

Recession and refill rates were similar across most lakes and years; however, the ranges of rates stimulated several key insights. First, we documented relatively extraordinary rates within a few recession and refill phases. For example, we observed maximum sequential recession rates > 50 cm/d for 4 recession phases reaching up to 188.4 cm/d and similarly found cumulative recession rates > 25 cm/d for 4 recession phases reaching up to 62.9 cm/d. Second, although median cumulative recession rates were similar across lakes, recession phases often contained rates ≥ 7.62 cm/d MassWildlife (2002) guideline. Although the percentage of these rates largely comprised a minority of rate records, several lakes consistently fell within or exceeded the recession rate guideline across WD periods. Few studies have investigated the effect of recession rates on ecological responses, but low mobile organisms like freshwater mussels are particularly susceptible to rapid dewatering. Galbraith et al. (2015) found most mussels were stranded under 4 cm/d and 8 cm/d recession rates but with variable species-specific mortality after stranding. Given many WD events in the current study possessed cumulative daily recession rates > 4 cm/d, increases in magnitude with similar recession rates will likely impact existing mussel assemblages, whose distributions are already limited by ongoing WD regimes (Carmignani et al. 2019). Also, rapid drawdowns can cause fish stranding and trap fish in shallow pools under stressful conditions (Nagrodski et al. 2012). More field-based studies are needed to estimate the effect of typical recession and extreme recession rates on littoral communities. Furthermore, more research is needed to estimate the impact of high outflows to downstream communities associated with drawdown recession phases, as these flow patterns are likely atypical to natural streamflows during fall months.

WD Management Implications

From our empirical observations and intercorrelations among WD hydrological metrics, we hypothesize deeper WD magnitudes restrict control on the timing, duration, and rates compared to smaller magnitudes because they are likely more dependent on local precipitation and temperature events. Therefore, deeper WD magnitude regimes may not be able to meet WD performance standards for timing and rates. The capacity to increase WD magnitudes will depend on a lake's water budget (e.g., inflows, outflows, residence time, evapotranspiration), as lakes with relatively high surface area to watershed area ratios are less sensitive to water level fluctuations (Keto et al. 2008). Simulating magnitude scenarios under various water budget conditions can estimate the duration and timing of WD phases, and the potential rates needed to achieve WD management goals while also meeting state recommendations.

The efficacy of WD regimes as a macrophyte control strategy is strongly dependent on winter weather conditions and the target species resistance to freezing and desiccation (Cooke 1980). Given that the majority of WD's were initiated in October, reached target water levels before or in the beginning of December likely before ice-on, and were refilled in April or later suggests WD timing and duration amply allows for possible exposure to rhizome-damaging conditions. Lonergan et al. (2014) experimentally found that sediment temperatures at -5°C sustained for ≥24 h, or below a sediment water content threshold for ≥48 h prevented regrowth of *Myriophyllum spicatum*, a widespread invasive species in the Northeast. However, the presence of ice and snow cover concurrent with freezing and dry exposed soil will dictate the level of rhizome mortality (Lonergan et al. 2014) and often weather conditions are difficult to predict. Early freezing of exposed lakebed followed by snow cover can sustain frozen soil conditions that may result in effective macrophyte rhizome mortality. In contrast, snow cover before the onset of freezing temperatures can effectively insulate sediment above freezing and regulate freeze-thaw cycles (Huntington et al. 2009 and references therein). Thus, enough time is needed to allow sediment dewatering before ice formation, along with exposure to consecutive subzero freezing days to control susceptible nuisance species. The among-winter variability of snow and ice cover relative to the timing of freezing and dry conditions has likely resulted in variable control of target macrophyte species within the exposure zone and is ineffective at controlling macrophytes in the rest of the photic zone. Further monitoring of exposed soil temperature and moisture, and ice and snow cover durations during WD periods could help determine the timing of refill once macrophyte mortality conditions are met and the lake is ice-free (Lonergan et al. 2014). Additionally, incorporating fine-scale estimates of bathymetry could help identify benthic areas of high topographic heterogeneity that may be less vulnerable to exposure (i.e., variable moisture and temperature conditions).

Likely changes in lake water level regimes from climate change are a top concern among lake management stakeholders (Magee et al. 2019). Climate change is projected to increase winter temperatures, increase winter rainfall, reduce the extent and duration of snow cover, increase the frequency of short-term droughts, and shift the timing of spring floods in the Northeast USA (Hayhoe et al. 2007; Huntington et al. 2009). Additionally, the current trend of earlier ice-out dates (Hodgkins et al. 2002) is expected to continue in the future along with the potential of shorter ice cover durations and reduced ice thickness (Huntington et al. 2009). Given these projections, climate change poses potential challenges for WD regimes as a macrophyte control strategy and for meeting timing guidelines to minimize ecological impacts and maintain recreational value. Specifically, warmer and wetter winters may limit macrophyte mortality by keeping exposed sediment above mortality threshold temperatures and by keeping sediments moist from rainfall and associated water level fluctuations. A major concern associated with climate change is delayed or incomplete refill to reference pool levels because of a spring drought (Magee et al. 2019). In several Connecticut lakes, McDowell (2012) documented refill phases that did not reach summer pool levels until mid-late May as a result of a springtime drought. Delayed refill extending into summer months could also decrease recreational opportunities for boating and angling (Miranda and Meals 2013) and may decrease lakefront property values (Hanson et al. 2002). Anticipation of these changes in precipitation and temperature regimes will help to guide WD regime management with potential changes to magnitude, duration, and even frequency in order to sustain ecological integrity and maintain recreational value. Due to heterogenous conditions of watershed (e.g., land use and cover, slope, drainage density) and lake-specific factors (morphometry, residence time) that regulate lake water levels (Molinos and Donohue 2014), management of WD regimes will require lake-specific adaptation strategies (Magee et al. 2019).

Data Needs & Conclusions

The scarcity of water level records and lake water level monitoring efforts poses a large challenge to assess WD impacts on lake ecosystems and understand the role of interacting anthropogenic stressors (e.g., climate change, watershed land use). Increased monitoring of lake levels at ecologically-relevant temporal resolutions and scales is a primary need (Magee et al. 2019). In this study, bihourly recording intervals enabled the documentation of short-term extreme events (e.g., high recession rates) and captured the overall inter- and intra-annual variability of WD regimes. Furthermore, given winter water level regulation could carry over into summer months because of climate change, year-round water levels need to be monitored as recent evidence suggests summer water level fluctuations impact water quality more (e.g., cyanobacteria blooms, Bakker and Hilt 2015) than winter drawdowns (Elchyshyn et al. 2018). Integrating knowledge of the natural range of variability of lake levels over long time scales (i.e., decades, Hofmann et al. 2008; Molinos et al. 2015) will help to predict future water level changes and direct management to mitigate and anticipate related water quality issues (Lisi and Hein 2018). We also need increased modeling efforts to understand the drivers and patterns of lake water level fluctuations. Application of recently developed models can improve our understanding of lake water budgets at local and regional levels and help to estimate the hydrological impacts of varying WD regimes in combination with watershed land use cover (Hanson et al. 2018). Fundamental lake characteristics that control in-lake abiotic and biotic dynamics including lake morphometry, water transparency, nutrient status, and watershed land use will help to contextualize the long-term efficacy of WD management with ongoing climate change.

Tables

Table 3.1. Summary of winter drawdown metrics.

Mean, minimum (min), and maximum (max) hydrologic metrics for 18 lakes and overall average based on 3-4 years of winter drawdowns (WD) per lake derived from 2-h water level records. Drawdown magnitude is based on water levels during the drawdown phase (i.e., excludes recession and refill water levels). Maximum lake and littoral area exposed are based on maximum magnitude (i.e., lowest drawdown water level) per WD period. Recession and refill rates represent water level decline (negative values) and rise (positive values) respectively.

Lakes	Years Monitored	Drawdown Magnitude (m)			Max Lake Area Exposed (%)			Max Littoral Area Exposed (%)			Recession Rate (cm/day)			Refill Rate (cm/day)		
		Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Ashmere	4	0.69	0.38	0.87	17.4	17.4	17.5	23.4	23.3	23.5	-2.6	-28.5	28.2	2.8	-16.2	30.9
Boon	4	0.30	0.24	0.38	6.5	5.7	7.0	15.2	13.4	16.5	-0.8	-22.5	23.7	1.3	-27.6	29.7
Brookhaven	4	0.26	0.10	0.36	9.0	7.3	11.7	12.0	9.8	15.6	-2.0	-28.0	39.2	2.7	-11.7	19.8
Buel	3	0.17	0.02	0.24	6.1	5.8	6.4	12.8	12.2	13.5	-1.2	-16.4	16.4	4.0	-9.2	17.6
Cranberry Meadow	4	0.24	0.13	0.42	11.9	10.2	13.5	12.0	10.3	13.7	-1.6	-12.9	11.7	1.7	-12.0	16.4
Garfield	3	1.77	1.56	1.92	35.3	33.1	37.6	66.8	62.6	71.1	-3.4	-41.6	82.0	3.0	-24.8	94.4
Goose	4	1.29	1.11	1.50	11.3	11.3	11.3	25.9	25.8	25.9	-3.6	-26.4	25.8	2.4	-32.4	45.0
Greenwater	4	0.43	0.23	0.51	3.9	3.9	3.9	9.3	9.2	9.4	-0.8	-17.4	28.8	2.5	-15.6	49.8
Hamilton	3	0.59	0.44	0.77	9.8	9.0	10.6	25.0	23.0	26.9	-3.8	-27.0	46.8	4.9	-7.6	32.8
Onota	4	0.98	0.72	1.39	20.0	11.4	32.5	34.9	19.9	56.5	-2.5	-66.9	280.8	2.5	-40.2	71.1
Otis	5	2.16	2.08	2.24	20.5	20.1	21.1	57.2	56.2	58.9	-4.8	-50.1	51.8	2.5	-48.8	48.9
Richmond	4	0.58	0.40	0.73	6.9	6.7	7.1	9.6	9.2	9.9	-3.6	-15.3	12.6	11.9	-13.2	60.6
Silver	4	0.03	-0.08[a]	0.09	25.8	25.7	25.9	37.7	37.6	37.8	-1.3	-11.4	4.2	1.2	-6.6	14.4
Stockbridge	4	0.73	0.47	1.22	13.9	9.4	16.4	43.8	29.5	51.7	-3.4	-32.1	62.4	5.8	-56.4	131.4
Watatic	4	0.29	0.07	0.37	1.3	1.3	1.3	34.3	33.6	35.4	-3.1	-20.7	30.6	2.9	-12.6	24.3
Wickaboag	3	0.44	0.14	0.55	6.5	6.5	6.5	15.3	15.3	15.4	-1.6	-53.4	27.0	3.4	-18.4	48.4
Wyman	4	0.36	0.36	0.37	12.6	7.6	17.3	15.6	9.5	21.5	-5.0	-22.3	27.1	4.9	-12.8	25.6
Wyola	3	0.56	0.01	0.87	9.0	7.8	10.2	12.7	11.0	14.3	-5.4	-15.0	4.8	12.3	-2.8	52.8
Overall	*NA*	*0.66*	*-0.08*[a]	*2.24*	*12.7*	*1.3*	*37.6*	*25.8*	*9.2*	*71.1*	*-3.0*	*-66.9*	*280.8*	*4.0*	*-56.4*	*131.4*

[a] Negative mean minimum drawdown refers to water level higher than reference level

Table 3.2. Drawdown phase durations.

Average mean, minimum, and maximum durations in days for recession (i.e., water level decline), drawdown (i.e., lowest WD water levels), and refill (i.e., water level rise) phases, and for entire winter drawdown (WD) periods.

Lake	Recession Phase			Drawdown Phase			Refill Phase			WD Period		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Ashmere	29	22	42	134	116	161	32	14	70	195	174	221
Boon	41	18	54	108	84	137	26	15	43	177	136	210
Brookhaven	25	8	41	139	101	197	10	4	19	155	152	161
Buel	29	12	51	101	33	176	9	0	17	137	84	201
Cranberry Meadow	10	7	16	166	141	190	9	7	11	186	156	210
Garfield	49	37	58	65	40	85	60	45	70	176	161	195
Goose	37	27	44	95	78	120	54	22	82	187	176	206
Greenwater	54	43	63	94	74	120	23	9	43	158	122	185
Hamilton	21	12	29	70	55	98	16	11	27	118	99	137
Onota	45	29	60	71	52	105	48	44	50	161	138	182
Otis	55	43	70	66	38	100	102	70	139	230	185	246
Richmond	20	15	27	85	47	127	17	1	34	121	74	153
Silver	4	3	5	167	120	215	6	1	17	177	126	223
Stockbridge	33	21	42	79	38	127	29	7	64	138	81	172
Watatic	14	5	19	149	122	171	16	4	26	180	167	191
Wickaboag	22	19	24	168	162	174	11	8	16	205	198	211
Wyman	10	4	19	0	0	1	12	1	45	22	5	55
Wyola	10	8	12	145	120	166	7	3	15	177	176	178
Overall	*28*	*3*	*70*	*106*	*0*	*215*	*27*	*0.4*	*139*	*161*	*5*	*246*

Figures

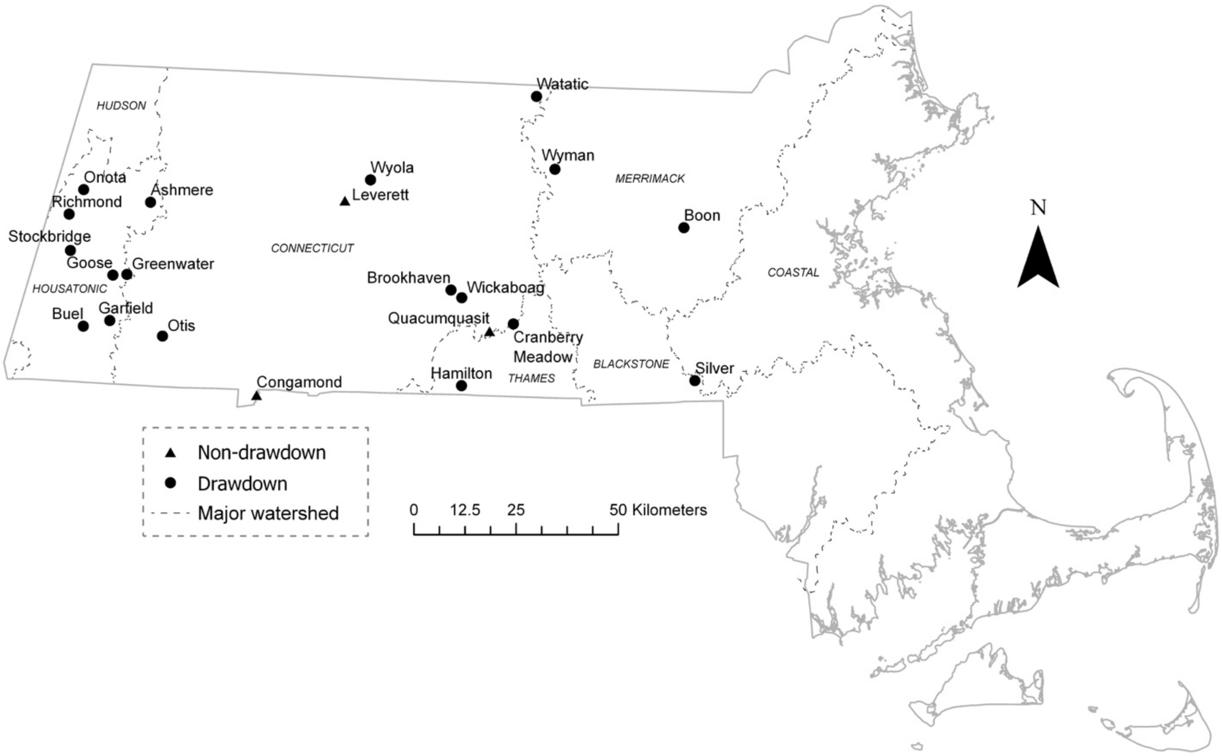


Figure 3.1. Map of study lake locations.
Circles represent lakes with annual winter drawdown water level regimes (WD) and triangles represent lakes with no history of WD's.

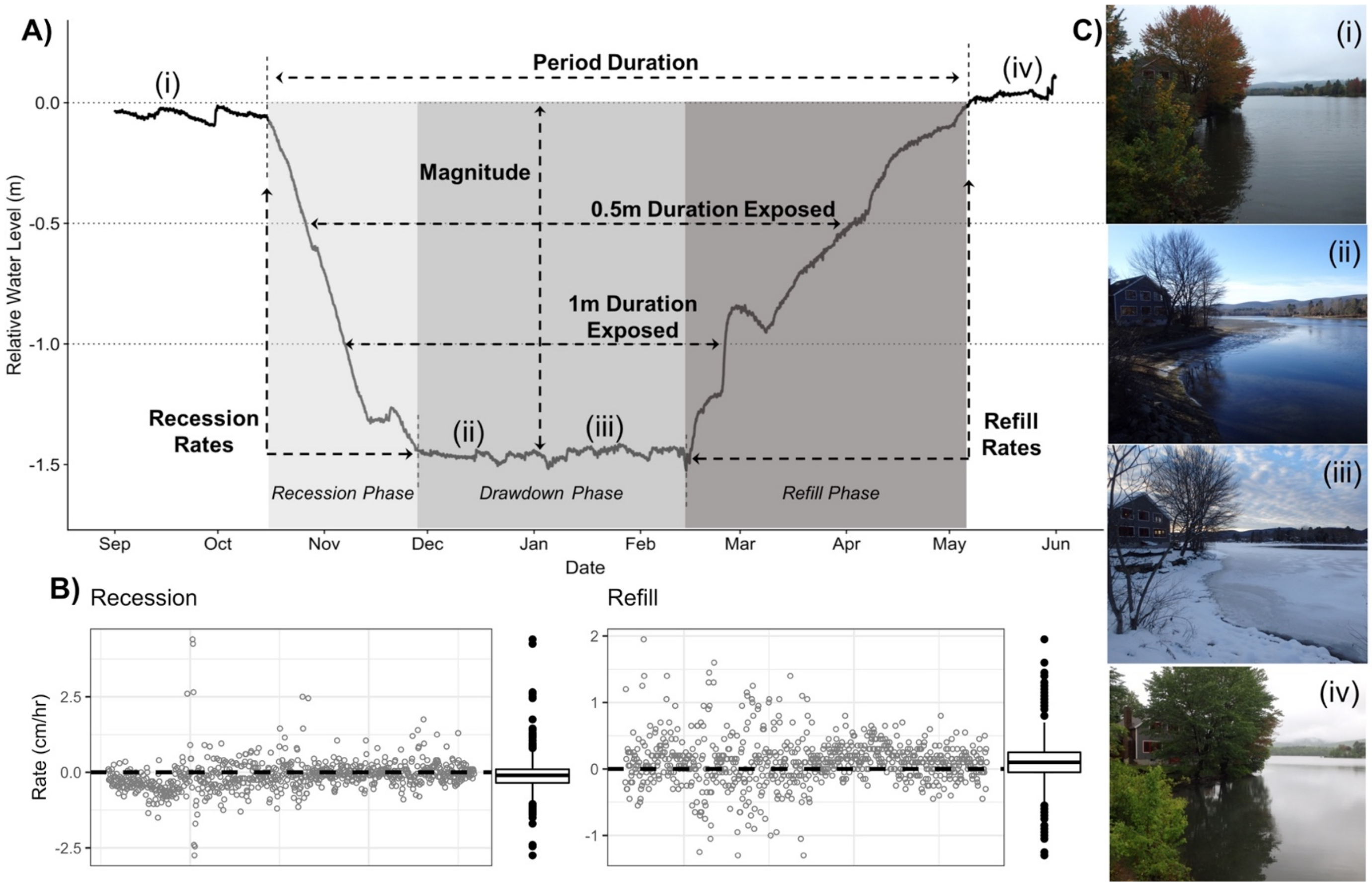


Figure 3.2. Winter drawdown metrics.

A) Example hydrograph and associated winter drawdown (WD) metrics calculated for a single WD period. Water levels (y-axis) are relativized to reference water level (e.g., summer/normal pool level) such that relative water level = 0 represents normal pool level. WD period phases (in italics and grey shades) include: the recession, drawdown, and refill phases. Vertical dotted lines and changes in background color indicate the start and end dates for WD phases. These dates are used to calculate WD duration, recession and refill rates, and WD magnitude. Duration exposed for a given depth (e.g., 0.5m, 1m) corresponds to elapsed time when relative waters exceeded this depth. B) Example of recession and refill rates through time for a WD period with boxplot displaying interquartile range and extreme values > 1.5 times the interquartile range, this can be inferred from plot. C) Photos corresponding to changes in water level throughout a WD period as labeled in panel A.

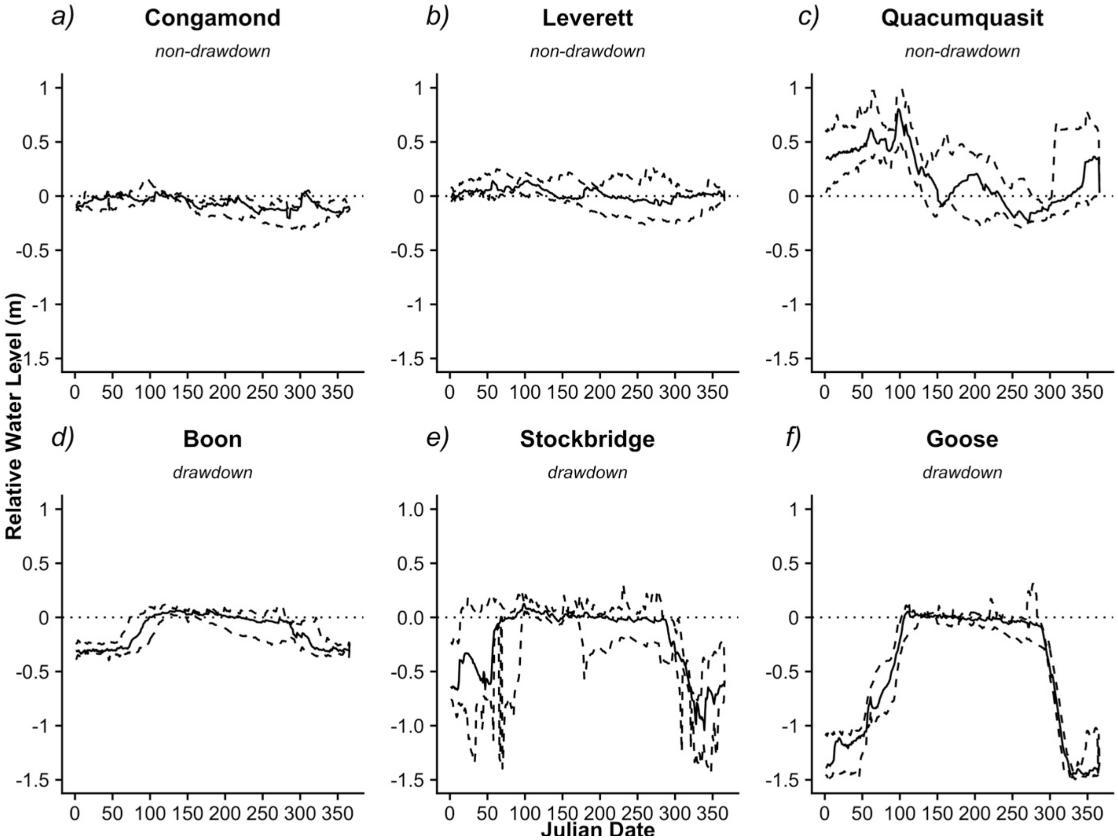


Figure 3.3. Empirical water level time series.
Water level time series for 3 non-drawdown (a-c) and 3 drawdown (d-f) lakes depicting within and among lake and year variability in drawdown magnitude, and timing. Water levels are expressed relative to reference pool level (relative water level = 0, dotted line). Solid water level lines indicate water level medians, and dashed lines represent the range per Julian date over 3–4 years.

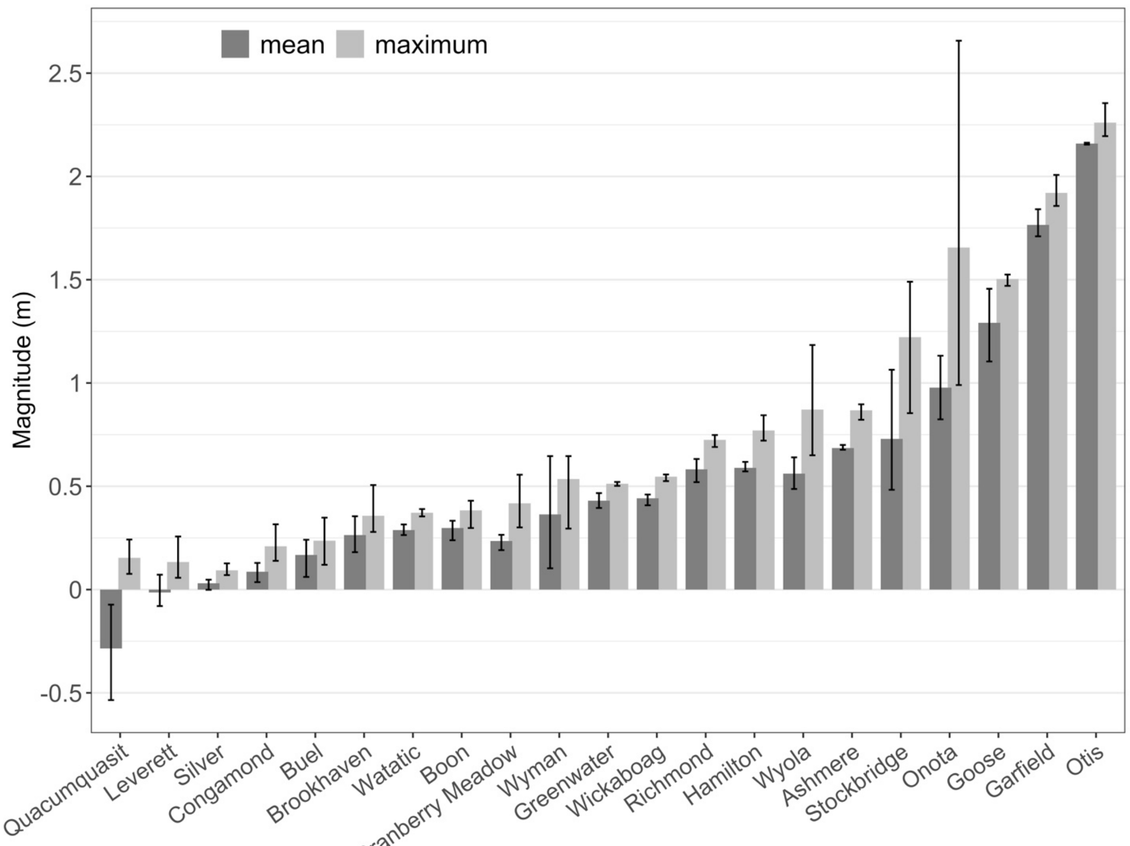


Figure 3.4. Drawdown magnitudes.

Interannual averages (± range) for magnitudes categorized as mean (dark grey bars) drawdown phase water levels and maximum (light grey bars) drawdown water levels. Non-drawdown lakes are Quacumquasit, Leverett, and Congamond.

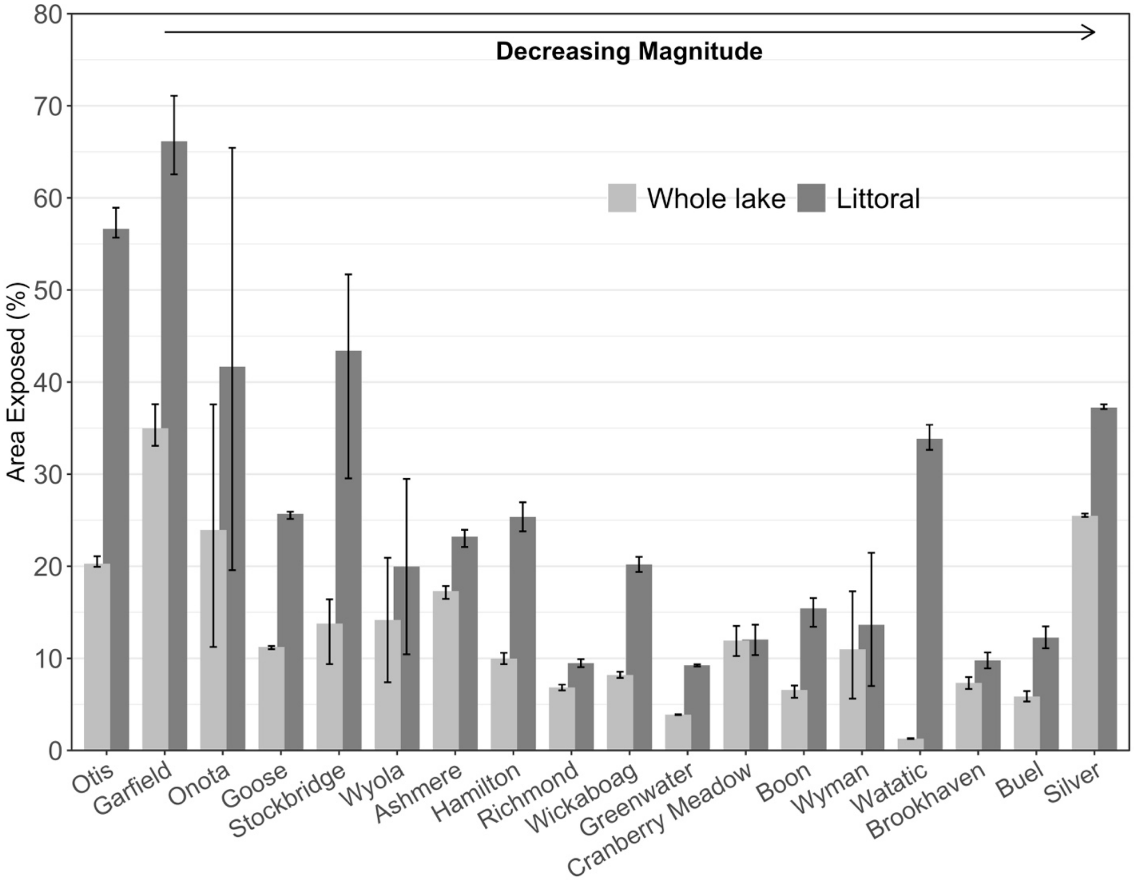
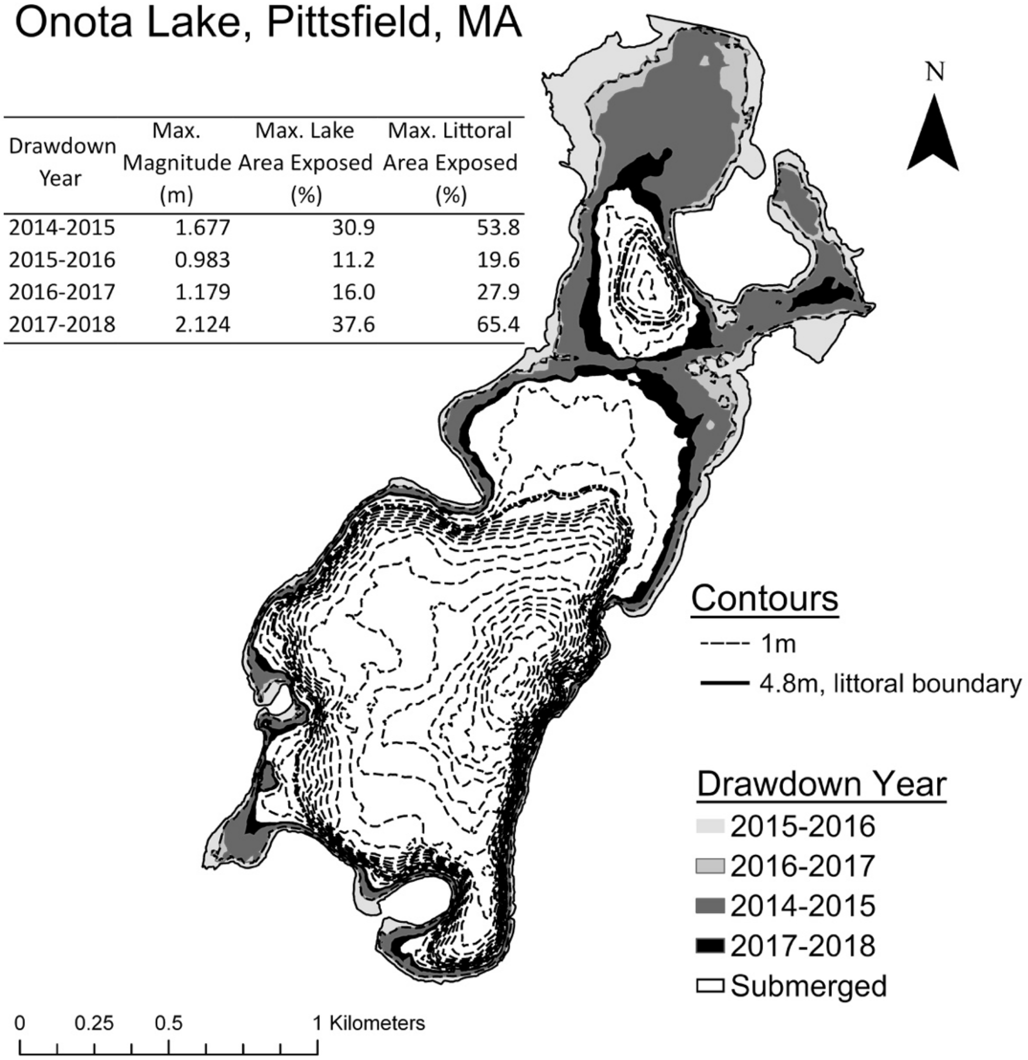


Figure 3.5: Percent lake and littoral area exposed.
Mean (± range) percent lake area and littoral area exposed at maximum drawdown magnitudes. Lakes are ordered by decreasing mean drawdown magnitude.



Drawdown Year	Max. Magnitude (m)	Max. Lake Area Exposed (%)	Max. Littoral Area Exposed (%)
2014-2015	1.677	30.9	53.8
2015-2016	0.983	11.2	19.6
2016-2017	1.179	16.0	27.9
2017-2018	2.124	37.6	65.4

Figure 3.6. Exposed area for Onota Lake.
Estimates of maximum (max) lake area exposure for Onota Lake across 4 years based on interpolated bathymetry data and daily mean water levels. Exposed areas are nested as drawdown magnitude increases. Submerged area (white) refers to depths perennially submerged throughout the study duration.

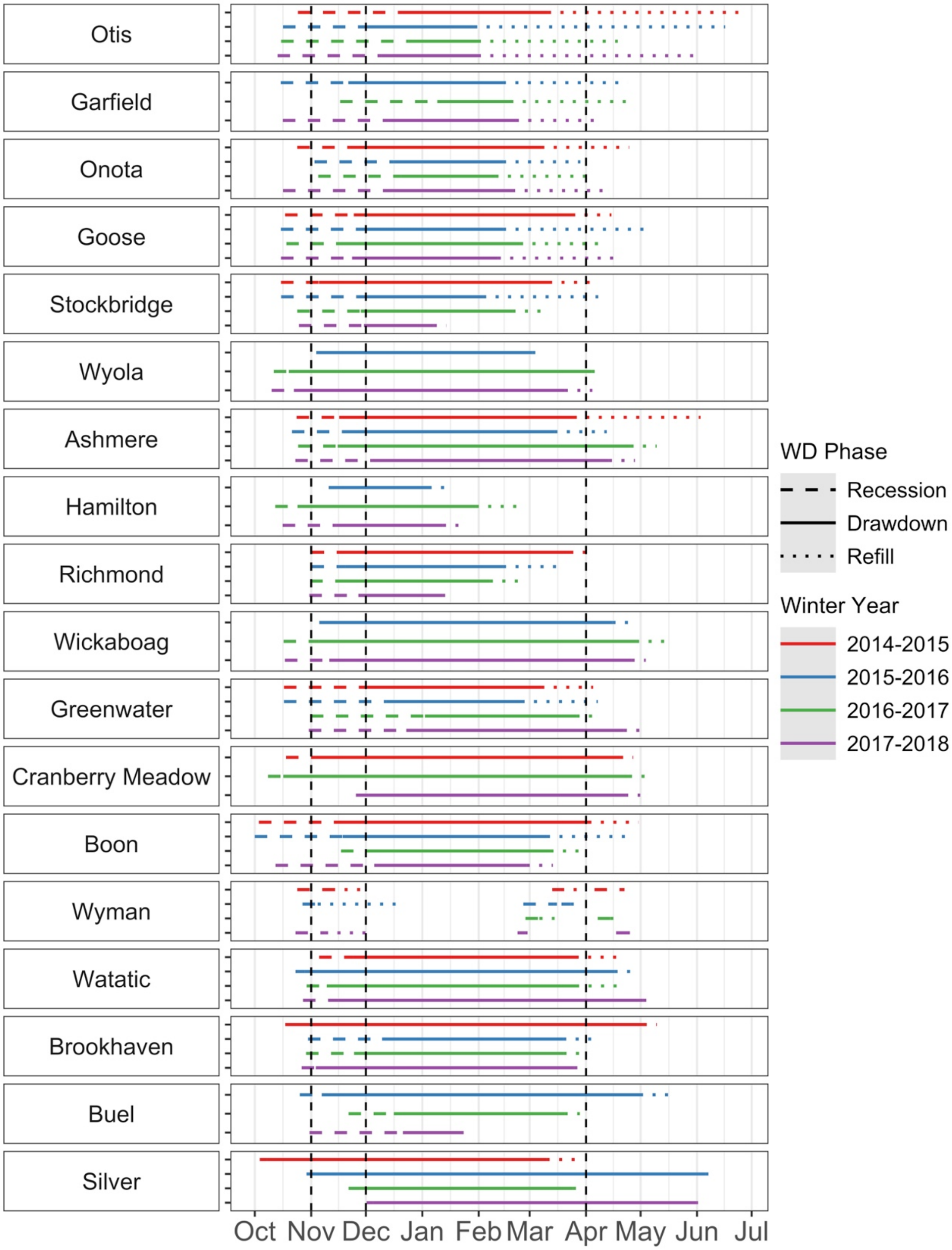


Figure 3.7. Timing and duration of drawdown phases.
WD period duration and timing for 3 or 4 drawdowns per lake (color coded by year). Each WD period is divided into recession, drawdown, and refill phases by line types. Vertical dashed lines represent the Generic Environmental Impact Report guidelines recommended for WD start and end dates. For Wyman, 2-3 WD's are conducted per winter year.

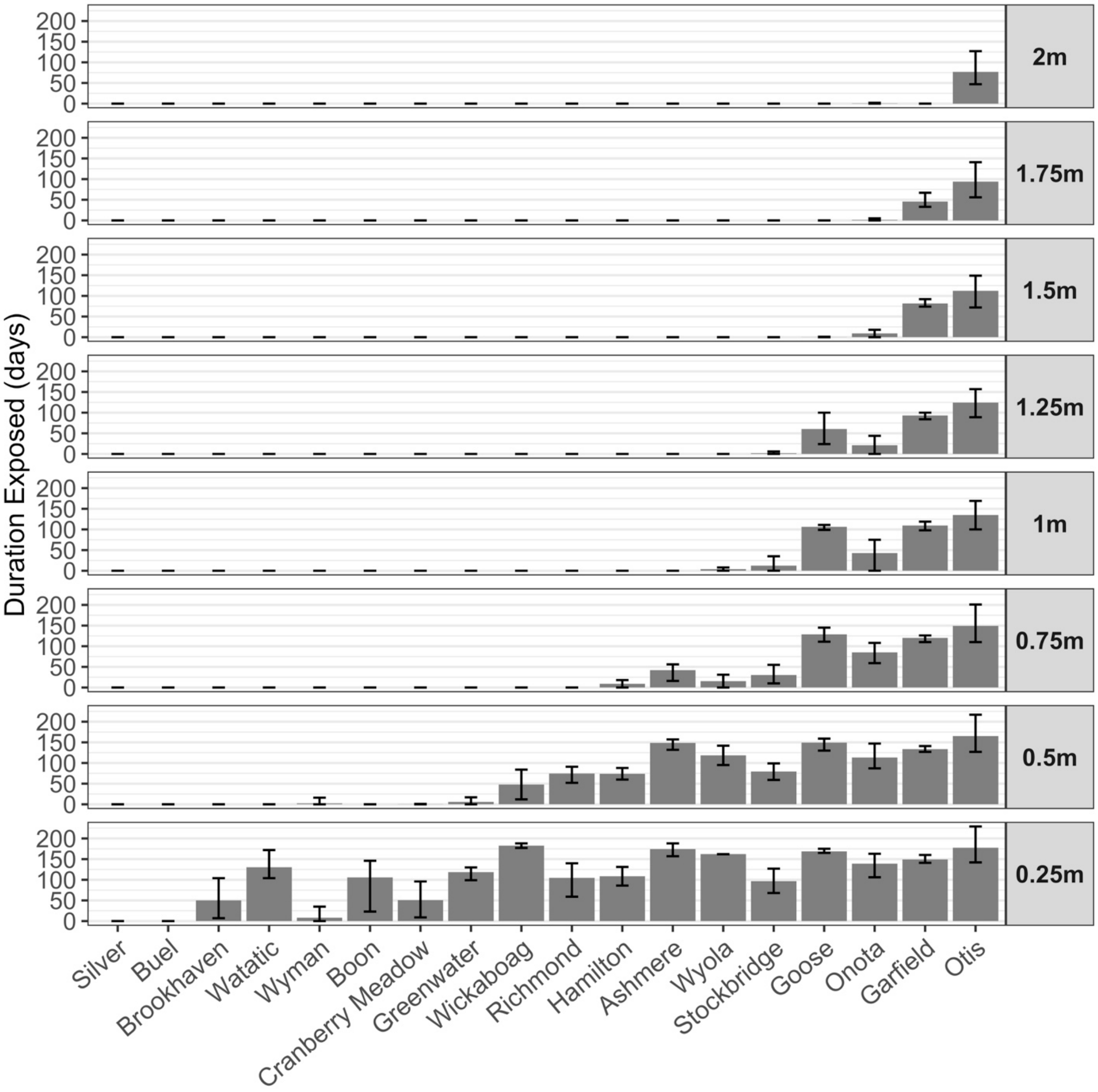


Figure 3.8. Duration exposure of depth contours.
Mean (± range) duration exposed for 8 depths per drawdown lake. Lakes are ordered by increasing mean drawdown magnitude.

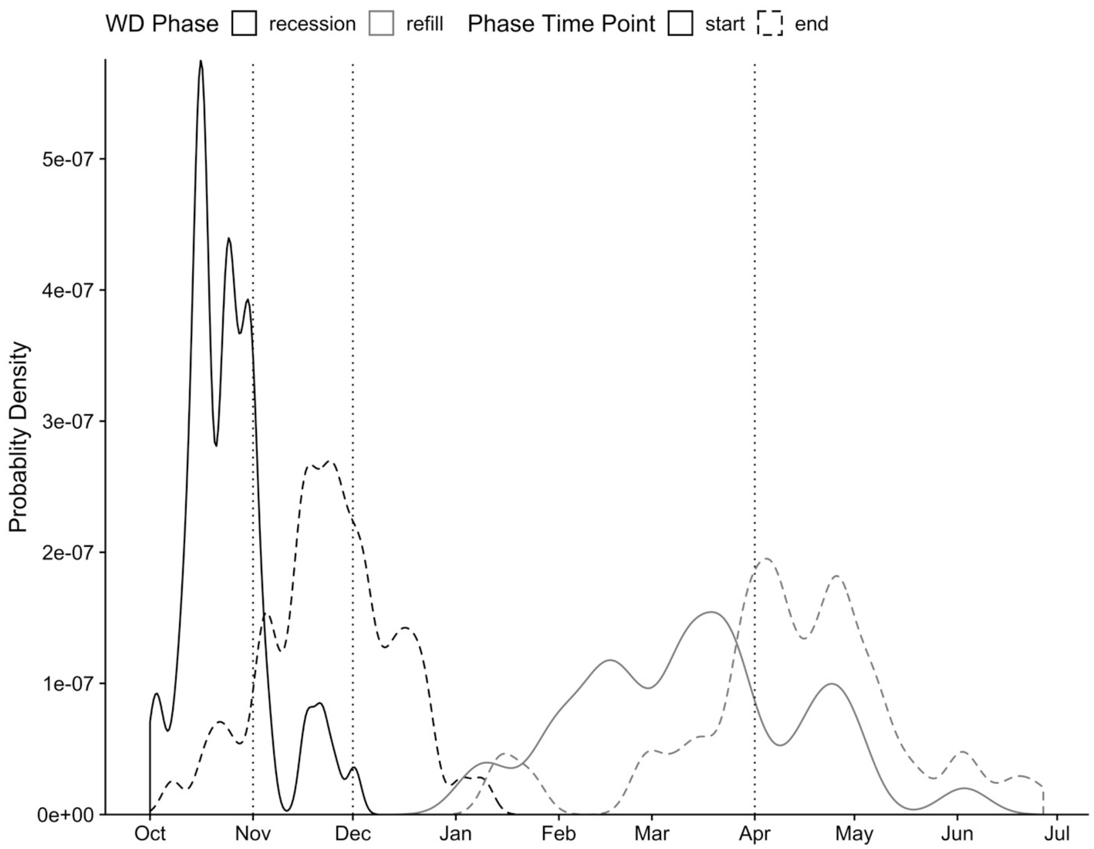


Figure 3.9. Probability density of drawdown phase timing.
Density of recession and refill start and end dates (see legend) aggregated across winter-years and lakes for WD periods. Dotted vertical lines indicate Mattson et al. (2004) timing recommendations for WD initiation start (Nov. 1st), recession end (Dec. 1st) and WD period end dates (Apr. 1st). Phase dates from late winter-spring WD periods in Wyman are not included.

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CHAPTER 4

ANNUAL WINTER WATER LEVEL DRAWDOWNS INFLUENCE LITTORAL ZONE PHYSICAL HABITAT STRUCTURE AND MACROPHYTES IN MASSACHUSETTS LAKES

Introduction

Natural water level fluctuations create spatiotemporal heterogeneity in the physicochemical habitat of lake littoral zones (Hofmann et al. 2008; Evtimova and Donohue 2015). Diverse littoral zone habitat (e.g., macrophytes, wood, bed texture) supports high within-lake diversity of invertebrates and fish (Weaver et al. 1997; Tolonen et al. 2001; White and Irvine 2003), provides fish spawning habitat (Winfield 2004; Lawson et al. 2011), mediates predator-prey interactions (Diehl 1992; Sass et al. 2006; Kornijów et al. 2015), contributes to whole-lake primary and secondary production (Vadeboncoeur et al. 2002; Vander Zanden et al. 2011), and may offer high ecosystem resiliency (Kovalenko et al. 2012) by supporting longer food chains (Ziegler et al. 2015). In impounded systems, anthropogenic alterations to water level—alterations beyond the natural range of timing, magnitude, and frequency of daily to seasonal water level fluctuations (Hofmann et al. 2008)— can impair the ecological integrity of littoral zones and hence lake ecosystems (Wantzen et al. 2008). Although scientific understanding of the role of natural (e.g., Evtimova and Donohue 2015) and modified (Leira and Cantonati 2008; Zohary and Ostrovsky 2011) water level fluctuations in structuring littoral zone physical habitat has improved, there are limited empirical data on the impacts from prescribed water level fluctuations regimes, including annual winter water level reductions or drawdowns (referred to hereafter as winter drawdowns; Carmignani and Roy 2017).

Winter drawdowns are a widespread management practice conducted in temperate and boreal lakes typically as a consequence of power demands and flood protection in hydroelectric reservoirs (e.g., Mjelde et al. 2012) or as a strategy to reduce submerged macrophyte densities that may affect some recreational activities (Cooke et al. 2005). Drawdowns are initiated in fall and winter months, whereby water levels are reduced to desired minimum levels, and rise to full pool levels upon spring flooding (Mattson et al. 2004). Through desiccation and accelerated erosional processes, drawdowns can reduce fine-textured sediment (Effler and Matthews 2004; Cooley and Franzin 2008), organic matter, and nutrients (James et al. 2001; Furey et al. 2004) in exposure zones, leaving behind primarily larger sediment particles with low nutrient storage capacity. These abiotic changes along with direct physiological stresses from desiccation and freezing conditions can reduce macrophyte abundance and alter assemblage composition within drawdown exposure zones (Wilcox and Meeker 1991; Wagner and Falter 2002; Turner et al. 2005). Specifically, winter drawdowns can reduce macrophyte species reliant on vegetative structures for future propagation (i.e., perennials) in favor of high seed-bearing taxa (i.e., annuals) or taxa with multiple viable propagation strategies (reviewed in Carmignani and Roy 2017). Ultimately, these littoral habitat changes with drawdown can result in less complex physical habitat structure with negative implications for invertebrate and fish assemblages (Wilcox and Meeker 1992; Meeker et al. 2017).

Where winter drawdowns occur, they are typically not the only disturbance contributing to loss in littoral zone habitat complexity (Kaufmann et al. 2014); lakeshore development, herbicide application, and nutrient loading also alter littoral habitat in drawdown lakes. Lakeshore development is associated with reduced coarse wood (Christensen et al. 1996; Francis and Schindler 2006), reduced emergent and floating-leaved vegetation (Radomski and Goeman 2001; Alexander et al. 2008; Hicks and Frost 2011), finer sediments (Jennings et al. 2003), and lower sediment organic matter content (Francis et al. 2007). Lake nutrient enrichment in combination with other pressures that affect food web dynamics (e.g., fish winterkills, invasive species) can enable declines of submerged macrophytes particularly in shallow lakes (Phillips et al. 2016). However, disentangling the individual and potentially collinear effects of these anthropogenic stressors can be challenging (Van Sickle 2013), and elucidating the interacting effects of winter drawdowns with co-occurring anthropogenic stressors offers a novel area for research.

We aim to determine the effects of winter drawdowns on physical habitat (i.e., coarse wood, sediment, macrophytes) of the littoral zone for lakes with decades of annual winter drawdowns. Given that littoral zone physical habitat can exhibit substantial inter-lake variability (Gasith and Hoyer 1998; Weatherhead and James 2001), our study included 21 lakes that encompass a gradient of drawdown magnitude while attempting to account for other environmental gradients (e.g., water chemistry, morphometry, herbicide application) that influence physical habitat. Finally, to address within-lake variability and specifically assess the interactive effect of local riparian development with drawdowns, we sampled paired forested and developed shorelines in each lake. Our study will help refine adaptive lake management strategies to minimize ecological impacts in the context of multiple anthropogenic stressors.

Methods

Lake Selection & Study Area

We selected lakes using a stratified random approach to primarily capture a winter drawdown magnitude gradient. Lakes were selected from local conservation commissions and lake associations that responded to a statewide email survey (i.e., 397 out of 2080 waterbodies). We targeted lakes in the Northeastern Highlands (e.g., Western New England Marble Valleys/Berkshire Valley/Housatonic and Hoosic Valleys) and two ecoregions in the Northeastern Coastal Zone (e.g., Connecticut River Valley, Lower Worcester Plateau) to help reduce water chemistry variation among waterbodies based on watershed land cover and geology (Griffiths et al. 2009). Where we received reported drawdown magnitude information (n = 21 lakes), we selected two lakes each from four drawdown magnitude classes (<0.5, 0.5–1, 1–1.5, >1.5 m) to ensure a drawdown magnitude gradient. We then selected 8 additional lakes with a history of annual winter drawdowns but without magnitude information that were stratified into four lakeshore development density classes (e.g., 0–155, >155-284, >284–395, 412–536 buildings/km^2) calculated within a 100 m buffer around shore and determined by natural breaks in the data distribution. The final four lakes had no history of annual winter drawdowns, and these lakes were randomly selected based on lake area (0.012–0.073 or 0.11–0.89 km^2) and lakeshore development density (<97 or >105 buildings/km^2). Where waterbodies were exhausted within a stratification (low drawdown magnitude class: <0.5 m), we extended our selection area to include the New England Coastal Plains and Hills in eastern MA, and randomly selected Silver Lake and Lake Boon. We were unable to sample five of the original 20 selected lakes in 2014 due to access issues and replaced those with 6 additional lakes that are within our study area and represent lakes with current drawdown regimes or with no history of annual winter drawdowns, for a total of 21 lakes (Table 4.1).

Study lakes were in the Northeastern Highlands and Northeastern Coastal Zones (level 3 ecoregions) located in the Housatonic, Connecticut, Thames, Merrimack, and Blackstone River watersheds (Figure 4.1). Inland Massachusetts has a continental temperate climate with four seasons. Mean minimum and maximum July and January temperatures for ecoregions in the Northeastern Highlands tend to be 1-3°C degrees lower than in Northeastern Coastal Zone (Griffith et al. 2009). Winter precipitation averages 21.6–25.4 cm (1981-2010) across the study area (National Oceanic and Atmospheric Administration, https://www.ncdc.noaa.gov/cdo-web/datatools/normals, last accessed 2018-06-28). Lake watersheds have mixed land use with variable urban development ranging from 2-40% (median = 9%) with a general increase from west to east, and relatively small proportions of pasture (0-15%) and agriculture (0-8%). Total watershed forest cover ranged from 20-83% (median = 64%) among lakes. Forests are primarily composed of mixed deciduous and conifer stands including northern, central, and transition hardwoods. Lakes located in the Northeast Highlands are characterized by coarse-loamy to loamy soils and metamorphic bedrock or limestone derived coarse-loamy soils and calcareous bedrock. In the Northeast Coastal Zone, lakes are underlain with sedimentary bedrock and alluvium soils, metamorphic bedrock with coarse-loamy soils, or coarse-loamy and sandy soils (see Griffiths et al. 2009 for more detail).

Physical Habitat Sampling

We sampled lakes once in 2014 (n = 15 lakes) or 2016 (n = 6 lakes) in July–August when water levels were at or near full pool and macrophytes were generally at peak biomass. Since annual drawdown regimes have been maintained for at least two decades (Table 4.1), our single season sampling was presumed to reflect a sustained drawdown effect. At each lake, we established two sampling sites that stretched along 20-m shoreline segments. One site was selected with predominant forest riparian cover and the other site by human development (i.e., houses, lawns), each buffered by 50 m of similar shoreline land cover composition on each end. Sites were selected to represent shorelines sheltered from predominant wind-wave action and with gently graded slopes (i.e., ≤10%) to ensure we sampled conditions that support macrophyte biomass (Duarte and Kalff 1990).

We aimed to capture the major physical littoral habitat components including coarse wood, sediment, and macrophytes. At the site level, we enumerated all coarse wood (i.e., wood ≥10 cm in diameter at its thickest cross-section) at depths ≤ 1 m along 100 m of shoreline centered around the 20 m sites. Using methods from Newbrey et al. (2005), we quantified the branching complexity for each coarse wood piece. For every site, we set three transects spaced 10 m apart and perpendicular to shore that extended to 1.5–2 m depths. Along each transect, we collected habitat data at 0.5-m, 1-m, and between 1.5-m and 2-m depth contours. Using a 1-m^2 quadrat we visually estimated percentages of submerged macrophyte cover and biovolume, sediment size classes (e.g., silt, sand, gravel, pebble, cobble, boulder), and leaf litter cover. We summed the gravel, pebble, and cobble sediment size-class proportions per quadrat to create an aggregate coarse sediment variable to attain more non-zero data for analysis.

For sites sampled in 2014 (n=15), we collected triplicate samples of the top 2 cm of sediment using 50 mL falcon tubes adjacent to a randomly selected 1-m^2 quadrat at each depth and site. Sediment samples were put on ice, kept frozen in the lab before percent organic matter content determination. Sediment was dried at 60°C for ≥24 hours, weighed, placed in a loss-on-ignition furnace for 4 h, and weighed again to determine percent organic matter content. Depth-specific samples <1 g were aggregated.

Within the 1-m^2 quadrat, we randomly placed a 0.25-m^2 quadrat, harvested the above-ground portion of macrophytes within the smaller quadrat, and brought the macrophytes to the lab for identification and biomass measurement. Macrophytes were identified to species using Crow and Hellquist (2000a, 2000b) except for *Utricularia* species and macroalgal taxa *Chara* and *Nitella,* which were left at genus. Individual macrophyte taxa were dried at 60°C for ≥ 24 hours and weighed. Quadrat-level data were averaged across transects for each depth contour per site.

We assigned macrophyte taxa to functional trait states based on morphology, longevity, amphibious capacity, fecundity, and native or nonnative status (Appendix K). Previous studies have suggested these traits are influenced by annual winter drawdown regimes (Wilcox and Meeker 1991; Cooke et al. 2005) and other water level fluctuation disturbances (Willby et al. 2000; Arthaud et al. 2012). Taxa were assigned morphology states (i.e., erect-caulescent, low-growth caulescent, low rosette, mat-former) based on leaf arrangement and general plant height following nomenclature from Wilcox and Meeker (1991) and Meeker et al. (2017). Longevity was categorized into perennial and annual taxa, along with perennials and annuals that possess storage organs (e.g., dormant buds in annuals, see Grime et al. 1990; Willby et al. 2000; Combroux et al. 2001; Hill et al. 2004; Capers et al. 2010; Arthaud et al. 2012). We divided taxa as amphibious or not following Willby et al. (2000); we expect amphibious taxa to be more tolerant of drawdown exposure. Lastly, fecundity was based on the number of reproductive organs (low <10, medium = 10-100, high = 100-1000 year^{-1} individual^{-1}) and divided by mode of reproduction as only seeds or as seeds and vegetative propagules following Willby et al. (2000) and Arthaud et al. (2012). We expect annuals and/or taxa with high reproductive output or multiple propagation strategies to be more tolerant of winter drawdowns. Species native status was determined using the PLANTS database (https://plants.sc.egov.usda.gov/java/index.jsp, last accessed 2019-05-16) and GoBotany databases (https://gobotany.nativeplanttrust.org/, last accessed 2019-05-16). If we could not locate trait information for taxa, we used descriptions from taxonomic keys (e.g., Hellquist and Crow 2000; PLANTS database).

Water Quality

We sampled water quality and determined secchi depth at the deepest part of each lake for two years between 2014 and 2017. In June, July, and/or August we collected surface water samples for total phosphorous (TP), total nitrogen (TN), alkalinity, and dissolved organic carbon (DOC) and were analyzed at the University of New Hampshire Water Quality Analysis Laboratory. TP and TN were directly sampled with acid-washed polyethylene bottles, frozen, and analyzed through alkaline persulfate digestion followed by colorimetric measurement for PO_4 and NO_3, respectively (Patton and Kryskalla 2003). Water samples for alkalinity and DOC were filtered through a pre-ashed microfiber glass filter, put on ice, cooled and kept frozen respectively. DOC was measured using US EPA (1979) with high temperature catalytic oxidation and alkalinity using the inflection point titration method.

Chlorophyll-*a* was filtered using a pre-combusted microfiber glass filter, put on ice, and kept frozen for < 2 weeks before processing at the University of Massachusetts Amherst. We followed EPA method 445.0 in vitro determination of chlorophyll-*a* by fluorescence. Briefly, chlorophyll was extracted from the filters using 90% acetone with 18-24 hours of extraction time. Extracted chlorophyll was measured using an *Aqua*Fluor fluorometer (Model 8000-010; Turner Designs, Sunnyvale, CA, USA) and then acidified using hydrochloric acid to determine chlorophyll-*b*. Chlorophyll-*b* values were back-calculated to determine chlorophyll-*a* concentration in the original sample volume (Arar and Collins 1997).

Lakeshore Development, Herbicide Use, and Fetch

At the lake-level, we used the 2011–2014 MassGIS Building Structures (2-D) data layer to estimate shoreline residential density as the number of buildings within a 100-m buffer around the shoreline. At the site level, we estimated effective fetch following methods from Häkanson and Jansson (1983) and Cyr et al. (2017). Over-water distances were measured in ArcGIS 10.3.1. Wind speeds and directions were taken from the United States National Oceanic and Atmospheric Administration using daily wind from Orange Municipal Airport, MA (USW00054756) running from 1998–2017. Our study lakes variably undergo herbicide application for nuisance macrophyte species during spring and summer seasons (Table 4.1). We assigned the presence or absence of herbicide application over the past two years for each site within each lake using annual herbicide use reported to the Massachusetts Department of Environmental Protection.

Lake Hydrology

We continuously monitored water levels for each lake from September/October of 2014 or 2015 to December 2017. We installed paired non-vented pressure transducers (Onset HOBO U20L-01, Bourne, MA, USA) at the point of outflow underwater and above water on shore and were both set to record at 2-h intervals. Paired pressure measurements were converted to water levels using HOBOWarePro (version 3.7.8, Onset Computer Corporation, Bourne, MA, USA). To calculate drawdown magnitude, we first isolated drawdown events using daily means by identifying the drawdown initiation date as the first record of consistent water level decline in the fall (i.e., October–November) and drawdown end date as the first record reaching pre-defined summer pool levels in winter-spring (i.e., drawdown end in January–June). We identified summer pool levels (i.e., drawdown refill target) as the median water level from non-drawdown phases in 2015 (n=15) or from spillway elevations (n=6). We determined drawdown magnitude as the lowest water level during drawdown relative to summer pool levels and used the average from the 2–3 drawdown events per lake for analyses.

Statistical Analyses

We analyzed habitat response variables (macrophyte biomass, macrophyte biovolume, silt-sized sediment, coarse-sized sediment, percent organic matter, coarse wood abundance, coarse wood complexity) using generalized linear mixed models to fit various probability distributions and account for non-independence inherent in our nested study design (Supplementary Table 4.2, Bolker et al. 2009; Zuur et al. 2009). Macrophyte biomass did not fit a normal (Shapiro-Wilk, W=0.41, $p < 0.001$) or log-normal error distribution (Shapiro-Wilk, W=0.95, $p < 0.001$), hence we used a gamma distribution with a log link and transformed the data using $x + 0.001$ g to elevate zero-values. We modeled percent sediment organic matter, macrophyte biovolume, and sediment size proportional data using a beta error distribution with a logit link, and applied the transformation derived from Smithson and Verkuilen (2006) to meet beta error distribution range values between 0 and 1 exclusive. We modeled site total coarse wood abundance and branching complexity count data by applying a negative binomial error distribution with a log link and an offset of coarse wood abundance for branching complexity counts.

We anticipated habitat responses to covary by sample depth along our drawdown magnitude gradient (Table 4.1), because of variable drawdown exposure and independent effects of depth on habitat. Thus, contour-level habitat response variables (i.e., all except coarse wood variables) were modeled with a drawdown magnitude-depth interaction, other potential environmental covariates, and lake as a random intercept (Appendix L). Since sediment organic matter was sampled in a subset of lakes (n=15) and can potentially influence macrophytes, we also developed a separate set of models for macrophyte biomass and biovolume with organic matter as a predictor. We also applied generalized linear mixed models to each macrophyte trait state with sufficient nonzero values across the drawdown magnitude gradient using the same predictor structure as macrophyte biomass and biovolume models. Models were not applied to annuals with storage organs (longevity), moderate and high numbers of reproductive organs with seeds only (fecundity), mat-former and low rosette (morphotype), and for non-native taxa (status). For coarse wood abundance and branching complexity, we tested an interaction between drawdown magnitude and shoreline type (e.g., forested/developed).

We started with full predictor sets (Appendix L) of known covariates that could affect habitat response variables and iteratively removed single non-significant ($p > 0.05$) predictors using Chi-square tests to simplify models and isolate important predictors. All continuous variables were Z-scored transformed before analyses. We checked for covariate collinearity using scatterplot matrices (e.g., Pearson $r < 0.7$) for continuous predictors, and generalized inflation factors (e.g., GVIF < 3) among continuous and categorical covariates using the car package in R (Fox and Weisberg 2011, version 2.1-5). We found secchi depth was strongly correlated with DOC ($r = -0.76$) and chlorophyll-*a* ($r = -0.70$), and consequently included only secchi depth in our models. We compared models using corrected Akaike Information Criterion (AIC_c) to determine the most parsimonious and plausible models for each habitat response variable (Burnham and Anderson 2004). Models were validated by examination of residual plots at predictor and model levels to ensure no patterns existed. We generated all regression models using the glmmTMB package (Brooks et al., 2017, version 0.2.1.0) performed in R (R Core Team, 2017, version 3.4.2).

We used non-metric multidimensional scaling ordination (NMDS) to assess potential relationships between macrophyte taxa composition, macrophyte traits, and environmental variables. We used contour-level, taxon-specific biomass data at 0.5-m and 1-m depths yielding 84 samples (i.e., 21 lakes, 2 sites/lake, 2 contours/site) with nonzero biomass. Before analysis, we first dropped rare taxa with fewer than five observations (n=20) and sites with no macrophyte biomass (n=10), and subsequently performed site row total standardization on the site by macrophyte taxa biomass matrix with the remaining 21 taxa (McCune and Grace 2002). We used Bray-Curtis dissimilarities in our NMDS to represent taxa dissimilarity across sites (Bray and Curtis 1957). We examined a scree-plot of stress with up to 5 NMDS axes and found a 3-axis solution provided a stress level (<0.15) after 20 random starts suggesting an interpretable result (Clarke 1993). We fit environmental variables (e.g., drawdown magnitude, secchi depth, alkalinity, shoreline type, coarse substrate, TP, herbicide use, and depth) and macrophyte traits based on biomass relative abundance (e.g., longevity, amphibiousness, native/nonnative, morphotype, fecundity) to the NMDS ordination solution using a permutation test (permutations=1000). NMDS and permutation tests were conducted using the vegan package (Oksanen et al. 2019, version 2.5-3) in R.

Results

Our stratified random lake selection captured a gradient of drawdown magnitude (0.07–2.26 m) and shoreline residential density (97.7–525.2 buildings km^{-2}; Table 4.1). Lakes also ranged in secchi depth (1.2–6.5 m), alkalinity (1.9–141.3 mg $CaCO_3$ L^{-1}), and total phosphorous (1.7–24.9 μg L^{-1}; Table 4.1). Most lakes (n = 15 of 21) had a history of herbicide use. These water quality gradients and herbicide categorization were not collinear with the drawdown magnitude gradient.

Coarse Wood

We found coarse wood at 20 of 21 forested sites and at 14 of 21 developed sites. There was significantly less coarse wood along developed shorelines (2.3 pieces ± 2.3) compared to forested shorelines (15.9 pieces ± 12.4, $\beta = -1.87$, SE = 0.27, $p < 0.001$;

Figure 4.2A, Table 4.2). Additionally, we found a negative correlation between coarse wood abundance and bed slope (β = -0.30, SE = 0.14, p = 0.027). We found no effect of drawdown magnitude on coarse wood abundance (β = 0.095, SE = 0.17, p = 0.510).

Simple branching complexities dominated our coarse wood samples across forested and developed sites (>71.8% had complexity ≤ 5, n=383). After accounting for coarse wood abundance, we found wood had less complexity along developed shorelines than forested shorelines (β = -0.87, SE = 0.39, p = 0.025; Figure 4.2B, Table 4.2). Surprisingly, we also found a positive effect of whole lake residential density on wood complexity (β = 0.63, SE = 0.22, p <0.001). Drawdown magnitude showed a marginally nonsignificant positive trend with wood complexity (β = 0.38, SE = 0.23, p =0.099); however, this trend was driven by a forested site at the lake with the deepest drawdowns (Otis) that had extremely high wood complexity.

Sediment

Silt and coarse sediment proportions were moderately correlated with each other (Pearson-r = -0.61) and this was reflected with similar predictor sets in our models (Table 4.2). Depth was significantly correlated with both silt and coarse substrate whereby silt increased with depth and coarse particles decreased with depth. Silt proportion was best explained by an interaction between depth and drawdown magnitude (Table 4.3), whereby silt cover significantly decreased with drawdown magnitude at the 0.5-m depth (Figure 4.3A). The top model for silt also included bed slope (steeper slopes had less silt), and shoreline type (less silt in developed than forested sites) was included as a predictor in the next plausible model (Table 4.2). Coarse substrate was best predicted by the drawdown magnitude-depth interaction (Table 4.2), whereby coarse substrate significantly increased with magnitude at 0.5-m and 1-m depths, with this effect waning with increased depth (Figure 4.4.3B, Table 4.3). Organic matter content was significantly lower along developed shorelines and steeper slopes (Table 4.3). Drawdown magnitude showed nonsignificant negative effects on organic matter content (Figure 4.3C), and this effect was strongest at the 0.5-m and >1-m depth contours.

Macrophyte Biomass and Biovolume

Macrophyte biomass varied by 2–3 orders of magnitude, with mean biomass ranging from 0.17–73.44 g among lakes. The top model included a drawdown magnitude-depth interaction, coarse substrate, alkalinity, and secchi depth. Models with the addition of shoreline type (developed/forested) and slope as predictors were also equally plausible models (i.e., $< 2\ \Delta\mathrm{AIC_c}$; Table 4.2). We found a negative correlation of drawdown magnitude on macrophyte biomass and the strength of this effect varied by depth (Figure 4.4A). At the 1-m depth, drawdown magnitude showed a significant negative effect on biomass, while magnitude showed nonsignificant negative effects at 0.5-m and >1-m depths (Table 4.3). Secchi depth and alkalinity had significant positive effects on macrophyte biomass, while coarse substrate was negatively correlated with macrophyte biomass (Table 4.3). The addition of organic matter as a predictor within a subset of lakes did not affect our interpretation on effects of winter drawdowns but had a significant negative effect on biomass ($\beta = -0.52$, SE = 0.23, $p = 0.021$).

Macrophyte biovolume also varied, ranging from 1.1–34% among lakes. The top biovolume model was similar to biomass (i.e., included a drawdown magnitude-depth interaction, coarse substrate, alkalinity, and secchi depth) with the addition of shoreline type, whereby biovolume was lower along developed shorelines (9.1% ± 14) than forested shorelines (16 % ± 16, Figure 4.4B). Other plausible models included a negative effect of TP (Table 4.2). As with macrophyte biomass, drawdown magnitude had a negative effect on macrophyte biovolume (Figure 4.4B), which was significant at the 1-m depth and nonsignificant at 0.5-m and >1-m depths (Table 4.3).

Macrophyte Taxa and Trait Composition

Univariate response models for macrophyte traits showed variable responses to drawdown magnitude. For longevity traits, drawdown magnitude had no effect on perennials at 0.5-m depths but showed a marginally insignificant negative correlation at the 1-m depth (Appendix M). Also, the proportion of perennials were lower at 1-m compared to 0.5-m depths. In contrast to perennials, drawdown magnitude was positively correlated with annuals at 0.5-m and 1-m depths, with a stronger effect at the 1-m depth. Further, the proportion of annuals was higher at 1-m vs 0.5-m depths and was positively correlated with alkalinity and herbicide use. Fecundity trait and morphotype proportions were not significantly correlated with drawdown magnitude or a drawdown magnitude-depth interaction (Appendix M). We found significantly lower proportions of the erect caulescent morphotype at the 1-m depth compared to the 0.5-m depth and found the converse for low caulescents. The proportion of amphibious taxa was positively correlated with drawdown magnitude at the 0.5-m depth (Appendix M). Additionally, we found higher amphibious proportions at 0.5-m compared to 1-m depths, and with higher alkalinity, higher effective fetch, with less coarse substrate, and the absence of herbicide use (Appendix M).

Macrophyte taxa composition varied among the 21 lakes (Figure 4.5). We achieved a stress level =0.107 after 20 random starts with a 3-axis NMDS solution.

Among the environmental covariates, drawdown magnitude, coarse substrate, alkalinity, secchi, and herbicide use were significantly correlated to NMDS axes (Table 4.4). The drawdown magnitude vector positively aligned with *Najas* species (*N. minor*, *N. flexilis*) and the macroalga genus *Chara*, and roughly corresponds to the low caulescent morphotype, annuals with seeds-only longevity strategy, and nonnative species on Axis 2 (Figure 4.5). Sites with higher alkalinities and secchi depths corresponded with higher proportions of *Chara*, *Myriophyllum spicatum*, and *Vallisneria americana*. In contrast, species such as *Nymphaea odorata*, *Brasenia schreberi*, *Potamogeton bicupulatus*, and the macroalga *Nitella* genus were typically of lower alkalinity and secchi sites (Figure 4.5A). Sites with higher alkalinities and secchi depths were also associated with the absence of herbicide use. Numerous macrophyte traits were significantly correlated with NMDS axes, including: species native status, amphibiousness, all longevity trait states, three morphotypes (low and high caulescent, and low rosettes), and medium to high reproduction output of seed and seed + vegetative reproduction modes (Table 4.4; Figure 4.5B&D).

Discussion

We provide evidence that annual winter drawdowns alter littoral zone physical habitat even at relatively mild magnitudes of < 2 m. At depths within drawdown exposure zones (i.e., ≤1 m), we found significant changes in sediment texture, macrophyte abundance, and macrophyte taxonomic and functional composition as a function of drawdown magnitude. Concordantly, at unexposed depths (i.e., > 1 m), drawdown magnitude was not correlated with physical habitat components, suggesting that impacts from winter drawdowns correspond with the depth of exposure. Drawdown magnitude poorly explained coarse wood abundance and complexity variability; instead, coarse wood abundance and complexity was greatly reduced at developed shorelines compared to forested shorelines, demonstrating distinct effects of different anthropogenic activities on littoral zone habitat.

Winter drawdown effects on littoral habitat

Winter drawdowns coarsened sediment with associated reductions in silt cover and organic matter content at depths within exposure zones. These patterns are consistent with previous winter drawdown studies (Wagner and Falter 2002; Cooley and Franzin 2008) and other water level fluctuation regimes (Evtimova and Donohue 2015) that suggest accelerated sediment focusing from exposure zones to depths below water level minimums. As water levels decline, fine sediment at depths typically protected from wave action at normal water levels become susceptible to resuspension and are transported to deeper depths (Effler et al. 1998; Dirnberger and Weinberger 2005). Furthermore, water column mixing likely temporally overlaps with water levels recession from drawdowns in October to December, which may enhance sediment focusing (Effler and Matthews 2004). Ultimately, the likely interaction between annual drawdowns conducted for several decades and short-term high wind/wave events (Hofmann et al. 2008) has coarsened exposure zones (Hall et al. 1999; Furey et al. 2004).

We found annual winter drawdowns affect the abundance, taxonomic, and functional composition of submerged macrophytes in drawdown exposure zones. Consistent with previous winter drawdown studies (Siver et al. 1986; Turner et al. 2005; Olson et al. 2012), measures of macrophyte abundance (e.g., biomass and biovolume) were negatively correlated with drawdown magnitude, particularly at the 1-m depth. Drawdowns did not affect macrophyte abundance at depths >1 m, presumably because they are rarely exposed during drawdown, and at the 0.5-m depth because other environmental factors (e.g., ice erosion, Renman 1989; Hellsten 1997), may be more important at shallow depths. The correlations between drawdown magnitude, coarse substrate, and macrophyte biomass suggest winter drawdowns reduce macrophytes directly through exposure to winter conditions, and indirectly through sediment coarsening over time. Wagner and Falter (2002) similarly found significantly lower macrophyte biomass on cobble substrate, which existed at higher frequencies in shallow-exposed depths in an annual winter drawdown lake. Macrophyte abundance tends to decrease with increasing sediment particle size (Anderson and Kalff 1988) because of low nutrient diffusion rates and nutrient capacity (Barko and Smart 1986), and its association with relatively high wind/wave energy and steeper littoral slopes (Duarte and Kalff 1986; Cyr 1998). Furthermore, winter drawdowns may decouple positive feedbacks between macrophyte beds, fine sediment accretion, and erosional reduction (Barko and James 1998), and enable sediment coarsening and further macrophyte reduction over time.

Taxa that appeared to be sensitive to winter drawdowns were *Nymphaea odorata, Brasenia schreberi,* and *Potamogeton robbinsii*. Previous studies have also shown declines of *B. schreberi* (Beard 1973; Richardson 1975) and *P. robbinsii* (Beard 1973; Nichols 1975; Crosson 1990) associated with winter drawdowns. These species are perennial taxa that primarily propagate via vegetative structures (e.g., rhizomes), which have been hypothesized to be sensitive to desiccation, freezing, and erosional disturbance related to winter drawdown (Rørslett 1989; Wagner and Falter 2002). Accordingly, we found a decline in perennial taxa, particularly at the 1-m depth. We found proportionally more perennials at the 0.5-m depth compared to 1-m depth and no effect of drawdowns at 0.5 m, suggesting that perennial taxa are variably susceptible to winter drawdown disturbance. Perennial taxa have plastic and variable propagation strategies (Barrat-Segretain et al. 1998; Combroux and Bornette 2004), high niche breadth (Alahuhta et al. 2017), and ability to colonize exposure zones late in the growing season (August-September). Furthermore, the inter-annual variability of drawdown exposure weather conditions (e.g., freezing temperatures, snowfall) could permit variable rhizome survival (Lonergan et al. 2014).

Winter drawdowns can select for drawdown-tolerant macrophyte assemblages (Siver et al. 1986; Richardson et al. 2002). Where macrophytes were present, several taxa were positively associated with drawdown magnitude. Consistent with other studies, we found positive associations of *N. flexilis* (Beard 1973; Nichols 1975; Tazik et al. 1982; Crosson 1990; Turner et al. 2005) and *N. minor* (Siver et al. 1986), and the macroalgae *Chara* (Wagner and Falter 2002) with drawdown magnitude. These taxa generally possess an annual longevity strategy that are largely dependent on sexual diaspores in the form of seeds (*Najas* species) or oospores (*Chara*). Concordantly, drawdown magnitude was positively related to annuals at exposed depths, consistent with ruderal life history strategies (Grime 1977; Rørslett 1989). We also found a positive, albeit weak correlation between amphibious taxa (*Gratiola aurea*, *Sagitarria*, *Elatine minima*) and drawdown magnitude at the 0.5-m depth, aligning with previous work (Rørslett 1989), although effects may be stronger under deeper drawdown magnitudes.

Several macrophyte traits were unrelated to drawdown magnitude. We observed no correlation between drawdown magnitude and taxa with moderate to high fecundity levels that produce both seeds and vegetative propagules, a finding consistent with Arthaud et al. (2012), suggesting several reproductive strategies may enable a taxa's persistence in annual drawdown regimes. We also found no distinct trends among macrophyte morphologies and drawdown magnitude. Previous studies found increases in mat-forming and low-rosette taxa with drawdowns (Wilcox and Meeker 1991); however, our dataset was insufficient to assess changes in these morphologies because of low sample sizes. Wilcox and Meeker (1991) also found declines in low and erect-caulescents with drawdowns; the lack of a relationship in our study may be explained by our relatively mild amplitudes in combination with co-occurring alkalinity and secchi gradients.

Lakeshore development effects on littoral habitat

We found lower coarse wood densities and branching complexity along developed shoreline sites compared to forested shorelines, supporting previous studies at similar spatial scales (Christensen et al. 1996; Jennings et al. 2003; Francis and Schindler 2006; Merrell et al. 2009). Coarse wood density in the littoral zone is largely a function of riparian tree density (Christensen et al. 1996, Francis and Schindler 2006) or riparian snags (Marburg et al. 2006). As such, lake riparian deforestation by humans restricts coarse wood recruitment to littoral zones. Additionally, humans directly remove coarse wood from littoral zones along adjacent shorelines (Francis and Schindler 2006). Wood density at forested sites showed more variation among lakes than developed sites suggesting other environmental factors (i.e., historical disturbance regime, riparian tree composition (Marburg et al. 2006; Francis and Schindler 2006) and beaver activity (France 1997) not included in this study may help to explain wood densities. As found in Newbrey et al. (2005), most of the coarse wood in our study had simple branching complexities across all sites. Lower structural complexity along developed shorelines compared to forested sites may be due recreational driven processes such as wave erosion from motorboats, physical removal of branches for firewood, or to reduce angling interference (Newbrey et al. 2005).

We observed reduced sediment organic matter along developed shorelines compared to more forested shorelines, supporting previous work estimated at the whole-lake scale (Francis et al. 2007). Loss of shoreline forest cover may decrease leaf-litter input to littoral zones, particularly in Southern New England where deciduous forests are dominant. Additionally, the reduction of coarse wood in littoral zones associated with lakeshore development may lessen organic matter retention particularly at shallower depths (Francis et al. 2007). This also supports the negative effect of developed shoreline sites on silt cover. Consequently, existing organic matter may be transported to deeper depths via erosional forces from wave action and drawdown, which matches previously reported depth distributions associated with lakeshore development (Francis et al. 2007).

Lakeshore development can impact macrophyte assemblages (Cheruvelil and Soranno 2008). Emergent and floating-leaf macrophytes generally decline along developed shorelines and with increasing whole-lake residential development; however, submerged taxa may increase (Hicks and Frost 2011) or display no response to shoreline disturbance (Radomski and Goeman 2001; Jennings et al. 2003; Dustin and Vondracek 2017). Submergent taxa were the dominant growth form and we detected emergent and floating-leaf taxa in only 5% and 17% of our sampling quadrats respectively. Despite the dominance of submerged taxa, we found lower macrophyte biovolume along developed vs. forested shorelines at the 1-m depth and a lesser effect at the 0.5-m contour. This likely corresponds to less floating-leaved taxa and tall-growing submerged taxa in our study. Macrophytes are directly removed (Asplund and Cook 1997; Radomski and Goeman 2001) via management strategies (e.g., hand-pulling, herbicide, mechanical harvesting) to facilitate recreational activities, particularly in front of active lakefront property (Payton and Fulton 2004).

Effects of water quality and herbicide use on littoral habitat

Water quality factors also influenced macrophyte composition and total abundance metrics. Macrophyte biomass and biovolume were positively correlated with alkalinity. The biomass-alkalinity trend supports previous observations (Duarte and Kalff 1990) and the positive correlation between biovolume and alkalinity may result from relatively short species (e.g., isoetids) associated with low alkaline lakes along with higher biomass in more alkaline lakes. Alkalinity is a major environmental factor controlling macrophyte species composition (Roberts et al. 1985; Vestergaard and Sand-Jensen 2000a; Alexander et al. 2008) because of its tight correlation with bicarbonate (HCO_3^-) concentrations that can be variably used as a carbon source for different macrophyte species (Madsen and Sand-Jensen 1991). Higher alkaline lakes tend to support more macrophyte species (Roberts et al. 1985) composed predominantly of the more species-rich elodeids and charophytes compared to soft-water lakes with more isoetids (Vestergaard and Sand-Jensen 2000b). We observed *Chara, P. pusillus, Vallisneria americana, and Myriophyllum spicatum* associated with moderate to high alkaline conditions and *Nitella, N. odorata, B. schreberi, Isoetes, Utricularia*, and *Potamogeton bicupulatus* associated with low alkalinities, which is consistent with previous studies (Alexander et al. 2008; Capers et al. 2010). Further, annual taxa were positively related to alkalinity, which likely derives from increased abundances of *Chara* beds in more alkaline conditions.

Water transparency directly influences the amount of colonizable area for macrophytes where increases in clarity allows for deeper macrophyte colonization (Chambers and Kalff 1985; Duarte and Kalff 1990; Vestergaard and Sand-Jensen 2000b) and increases in macrophyte biomass and cover (Barko et al. 1982; Cheruvelil and Soranno 2008). Low-lying species can persist at deeper depths in high clarity conditions (e.g., *Isoestes*, Mjelde et al. 2012), as we found for proportions of low-caulescent taxa. Although the effect of water clarity on abundance is typically more important at deeper depths (>2m, Duarte and Kalff 1990), we were able to detect an effect because several lakes exhibited relatively low clarity (e.g., <2 m visibility). In our study, secchi depth was negatively correlated with DOC and chlorophyll-*a*, which influence water transparency (Canfield and Hodgson 1983; Brezonik et al. 2019). Although the importance of specific drivers of water clarity variability is lake-specific, high chlorophyll-*a* concentrations (Kissoon et al. 2013) or DOC (McElarney et al. 2010) can limit depth range distributions and growth of submerged macrophytes.

Herbicide use also structured macrophyte taxa composition. Herbicide use tended to be absent from lakes with relatively higher alkalinity and secchi depths, which included taxa associated with these water chemistry conditions including the nonnative invasive species *M. spicatum*. Interestingly, annual taxa were positively correlated with herbicide use. Annual taxa emerging from seed banks may become relatively abundant in the following growing season after targeted taxa are treated (Hussner et al. 2017).

Implications for littoral habitat management

A primary reason for the implementation of annual winter drawdowns is to reduce nuisance densities of aquatic vegetation that inhibit recreational activities (Cooke et al. 2005). Our results show that drawdowns can partially meet this objective, as we observed a general decrease in macrophyte biomass and biovolume at depths exposed during drawdown across various ambient water quality conditions. However, macrophytes are not completely lost from exposure zones and considerable variability exists among lakes. Macrophytes can recolonize into exposure zones after a drawdown via seed banks or vegetative propagules from macrophytes at deeper unexposed depths and eventually resulting in a drawdown-tolerant macrophyte assemblage (e.g., Turner et al 2005). Species that can rapidly colonize exposure zones upon refill are at an advantage over slow-growing species and can include potentially invasive species (Crosson 1990). The widespread invasive Eurasian milfoil (*M. spicatum*) is a frequent target of winter drawdowns, and we found relatively low biomass of *M. spicatum* in drawdown-exposed areas of 4 lakes, consistent with previous studies (Lonergan et al. 2014). This suggests drawdown can limit but not eliminate this species probably because of specific freezing and/or drying threshold conditions needed to prevent regrowth (Lonergan et al. 2014) and the ease of dispersal via fragmentation from unimpacted, deeper depths. Other invasive species tolerant to drawdown conditions, such as *N. minor*, may proliferate in drawdown exposure zones. After declines of *M. spicatum* from two winter drawdowns, Siver et al. (1986) observed increases in *N. minor* and *N. flexilis* in exposure zones in a Connecticut lake. Often, other macrophyte management strategies (e.g., herbicide application) are needed to supplement winter drawdowns to sufficiently control or eradicate target species over longer time periods (Cooke et al. 2005).

Our data suggests macrophyte responses to drawdown magnitude are likely modified by the environmental context in littoral zones and lakes. Winter drawdown regimes may impact macrophytes relatively more in littoral zones with low water clarity or low alkalinity than under high alkaline or high water clarity conditions where macrophyte colonization and biomass production can be extensive. Furthermore, lakes with high clarity or alkalinity may have a higher probability to develop a drawdown-tolerant macrophyte assemblage because of a richer species pool (Vestergaard and Sand-Jensen 2000b). Therefore, applying an equal drawdown magnitude across lakes with varying water quality conditions will have varying macrophyte impacts. Identification of winter drawdown tolerant and sensitive taxa associated with different water quality conditions will require macrophyte surveys across many lakes within lake water quality classifications as seen in Mjelde et al. (2012) with oligotrophic and low alkaline lakes.

This study also identified the importance of maintaining forested shorelines within developed lakes to provide coarse wood habitat and retain sediment organic matter. These habitats provide numerous lake ecosystem functions including refuge and spawning habitat for invertebrates and fish, increased abundance and diversity of invertebrates and fish, and mediation of food web dynamics among others (reviewed by Czarnecka 2016). Recreational-driven processes such as wave erosion from motorboats and physical removal of branches for firewood, reduce angling interference, or maintain valued aesthetics may accelerate rates of branching complexity loss (Newbrey et al.

2005). Management to reduce these activities may be beneficial to lake ecosystem function.

Conclusion

Multiple anthropogenic stressors degrade littoral zone habitat structure important for littoral zone biota (Miranda et al. 2010). In recreational lakes of Massachusetts, annual winter water-level regimes, lakeshore development, and herbicide application impact physical habitat through changes in littoral zone sediments, macrophyte assemblages, and coarse wood. Drawdown impacts are depth-specific and observed even at relatively mild drawdown magnitudes. Additionally, the variable state of macrophyte assemblages (i.e., tolerant taxa) in exposure zones suggests the importance of environmental context (e.g., water quality, spatial dynamics) at lake- and watershed-levels (e.g., land use) as seen in larger studies (e.g., Sass et al. 2010). Incorporating lake-specific, ambient environmental conditions into winter drawdown management will help to improve implementation of winter drawdowns while conserving ecological integrity. The alteration and reduction of complex littoral habitat will modify predator-prey interactions (Diehl 1992; Sass et al. 2006; Kornijów et al. 2015) and shape nutrient and energy flow in lake food webs (Barko and James 1998). Climate change will likely further affect littoral zone habitat availability through changes in lake water level fluctuations. Summer drought conditions may become more frequent with climate change in the northeastern United States (Hayhoe et al. 2007) causing reductions in lake water levels and altering fish population dynamics (i.e., decreased fish growth) because of inaccessibility to critical spawning, predator refuge, and feeding habitat in littoral zones (Gaeta et al. 2014, Hardie and Chilcott 2016). Limiting further habitat loss by protecting areas of complex habitat structure (e.g., inlets, forested shorelines) in these impaired lake ecosystems will be essential to preserve current ecosystem resilience to anticipated effects of climate change on lake water levels.

Tables

Table 4.1. Study lake environmental characteristics.
NA = not applicable because these lakes have no history of annual winter drawdowns, and NK = data is not known.

Lake	Year Sampled	Decade Drawdown Implemented	Drawdown Magnitude (m)	Surface Area (km^2)	Mean/Max Depth (m)	Mean Effective Fetch	TP (µg L^{-1})	Secchi (m)	Alkalinity (CaCO$_3$ mg L^{-1})	Lakeshore Development (buildings km^{-2})	Herbicide Application
Leverett†	2014	NA	0.07	0.39	1.7/6.5	129.6	8.4	2.7	35.8	97.7	Yes
Silver	2014	2000s	0.09	0.19	1.5/2.8	69.5	11.9	1.8	23.5	348.7	Yes
Quacumquasit†	2014	NA	0.12	0.94	7.6/25.7	254.6	13.5	4.9	11.7	325.2	Yes
Congamond†	2016	NA	0.13	1.93	5.6/14.1	169.7	22.3	3.1	49.2	376.7	Yes
Buel	2016	2010s	0.21	0.83	5.1/14.4	267.5	12.9	4.3	141.3	291.6	No
Brookhaven	2014	1970s	0.32	0.14	1.5/3.8	88.5	24.9	1.2	15.5	187.7	No
Boon	2014	2000s	0.35	0.73	2.8/7.7	71.02	5.6	1.9	15.6	496.1	Yes
Watatic	2014	NK	0.36	0.56	2.0/4.6	83.3	14.1	1.3	1.9	298.9	Yes
Cranberry Meadow	2014	NK	0.40	0.30	1.5/3.0	95.1	22.6	1.9	15.6	383.0	Yes
Wyman	2014	1990s	0.48	0.87	1.6/5.4	57.5	12.5	2.6	7.0	377.7	Yes
Greenwater	2014	1950s	0.51	0.38	5.0/18.6	89.8	4.1	6.5	24.8	178.2	Yes
Wickaboag	2016	1960s	0.58	1.30	1.9/3.8	219.9	14.3	1.3	8.9	479.3	Yes
Richmond	2014	1960s	0.70	0.95	2.9/17.2	300.3	6.4	4.4	74.9	259.7	Yes
Wyola	2016	1970s	0.71	0.50	3.4/10.1	229.4	10.3	3.6	2.9	476.9	No
Hamilton	2016	1990s	0.77	1.68	1.8/6.4	222.6	1.7	1.9	8.9	525.2	Yes
Ashmere	2014	1950s	0.83	1.14	3.4/8.3	93.1	6.1	3.1	30.6	322.2	Yes
Stockbridge	2014	1980s	1.13	1.60	5.4/15.9	371.7	6.0	5.2	122.4	257.6	No
Onota	2014	1970s	1.25	2.66	4.1/24.7	291.1	10.0	5.2	72.2	237.6	Yes
Goose	2014	1920s	1.50	1.30	5.0/16.3	222.1	8.7	5.0	18.2	194.0	Yes
Garfield	2016	1970s	1.91	1.11	3.8/10.8	246.0	23.1	4.2	49.0	217.3	No
Otis	2014	1960s	2.26	4.21	4.5/17.4	182.7	4.8	3.3	9.7	289.3	No
Mean			*0.70*	*1.13*	*3.4/11.3*	*178.8*	*11.6*	*3.3*	*35.2*	*315.3*	
Minimum			*0.07*	*0.14*	*1.5/2.8*	*57.5*	*1.7*	*1.2*	*1.9*	*97.7*	
Maximum			*2.26*	*4.21*	*7.6/25.7*	*371.7*	*24.9*	*6.5*	*141.3*	*525.2*	

†Indicates non-drawdown lakes such that drawdown magnitude represents average low winter water levels.

Table 4.2. Model comparisons of top habitat models.
Summary of the top models (ΔAIC_c <2) for habitat response variables compared to random intercept of lake models or intercept-only models. K represents the number of parameters and model weights are derived from models from full predictor sets to the top model. Rand(Lake) = random intercept of lake. Predictor abbreviations are Mag = drawdown magnitude, Alka = alkalinity, Csub = coarse substrate, ShoreType = shoreline type (developed/forested), Herb = herbicide use (presence/absence), ResDens = shoreline residential density, Fetch = effective fetch, TP = total phosphorous, Secchi = secchi depth, OM = organic matter content, CWD = coarse wood abundance, Mag*Depth = magnitude–depth interaction.

Habitat Models	K	AIC_c	ΔAIC_c	Weight
Coarse Wood Abundance				
ShoreType + Slope	4	247.7	0	0.84
Intercept	2	275	27.3	<0.001
Coarse Wood Complexity				
ShoreType + Mag + ResDens	5	403.4	0	0.46
ShoreType + ResDens	4	403.8	0.4	0.38
Intercept	2	413.1	9.7	0.0036
Silt Sediment				
Mag*Depth + Slope + Rand(Lake)	9	-267.1	0	0.51
Mag*Depth + Slope + ShoreType + Rand(Lake)	10	-266.2	0.9	0.33
Rand(Lake)	3	-231.6	38.1	<0.001
Coarse Sediment				
Mag*Depth	7	-427.6	0	0.53
Rand(Lake)	3	-375.4	52.3	<0.001
Organic Matter				
Mag*Depth + ShoreType + Slope	10	-153.3	0	0.70
Rand(Lake)	3	-131.7	21.5	<0.001
Macrophyte Biomass				
Mag*Depth + Alka + Secchi + Csub + Rand(Lake)	11	627.8	0	0.36
Mag*Depth + Alka + Secchi + Csub + ShoreType + Rand(Lake)	12	628	0.2	0.33
Mag*Depth + Alka + Secchi + Csub + ShoreType + Slope + Rand(Lake)	13	629.1	1.3	0.19
Rand(Lake)	3	654.9	27.1	<0.001
Macrophyte Biovolume				
Mag*Depth + Alka + Secchi + Csub + ShoreType +Rand(Lake)	12	-284.1	0	0.56
Mag*Depth + Alka + Secchi + Csub + ShoreType + TP + Rand(Lake)	13	-282.8	1.3	0.29
Rand(Lake)	3	-265.9	22.3	<0.001

Table 4.3. Parameter estimates of top habitat models.

Top habitat response models for macrophytes and substrate size classes that include a drawdown-depth interaction. Model terms include estimates (β) for drawdown magnitude at 0.5m, 1m, and >1m depths (subscripted), depth contrasts (0.5 m, 1 m, >1 m), drawdown magnitude-depth slope contrasts (i.e., interactions), and other environmental covariates (subscripted). Other environmental covariates include Secchi = secchi depth, Alka = alkalinity, Csub = coarse substrate, Slope = bed slope, Dev-For = developed – forested shorelines, and a random intercept of lake ($\mathrm{RandI}_{\mathrm{Lake}}$). Absence of a random lake intercept indicates a negligible variance term (e.g., <0.001). Associated standard errors for estimates are in parentheses. Bolded values indicate a significant correlation at $p = 0.05$.

Habitat Response	Drawdown Magnitude		Depth		Drawdown Magnitude*Depth		Other Covariates	
Sediment Size	β	*p*	β	*p*	β	*p*	β	*p*
Silt	**$\beta_{0.5m}$ = -0.52(0.23)**	**0.024**	**$\beta_{1\text{-}0.5m}$ = 0.73(0.26)**	**0.005**	$\beta_{1\text{-}0.5m}$ = 0.32(0.27)	0.236	**β_{Slope} = -0.28(0.13)**	**0.037**
	β_{1m} = -0.20(0.21)	0.364	**$\beta_{>1\text{-}0.5m}$ = 1.80(0.31)**	**< 0.001**	$\beta_{>1\text{-}0.5m}$ = 0.32(0.27)	0.229	$\mathrm{RandI}_{\mathrm{Lake}}$ = 0.29	
	$\beta_{>1m}$ = -0.19(0.23)	0.398	**$\beta_{>1\text{-}1m}$ = 1.07(0.28)**	**< 0.001**	$\beta_{>1\text{-}1m}$ = 0.0084(0.27)	0.975		
Coarse	**$\beta_{0.5m}$ = 0.81(0.14)**	**<0.001**	**$\beta_{1\text{-}0.5m}$ = -0.92(0.21)**	**< 0.001**	$\beta_{1\text{-}0.5m}$ = -0.25(0.20)	0.209		
	β_{1m} = 0.56(0.15)	**<0.001**	**$\beta_{>1\text{-}0.5m}$ = -1.37(0.22)**	**< 0.001**	**$\beta_{>1\text{-}0.5m}$ = -0.86(0.21)**	**< 0.001**		
	$\beta_{>1m}$ = -0.056(0.16)	0.722	**$\beta_{>1\text{-}1m}$ = -0.45(0.22)**	**0.039**	**$\beta_{>1\text{-}1m}$ = -0.61(0.22)**	**0.005**		
Organic Matter	$\beta_{0.5m}$ = -0.39(0.25)	0.115	$\beta_{1\text{-}0.5m}$ = 0.30(0.25)	0.222	$\beta_{1\text{-}0.5m}$ = 0.31(0.27)	0.250	**$\beta_{Dev\text{-}For}$= -0.67(0.21)**	**0.001**
	β_{1m} = -0.075(0.22)	0.740	**$\beta_{>1\text{-}0.5m}$ = 1.13(0.25)**	**< 0.001**	$\beta_{>1\text{-}0.5m}$ = 0.015(0.25)	0.949	**β_{Slope} = -0.27(0.13)**	**0.038**
	$\beta_{>1m}$ = -0.37(0.20)	0.067	**$\beta_{>1\text{-}1m}$ = 0.83(0.24)**	**< 0.001**	$\beta_{>1\text{-}1m}$ = -0.30(0.23)	0.204	$\mathrm{RandI}_{\mathrm{Lake}}$ = 0.27	
Macrophytes								
Biomass	$\beta_{0.5m}$ = -0.33(0.28)	0.234	$\beta_{1\text{-}0.5m}$ = -0.22(0.42)	0.599	**$\beta_{1\text{-}0.5m}$ = -0.89(0.38)**	**0.019**	**β_{Secchi} = 0.59(0.25)**	**0.017**
	β_{1m} = -1.22(0.33)	**< 0.001**	$\beta_{>1\text{-}0.5m}$ = 0.28(0.44)	0.519	$\beta_{>1\text{-}0.5m}$ = 0.023(0.36)	0.949	**β_{Alka} = 0.68(0.22)**	**0.002**
	$\beta_{>1m}$ = -0.31 (0.28)	0.263	$\beta_{>1\text{-}1m}$ = 0.50 (0.34)	0.143	**$\beta_{>1\text{-}1m}$ = 0.92 (0.36)**	**0.011**	**β_{Csub} = -0.75(0.21)**	**< 0.001**
							$\mathrm{RandI}_{\mathrm{Lake}}$ = 0.30	
Biovolume	$\beta_{0.5m}$ = -0.33(0.20)	0.104	$\beta_{1\text{-}0.5m}$ = 0.21(0.21)	0.300	$\beta_{1\text{-}0.5m}$ = -0.19(0.23)	0.414	**β_{Secchi} = 0.27(0.12)**	**0.025**
	β_{1m} = -0.52(0.18)	**0.003**	$\beta_{>1\text{-}0.5m}$ = -0.014(0.23)	0.950	$\beta_{>1\text{-}0.5m}$ = 0.18(0.23)	0.436	β_{Alka} = 0.21(0.11)	0.057
	$\beta_{>1m}$ = -0.15(0.17)	0.295	$\beta_{>1\text{-}1m}$ = -0.23 (0.19)	0.219	$\beta_{>1\text{-}1m}$ = 0.37(0.20)	0.069	**β_{Csub} = -0.25(0.12)**	**0.034**
							$\beta_{Dev\text{-}For}$= -0.58(0.16)	**< 0.001**
							$\mathrm{RandI}_{\mathrm{Lake}}$ = 0.084	

Table 4.4. NMDS correlations with environmental vectors.
Fitted environmental and macrophyte trait variables against macrophyte composition NMDS across 3 axes with r^2 and p values derived from permutational tests (n=1000). Bolded rows indicate significant correlations at $p < 0.05$. Refer to Figure 3 for fitted variable codes.

	NMDS 1		NMDS 2		NMDS 3	
Fitted Variable	r^2	*p*	r^2	*p*	r^2	*p*
Environmental						
Alkalinity	**0.283**	**0.001**	0.039	0.099	<0.001	0.818
Secchi	**0.265**	**0.001**	0.008	0.459	**0.055**	**0.049**
Drawdown magnitude	**0.100**	**0.006**	**0.117**	**0.004**	**0.130**	**0.001**
Coarse substrate	0.024	0.186	0.043	0.080	**0.160**	**0.001**
TP	0.001	0.783	0.001	0.768	0.014	0.306
Depth	<0.001	0.951	0.042	0.082	0.002	0.736
Shoreline type	0.026	0.187	<0.001	0.798	<0.001	0.828
Herbicide use	**0.139**	**0.002**	0.005	0.553	**0.065**	**0.035**
Macrophyte Traits						
Native	**0.054**	**0.036**	**0.070**	**0.022**	**0.059**	**0.033**
Non-native	**0.054**	**0.036**	**0.070**	**0.022**	**0.059**	**0.033**
Low caulescent	0.033	0.126	**0.360**	**0.001**	0.027	0.154
Erect caulescent	0.004	0.546	**0.276**	**0.001**	0.007	0.468
Mat former	<0.001	0.940	**0.086**	**0.011**	0.003	0.661
Low rosette	0.044	0.077	0.003	0.656	**0.264**	**0.001**
Perennial	0.028	0.153	0.002	0.735	**0.113**	**0.002**
Perennial, storage organs	<0.001	0.791	**0.464**	**0.001**	**0.070**	**0.03**
Annual	0.043	0.080	**0.600**	**0.001**	0.006	0.546
Annual, storage organs	0.015	0.266	0.004	0.595	**0.347**	**0.001**
Amphibious	0.021	0.227	**0.072**	**0.026**	0.038	0.088
Non-amphibious	0.021	0.227	**0.072**	**0.026**	0.038	0.088
Fecundity – low, seeds + veg.	0.005	0.573	0.011	0.395	<0.001	0.978
Fecundity – mod., seeds	0.002	0.730	**0.057**	**0.027**	**0.062**	**0.026**
Fecundity – mod., seeds + veg.	<0.001	0.826	**0.380**	**0.001**	0.001	0.745
Fecundity – high, seeds	0.041	0.081	0.025	0.175	**0.218**	**0.001**
Fecundity – high, seeds + veg.	0.007	0.495	**0.265**	**0.001**	**0.128**	**0.004**

Figures

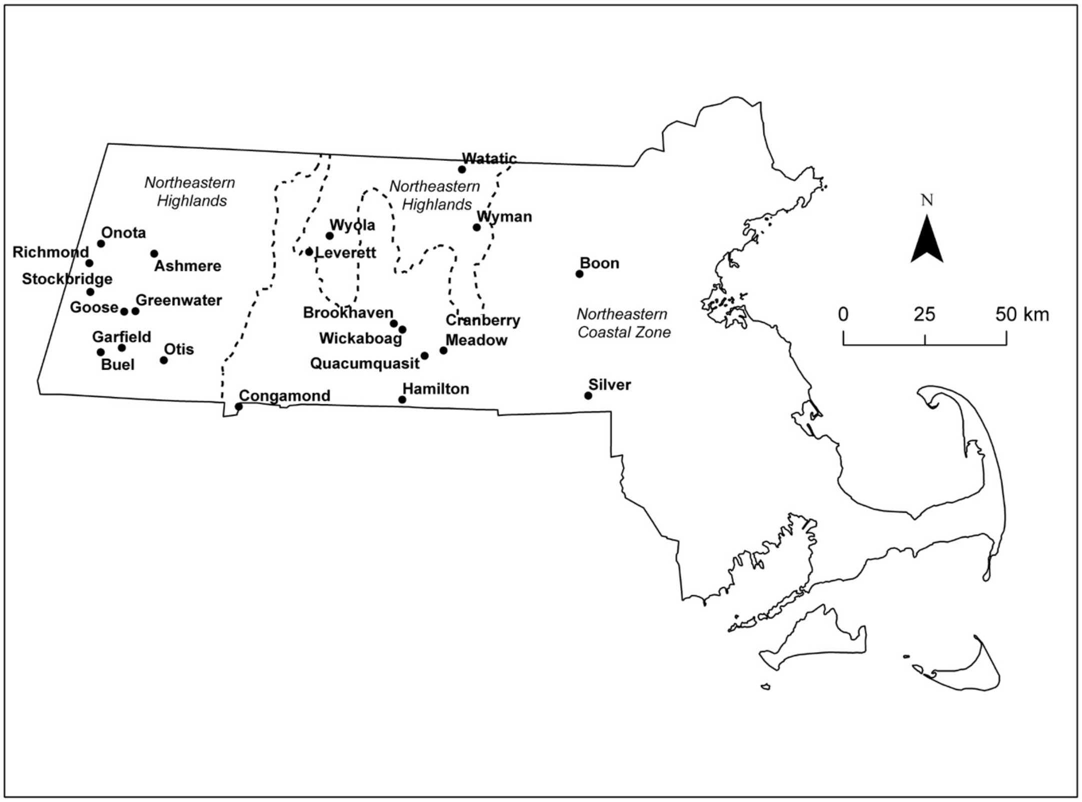

Figure 4.1. Map of study lakes.
Study lake locations across Massachuestts, USA. Dotted line delineates level 3 ecoregions, the Northeastern Highlands and the Northeastern Coastal Zone, derived from the U.S. Environmental Protection Agency.

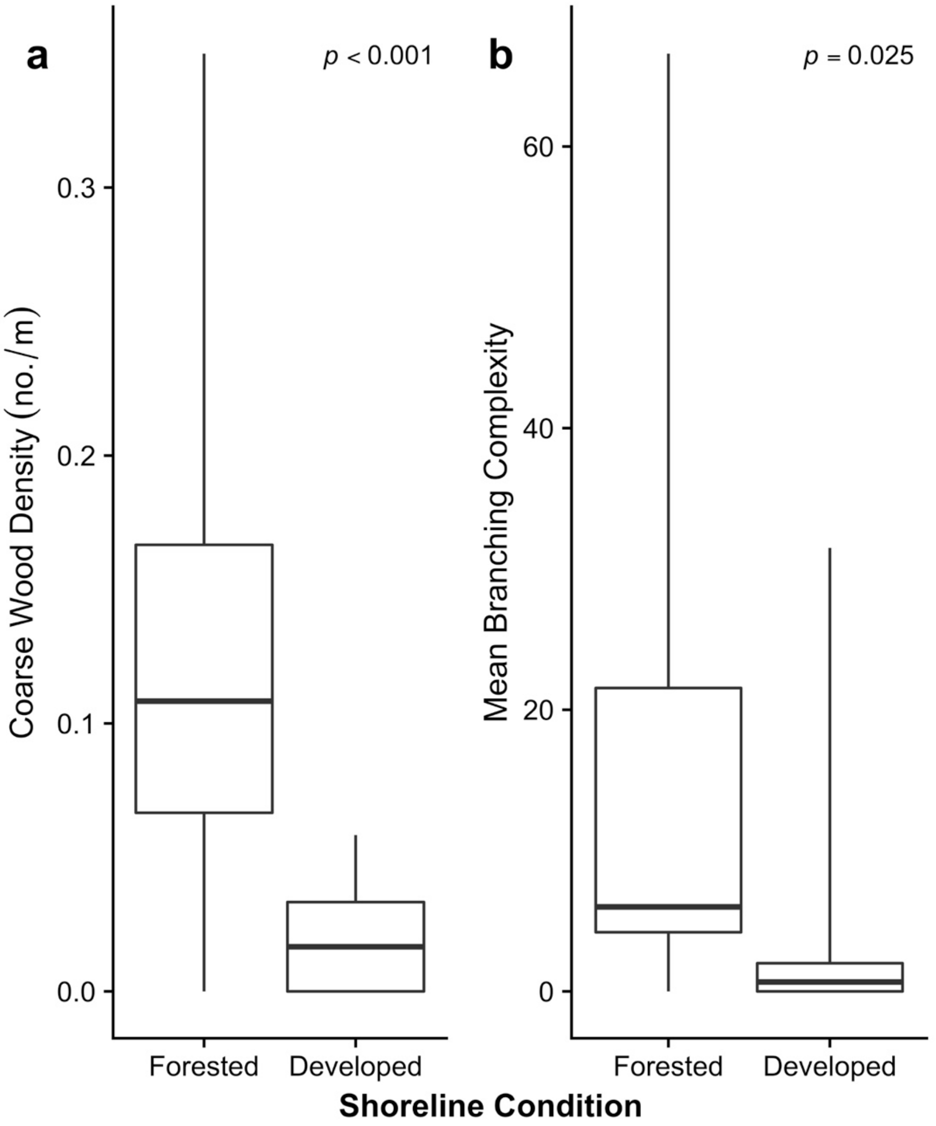

Figure 4.2. Coarse wood density and complexity.
Total coarse wood density (a) and branching complexity (b) among forested and developed shorelines (n = 42) for 21 lakes. Boxes represent median and interquartiles, and whiskers represent minimum and maximum values. *p*-values derive from negative binomial regressions.

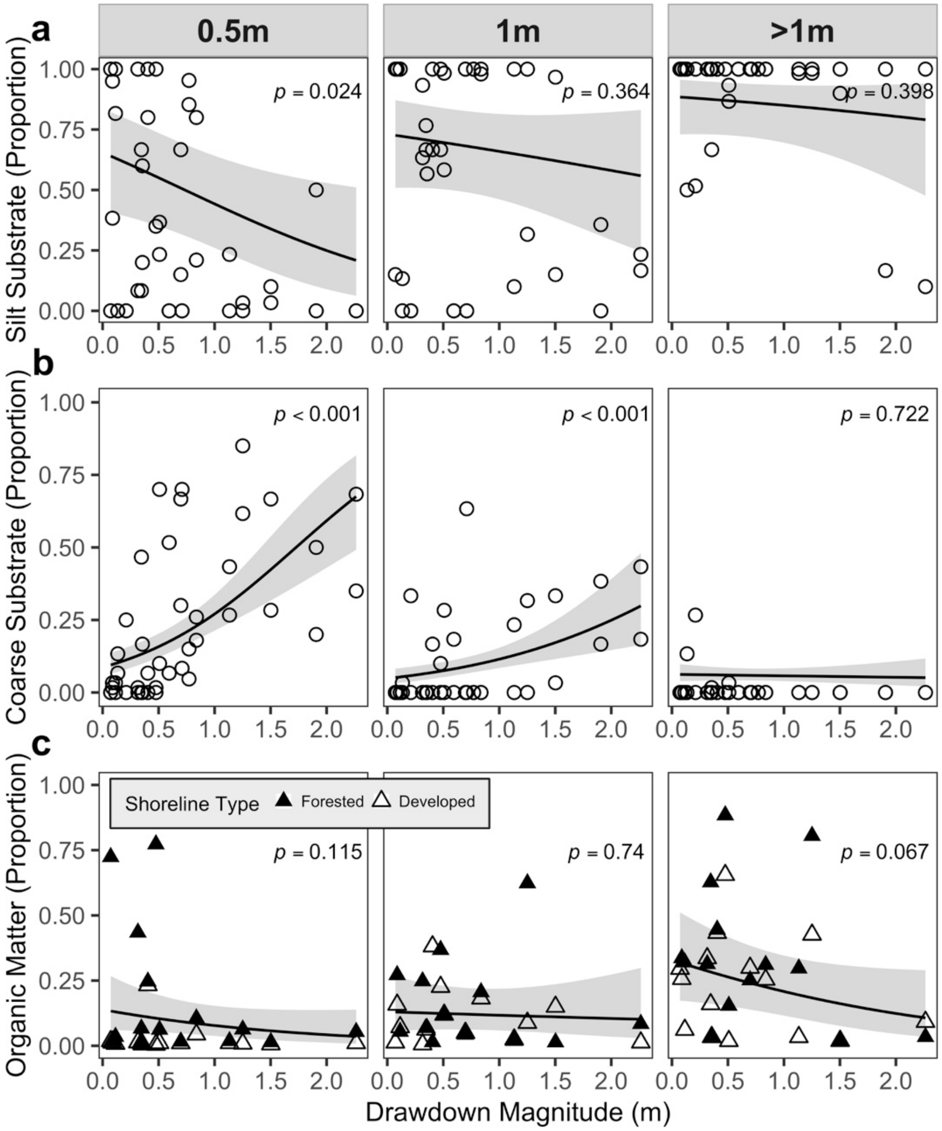

Figure 4.3. Substrate properties as a function of magnitude.
Silt (a), coarse substrate (b), and organic matter (c) proportions along a drawdown magnitude gradient. Substrate proportions are paneled by depth, each with model predicted lines with one standard error bands. *P*-values are associated with depth-specific effects of drawdown magnitude on sediment size classes. Organic matter derives from 15 lakes and is coded by shoreline type (forested, developed). Silt and coarse substrate derive from all 21 study lakes.

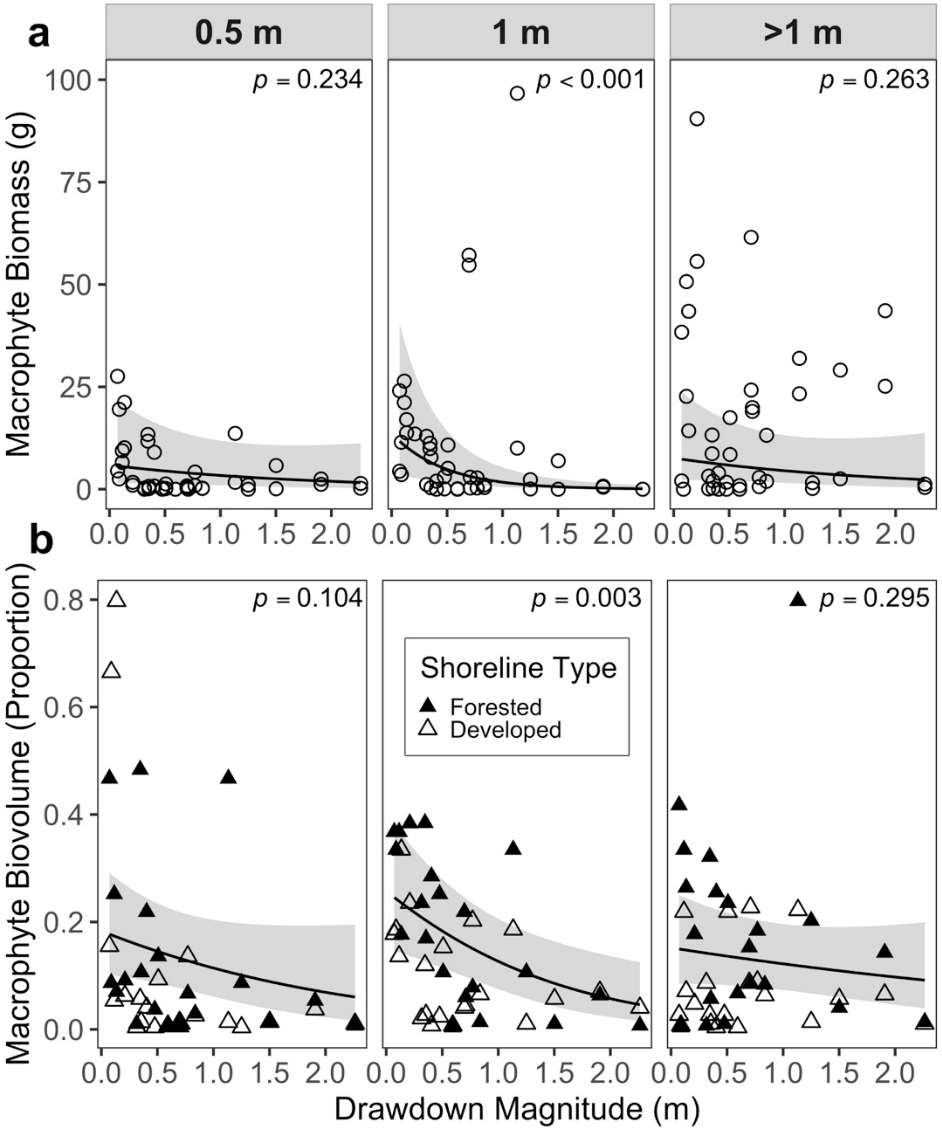

Figure 4.4. Macrophytes abundance as a function of magnitude.
Macrophyte biomass (a) and macrophyte biovolume (b) along a drawdown magnitude gradient. A) Biomass is divided by depth with depth-specific model predictions and one standard error bands. B) Model predictions for biovolume are parsed by forested (filled triangles, solid line) and developed (open triangles, dashed line) shoreline types. *P*-values are associated with drawdown magnitude-biomass and magnitude-biovolume effects.

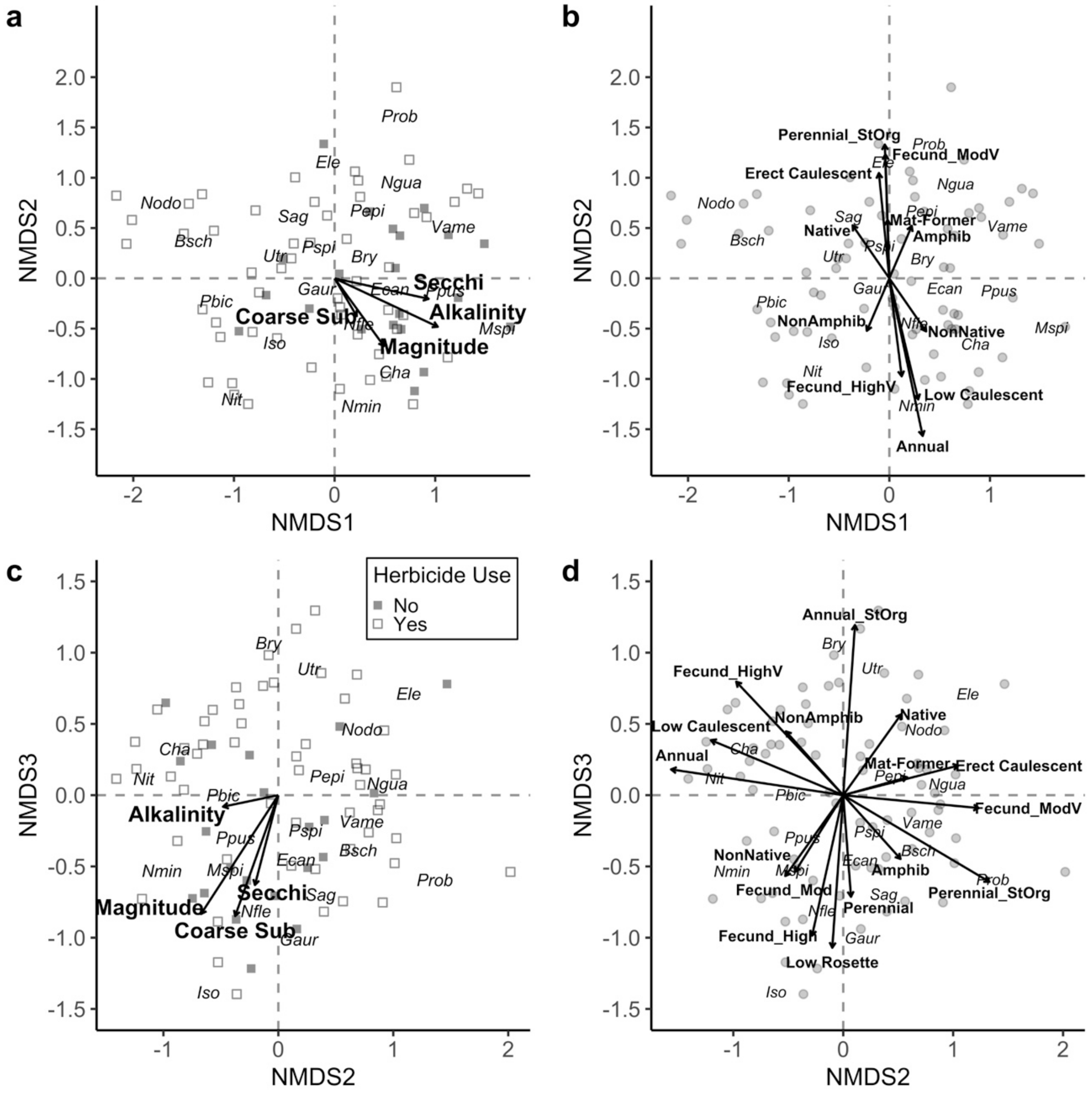

Figure 4.5. Non-metric multidimensional scaling of macrophyte taxa.
NMDS ordination of macrophyte taxa by biomass (stress = 0.107). Vectors represent fitted environmental (a, c) and macrophyte trait (c, d) variables. The top row (a, b) represents the first and second NMDS axes, and the bottom plots (c, d) axes are the second and third NMDS axes. Points represent site scores (i.e., 0.5m and 1m depths) coded by herbicide use for the plots a and c (filled square = no, open square = yes, see legends). Only fitted variables with $p < 0.05$ via permutational tests are shown. Note difference in scales among NMDS plots. Abbreviated environmental and trait vectors are (bolded) Coarse Sub = coarse substrate proportion, macrophyte trait vectors are Perennial_StOrg = perennial with storage organ, *A* = annual without storage organ, Annual_StOrg = annual with storage organ, Fecund_Mod = moderate number of reproductive organs, seeds only, Fecund_ModV = moderate number of reproductive organs, seeds and vegetative propagules, Fecund_High = high number of reproductive organs, seeds only, Fecund_HighV = high number of reproductive organs, seeds and vegetative propagules. Taxa scores are represented as abbreviated taxa codes and include Bry = bryophyte species, Bsc = *Brasenia schreberi*, Cha = *Chara* species, Ecan = *Elodea canadensis*, Ele = Eleocharis species, Gaur = *Gratiola aurea*, Iso = *Isoetes*, Mspi = *Myriophyllum spicatum*, Nfle = *Najas flexilis*, Ngua = *N. guadalupensis*, Nmin = *N. minor*, Nit = *Nitella* species, Nodo = *Nymphaea odorata*, Pbic = *Potamogeton bicupulatus*, Pepi = *P. epihydrus*, Ppus = *P. pusillus,* Prob = *P. robbinsii*, Pspi = *P. spirillus*, Sag = *Sagitarria* species, Utr = *Utricularia* species, Vame = *Vallisneria americana*.

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CHAPTER 5

ANNUAL WINTER WATER LEVEL DRAWDOWNS LIMIT SHALLOW-WATER MUSSEL DENSITIES IN SMALL LAKES

Introduction

Annual winter drawdown, whereby lakes are drawn down in the fall and refilled in the spring, is a common water level management regime in temperate and boreal climates. Annual winter drawdowns are conducted for various purposes including as a consequence of hydroelectric power generation (Hellsten, 1997) or to help improve recreational value. For example, in Massachusetts (MA) USA recreational lakes, winter drawdowns are an active management tool to reduce nuisance densities of submerged aquatic vegetation, prevent ice damage to human structures along shorelines (e.g., docks, retaining walls), and allow shoreline cleanup among other reasons (Mattson, Godfrey, Barletta, & Aiello, 2004). In this region, lakes are typically drawn down after October 1st and refilled by April 1st to abide by standards (Mattson, Godfrey, Barletta, & Aiello, 2004); however, the exact timing, magnitude, and duration of drawdown varies based on lake characteristics, precipitation, and management goals.

Despite purported benefits, winter drawdowns can alter littoral zone community structure (i.e., composition, distribution, and abundance) and function (reviewed by Carmignani & Roy, 2017; Hirsch et al., 2017). Freshwater mussels (Bivalvia: Unionida) are expected to be particularly susceptible to annual winter drawdowns because of their generally low mobility, consistent with other low mobility benthic invertebrates (e.g., clams - Sphaeridae) in annual winter drawdown lakes (White, Xenopoulos, Metcalfe, & Somers, 2011). Moreover, drawdowns can alter physical habitat and water quality of littoral zones, thus indirectly affecting freshwater mussel distribution, density, and size. Lake mussel populations are generally found above the thermocline in stratifying lakes (Cyr, 2008; Cyr, Phillips, & Butterworth, 2017). Within this limit, a suite of physical factors controlled by bathymetry and wave action predict mussel distribution, density, and size (Bossenbroek et al., 2018; Cyr, 2008). For example, the depth of maximum mussel density increases with effective fetch and lake area (Cyr, 2008; Cyr et al., 2017) and shell length of some species decreases with increasing water depth (Cyr, 2008; Ghent, Singer, & Johnson-Singer, 1978; Hanson, Mackay, & Prepas, 1988; Strayer, Cole, Likens, & Buso, 1981). Mussel density peaks often occur in shallow waters along low-grading slopes (Cyr et al., 2017). Most species of mussels occur in soft substrates (Bossenbroek et al., 2018), but densities can be constrained by silt (Burlakova & Karatayev, 2007). Further, fine sediment depth shows a unimodal relationship with mussel density with increasing densities up to 30 cm and declining thereafter, and more unexplained variability in coarser, low-penetrable substrates (Cyr, Storisteanu, & Ridgway, 2012). Mussel length also has a unimodal relationship with sediment depth (Cyr et al., 2012), and shell growth can vary among sediment size classes (Kesler & Bailey, 1993). Further, mussels buried during the growing season tend to be smaller and younger compared to mussels at the sediment surface (Amyot & Downing, 1991; Balfour & Smock, 1995). Finally, macrophyte cover is positively correlated with mussel presence (Bossenbroek et al., 2018), but dense macrophyte beds can limit mussel densities

(Burlakova & Karatayev, 2007) suggesting a potential unimodal relationship between mussel density and macrophyte cover.

Water level fluctuations further add to the physical disturbance constraining mussel distributions. Studies have demonstrated mussel mortality from natural (e.g., Bowers & De Szalay, 2004) and regulated water drawdowns in lentic systems (Burlakova & Karatayev, 2007; Howells, Mather, & Bergmann, 2000; Newton, Zigler, & Gray, 2014; Richardson, Hanson, & Locke, 2002). Previous winter lake drawdown studies have found negative effects of drawdowns on mussel densities and distribution. In a Maine lake, Samad and Stanley (1986) estimated a 98% loss of the mussels *E. complanata* and *Lampsilis radiata* after exposing the majority of mussel habitat (e.g., all habitat < 4 m depth) during two annual winter drawdowns, such that surviving mussels only resided in a perennially submerged inlet. Similarly, other studies documented continued mussel abundance declines in exposure zones after three consecutive winter drawdowns (Richardson et al., 2002) and across three drawdowns over six years (Howells et al., 2000). These studies demonstrate that mussel densities decline following one to several winter drawdowns; however, no study has estimated mussel responses to the effects of winter lake drawdown regimes with repeated (e.g., >3 years) annual winter drawdowns and at relatively mild amplitudes (e.g., <1 m). Specifically, we need a better understanding of whether annual drawdown regimes permanently constrain mussel populations to deeper depths in lakes or whether impacts are temporary, and mussels can compensate for drawdown disturbances.

We aimed to assess the effects of annual winter drawdowns on mussel density and size distribution in lakes with ongoing annual drawdown regimes that have existed for several decades. We estimated mussel densities and associated shell length distributions at depths within and deeper than drawdown exposure zones in between annual drawdown events when lake water levels are normal (i.e., early fall months). We further estimated mussel mortality in exposure zones after drawdown initiations. We also estimated the effects of region and other physical habitat covariates (e.g., submerged aquatic vegetation, sediment properties, fetch) on mussel densities to understand variation in mussel densities across sites and to isolate drawdown impacts.

Methods

Study Area & Lake Selection

The study included 13 lakes located in the Housatonic River Basin in western MA and the Connecticut River and Thames River Basins in central MA, USA (Figure 5.1). The Housatonic River Basin is bordered by the Taconic Mountains and Berkshire Plateau, with the highest elevation in the state (1064 m). Lakes in the Housatonic River Basin (n = 8) are located in valleys underlain by carbonate bedrock, and, in the Lower Berkshire Hills and Berkshire Highlands, predominantly composed of metamorphic, granite, mafic bedrock. Lakes in the Connecticut River and Thames River Basins (n = 5) are located in the Connecticut Valley and Lower Worcester Plateau ecoregions, predominantly composed of basin sedimentary and metamorphic bedrock, respectively (Griffith et al., 2009). The underlying geology results in higher alkalinity in western lakes (Table 5.1). Mean minimum/maximum July and January temperatures for ecoregions in western MA tend to be 1-3°C degrees lower than in central MA (Griffith et al., 2009). Winter precipitation averages 21.6–25.4 cm (1981-2010) across western and central MA

(National Oceanic and Atmospheric Administration, 2018) and ice out varies from February to early May for MA lakes (Hodgkins & James, 2002).

For assessing the effects of winter drawdown on live mussel densities and size distribution, we selected six drawdown lakes and three control lakes. Drawdowns have been conducted annually for several decades at most of our study lakes (Table 5.1); thus, observed mussel densities are a result of many years of drawdowns. Drawdowns are initiated in October–December, meet a target winter water level, and are refilled beginning in January–April, returning to normal pool levels in February–June. Average drawdown durations (i.e., time from initiation to refill) exceed 130 days across lakes (Table 5.1). The six drawdown lakes had average annual drawdown magnitudes between 0.5 m and 1.0 m between 2014 and 2017, annually exposing the 0.5-m depth contour. Control lakes had natural fluctuations or minor drawdowns that resulted in low water levels < 0.25 m below full pool levels (Table 5.1). Because differences in alkalinity and temperature between the western and central regions may affect mussel densities, we selected drawdown and control lakes within both regions (Table 5.1).

For assessing acute effects, we included nine drawdown lakes: five of the six drawdown lakes (all but Greenwater) in the pre-drawdown assessment and 4 additional lakes with larger drawdown magnitudes (1.25–2.26 m). We could not sample mussel mortality in Greenwater because drawdown initiation occurred in late December by which time snow and ice covered the exposure zone that created difficult conditions for mussel detection. Lakes vary in size (0.38–4.21 km^2), lakeshore development (178.2–525.2 buildings km^{-2} within a 100 m buffer), and water quality (Table 5.1).

Pre-drawdown Mussel Sampling

We estimated mussel densities in early to mid-fall (9/13–10/13) before annual winter drawdown initiation. Drawdown lakes were sampled in either 2015 (n = 3) or 2017 (n = 3), whereas control lakes were sampled in both 2015 and 2017. In each drawdown lake we selected 3 sites, and in control lakes we sampled 6 unique sites (3 sites in 2015, and 3 sites in 2017). We selected sites in areas with limited lakeshore development, shallow to moderately grading bed slopes, substrates not dominated by silt or boulder, and mussels present at >1-m depths as identified by snorkeling. Thus, sites were not selected randomly, but represented locations in the lake that were mostly likely to have mussels if they were present. Additionally, sites were at least 100 m apart. At each site, we established a 20-m long by 2-m wide transect centered on the 0.5-m and 1.0-m depth contours, parallel to the shoreline. Along each transect, a single snorkeler identified and enumerated each visible, surface mussel, and returned mussels to the same location. In 2015, mussels were also measured for shell length along the longest axis. Due to time constraints, if surface mussel densities were high (>14 mussels/m^2; n = 12 transects at 1-m depth), densities and shell lengths were subsampled using 4–5, 0.25-m^2 quadrats equally spaced along the transect.

Mussels were additionally sampled in 2017 at three drawdown and three control lakes using excavated quadrats to estimate surface and buried mussel density. We used a quadrat-based systematic sampling design (sensu Strayer & Smith, 2003) within the same transects visually sampled by snorkeling at the 0.5-m depth only. Systematic sampling has been shown to more precisely estimate mussel abundance over simple random sampling designs (Pooler & Smith, 2005) and is relatively easy to implement because of regular interval quadrat placing (Strayer & Smith, 2003). Following the snorkel surveys, we randomly determined three starting locations within a 5x4 grid of 0.25-m^2 cells at one end the transect, and then regularly placed five additional, 0.25-m^2 quadrats 2.5 m apart, for a total of 18 quadrats per 0.5m transect. Within each quadrat we first collected surface mussels. Then, we excavated the top 10 cm of sediment, sieved it through a 6.25-mm hardmesh wire, and collected buried mussels. All surface and excavated mussels were identified and shell lengths were measured. Transect-level density and associated variance were estimated following equations from Strayer and Smith (2003).

Post-drawdown Mussel Sampling

We quantified drawdown-related mussel mortality in the exposure zones of nine drawdown lakes in November and December of 2017 (Table 5.1). We chose to sample around water level decline cessation (e.g., 25-55 days after drawdown initiations) because of the unpredictability of snow and ice cover over exposed lakebed that would impede our mussel detectability (Appendix N). When water levels reached the approximate median drawdown level (based on 2-3 winter drawdown events per lake, see Water Level Section), we collected stranded mussels along three 50-m long sites contiguous to pre-drawdown sampling sites and at three sites in lakes with drawdown magnitudes >1m (Table 5.1). We surveyed the entire exposed width (i.e., from the waterline to wrack line) at each site and collected, identified, and measured shell length for stranded mussels that contained flesh/viscera that we considered to be recently deceased via drawdowns. Exposure zone width was measured at five equidistant points to calculate area of the exposed zone and determine mussel mortality density.

Physical Habitat Measurements

We measured physical habitat covariates at the quadrat, transect, and site scales, corresponding to the pre-drawdown density assessments. For each quadrat we measured depth to refusal using a 6.35-mm diameter metal rod as a proxy of sediment penetration and visually estimated dominant substrate size (using the Wentworth scale; Wentworth, 1922), percent macrophyte cover, and percent other organic matter cover (e.g., sticks, needles, leaves). Water depth was measured at the center of each quadrat and we calculated a quadrat's relative depth to the contour as the difference between the quadrat's depth and the contour depth (0.5 m), such that positive values represent depths deeper than the contour. Quadrat relative depths were further expressed as duration exposed (in days) during the 2016-2017 winter drawdown event. At each transect (e.g., 0.5-m and 1.0-m depth contours) we determined bed slope from the shoreline and visually estimated dominant substrate size and percent macrophyte cover. Additionally, we determined the median bed texture using a haphazard, 50-particle count (Wolman, 1954) along the stranded survey transects. We estimated effective wind fetch length as a proxy variable for potential wave action, for each site following methods from Häkanson and Jansson (1983) and Cyr et al. (2017). Over-water distances were measured in ArcGIS 10.3.1 (ESRI, 2015)**.** Wind speeds and directions were taken from the United States National Oceanic and Atmospheric Administration using daily wind from Orange Municipal Airport, MA (USW00054756) running from 1998-2017.

Water Level Monitoring and Metrics

We continuously monitored water levels for each lake from September/October of 2014 or 2015 to December 2017. At each lake, we installed a non-vented pressure transducer (Onset HOBO U20L-01, Bourne, MA, USA) under water near the point of outflow and a matching pressure transducer above water to account for barometric pressure. Pressure transducers were suspended on non-stretch cable within perforated PVC housing units and were set to record pressure every 2 h. We downloaded loggers at least twice per year and recorded relative height from a secondary fixed location (e.g., staff gauge, spillway, dam abutment) to help identify unintentional logger movement (e.g., from ice formation/melt) and measurement accuracy drift. For Otis Reservoir we used water level data recorded by the Massachusetts Department of Conservation and Recreation and filtered the data to match our 2-h recording interval and timing. We used HOBOWarePro (version 3.7.8, Onset Computer Corporation, Bourne, MA, USA) to convert pressure measurements to water levels from matching data logger pairs per lake. Next, we used the ContDataQC package (Leppo, Lincoln, Stamp, & Van Sickle, 2017, version 2.0.2.9001) in R (R Core Team, 2017, version 3.4.2) to identify potential inaccurate water level measurements based on absolute water level change and gross water level thresholds. We flagged records with an absolute change ≥ 3 cm and adjusted data to account for apparent transducer movement or drift. We removed water level records with negative values and within pressure transducer accuracy (i.e., values < 1 cm).

We defined two water level time periods as the winter drawdown phase and the normal spring-summer phase to calculate water level metrics. Using daily means, we determined drawdown initiation dates by identifying the first day of consistent water level decline and drawdown end dates by locating the first day reaching pre-defined normal pool levels in winter-spring (i.e., January-June). We identified normal pool levels (i.e., drawdown refill target) as the median water level from self-evident non-drawdown phases in 2015 (n=5) or from spillway elevations (n=8). We determined drawdown magnitude as the lowest water level during drawdown and then averaged across drawdown events. We also calculated mean and maximum drawdown rates from the time of drawdown initiation to the time of the mortality survey or the time of water level stabilization.

Water Quality

We measured summer water quality and determined secchi depth at the deepest part of each lake for two years between 2014-2017. In June, July, and/or August water samples were collected from the lake surface for total phosphorous (TP), alkalinity, and chlorophyll-a. TP was directly sampled with acid-washed polyethylene bottles, frozen, and analyzed through alkaline persulfate digestion followed by colorimetric measurement for PO_4. Water samples for alkalinity were filtered through a pre-ashed 0.7-μm Whatman microfiber glass filter, kept cool, and measured using the inflection point titration method. TP and alkalinity were analyzed at the University of New Hampshire Water Quality Analysis Laboratory. Chlorophyll-a was filtered using a pre-combusted microfiber glass filter, put on ice, and kept frozen for < 2 weeks before processing at the University of Massachusetts Amherst. We followed EPA method 445.0 in vitro determination of chlorophyll-a by fluorescence using an *Aqua*Fluor fluorometer (Model 8000-010; Turner Designs, Sunnyvale, CA, USA).

Data Analyses

We used generalized linear mixed models to estimate the winter drawdown effect on surface mussel densities at the transect scale, and surface and buried abundances and densities at the quadrat and transect scale. To match our discrete mussel count data, we used Poisson or negative binomial error distributed regressions (Bolker et al., 2009) and used an offset term to account for area sampled to effectively model mussel density (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). For each depth (0.5 m and 1m) we modelled surface density from transects (n=36 per depth) with drawdown presence as a fixed effect and lake as a random effect to account for spatial autocorrelation and pseudoreplication because of our inherently nested study design (Bolker et al., 2009). To assess effects of other environmental variables, we also included bed slope (water line to transect), macrophyte cover, effective fetch, and two geographic regions (i.e., western or central MA), as potential fixed effect predictors. We used 2-term interactions between drawdown and the other environmental covariates along with additive predictor terms.

We modeled surface and buried mussel densities at the transect level using a Poisson or negative binomial error distribution with an offset term for area sampled. Since we had a small dataset (n=18), we limited the regressions to two additive environmental predictors and considered a random intercept of lake. Environmental predictors included drawdown presence, transect slope, depth to refusal, macrophyte cover, and surface mussel density at the 1-m depth. We expect surface mussel density at the 1-m depth to help predict surface and buried mussel density at 0.5 m due to source population dispersal into colonizable habitat during normal water levels. We further modeled abundance at the quadrat-level (n=324) using Poisson error distributed regressions with a random intercept of site nested within lake to account for spatial autocorrelation (Bolker et al., 2009). We tested whether the addition of a zero-inflation term improved model fit because the high frequency of zeros (58.6%) suggested low mean quadrat abundance (Warton, 2005). Environmental predictors included drawdown presence, relative depth, depth to refusal, macrophyte cover, and dominant substrate class. We tried all predictor combinations including two-term interactions for conditional and zero-inflated formulas.

We modeled transect-level density of dead mussels (n=27) using a Poisson or negative binomial error distribution with a log link and offset term to account for area sampled. We also included a random intercept of lake. We tested median particle size, mean and maximum two-hour drawdown rate, mean drawdown magnitude, slope, and effective fetch as additive and two-way interaction terms. We further calculated site-level percent mortality as the ratio of mortality densities to transect surface and buried densities at 0.5-m depths. Percent mortality could only be calculated for two drawdown lakes (Hamilton and Wickaboag) where we performed both mussel excavations and mortality surveys.

We performed non-parametric Kolmogorov-Smirnov two-sample tests (KS-test) to determine differences between mussel shell length distributions across control and drawdown lakes and surface and buried mussels. We compared length distributions for: 1) buried versus surface mussels in control lakes pooled across species (*E. complanata* and *P. cataracta*), 2) buried mussels between drawdown and control lakes by species, 3) buried mussels in drawdown lakes and stranded mussels pooled across species. Sample size was too low for buried *P. cataracta* to estimate species-specific size-distribution differences between drawdown and control lakes.

For all regression models, we performed single-term deletion Chi-square tests to simplify models and used Akaike Information Criterion corrected for small sample size

(AICc) to compare models using the bbmle package (Bolker & R Core Team, 2017, version 1.0.20) in R. We report models within 5 ΔAICc units. All continuous covariates were Z-score transformed before analyses. We checked for collinearity among predictor variables using scatterplot matrices and among all covariate types using generalized variance-inflation factors (e.g., GVIF < 3) calculated using the car package in R (Fox & Weisberg, 2011, version 2.1-5). We also performed non-parametric Mann-Whitney tests for continuous covariates compared between drawdown and control lake treatments. Predictor variables were considered significant with *p*-values <0.05 and marginally insignificant with *p*-values >0.05 and <0.1. All regression models were generated using the glmmTMB package (Brooks et al., 2017, version 0.2.1.0) and KS-tests from the R Stats package performed in R (R Core Team, 2017, version 3.4.2).

Results

Water Level and Physical Habitat

Mean drawdown magnitudes ranged from 0.51–2.26 m in drawdown lakes and the lowest average winter water levels in control lakes ranged from 0.12–0.21 m (Table 5.1). Mean drawdown rates for the 2017-2018 winter drawdown events ranged from 1.42–5.01 cm/d and maximum rates ranged from 12.2–86.4 cm/d (Appendix N).

Correlation matrices among continuous habitat predictors indicated no collinearity. However, there were a few differences in physical habitat between control and drawdown lakes. At the quadrat level, we sampled significantly higher macrophyte cover at the 0.5-m depth in control lakes (Mann-Whitney: W = 17156, *p* <0.001; Appendix O). We also found higher macrophyte cover at the transect level in control lakes compared to drawdown lakes at the 1.0-m depth (Mann-Whitney: W =253.5, p = 0.004). However, we do not believe these correlations confounded our subsequent interpretation of any drawdown effect because we anticipated a negative correlation between dense macrophyte cover and mussel density (per Burlakova and Karatayev 2007). On average, we sampled significantly deeper relative depths (> or < 0.5-m contour) in drawdown lakes than in control lakes for quadrat surveys (Mann-Whitney: W=8552, p <0.001: Appendix O). In the three drawdown lakes, quadrats sampled deeper than the 0.5-m contour were submerged for 2 to 53 days longer in Wickaboag (0.5m – 5 cm deeper), 1 to 39 days longer in Hamilton (1 – 15cm deeper), and remained submerged in Greenwater compared to the 0.5-m contour. Thus, any observed negative drawdown effect is likely conservative, as we expected more mussels at deeper relative depths in drawdown lakes. Lastly, we sampled coarser substrates in drawdown lakes compared to control lakes (Appendix O). Other covariates showed no clear differences among drawdown and control lakes and depths.

Drawdown Effects on Surface Mussels: Transect Sampling

Across six drawdown and three control lakes we sampled 3,503 surface mussels comprised of *E. complanata* (83%), *P. cataracta* (16%), and *Lampsilis radiata* (1%). We observed *P. cataracta* in all lakes, *E. complanata* in 8 of 9 lakes (not found in Ashmere), and *L. radiata* only in Quacumquasit. Mussel densities ranged from 0–252 mussels/m^2, with 63% of transects with <1 mussel/m^2 and 19% of transects with >10 mussels/m^2. At the 1-m depth (i.e., not exposed during drawdown at any of the sites) we found the highest mussel densities in Wickaboag (mean = 137.6 mussels/m^2) and the lowest at Stockbridge (mean = 0.3 mussels/m^2) (Figure 5.2). There were significantly higher mussel densities in central MA lakes compared to western MA lakes (depth-specific model, $p < 0.001$; Figure 5.2). We did not detect surface mussels at 16 of 18 transects at the 0.5-m depth in drawdown lakes, with the exception of single transects at Stockbridge (0.03 mussels/m^2) and Hamilton (0.2 mussels/m^2). In contrast we detected mussels at all 0.5-m depth transects in control lakes (range = 0.03–9.6 mussels/m^2).

At the 0.5-m depth, which is exposed during winter drawdowns, we found significantly lower surface mussel densities in drawdown lakes (mean = 0.01) compared to control lakes (mean = 2.8, $p < 0.001$; Figure 5.2, Table 5.3A). We also found a significant interaction between drawdown and bed slope at the 0.5-m depth, with a more positive relationship between mussel density and slope in drawdown lakes than in control lakes (Table 5.3A). This interaction was driven by an extreme data point whereby the highest surface mussel density was observed at the steepest bed slope across drawdown lakes. In contrast to shallow depths, surface mussel densities were significantly higher at the 1-m depth (i.e., submerged) in drawdown lakes (mean = 30.5) than in control lakes (mean = 11.8, $p = 0.006$; Figure 5.2, Table 5.3B). At the 1-m depth, geographic region was the strongest predictor of surface mussel density followed by drawdown presence (Table 5.3B).

Drawdown Effects on Surface and Buried Mussels: Quadrat Sampling

Extrapolated transect surface and buried mussel densities from systematic quadrat sampling ranged from 0–5.3 mussels/m^2 in drawdown lakes and 0–39.0 mussels/m^2 in control lakes. If present, mussels were primarily buried in drawdown lakes. Within the 3 drawdown lakes, quadrat systematic sampling yielded surface mussels at 1 of 9 sites and buried mussels at 6 of 9 sites. Control sites showed more variability in the ratio of surface to buried mussel densities than drawdown lakes (Figure 5.3). We found a significant negative effect of drawdown on surface and buried mussel densities at the 0.5-m depth (Figure 5.4, Table 5.3C).

In predictive models, we found a marginally insignificant positive effect of surface mussel density at the 1-m depth on surface and buried mussel densities at the 0.5-m transect (Table 5.3C). When drawdown presence was included in the model, we found no additional significant effects of other covariates (Table 5.2) including depth to refusal (beta = 0.65, $p = 0.450$), transect slope (beta = 0.48, $p = 0.387$), effective fetch (beta = 0.26, $p = 0.491$), and macrophyte cover (beta = -0.67, $p = 0.138$).

We found a significant negative effect of drawdown presence and a significant positive effect of relative depth on quadrat-level mussel abundance (Table 5.3D). There was an additional significant interaction effect of drawdown presence and relative depth on mussel abundance whereby mussel abundance increased faster with relative depth in drawdown lakes compared to control lakes (Figure 5.5). Additionally, relative depth accounted for mussel absences in the zero-inflation component of the model, showing a higher chance of observing mussel absence at shallower relative depths. Macrophyte cover had a weak, significant positive effect on mussel abundance (Table 5.3D).

Across all lakes and species, surface mussels were larger than buried mussels (D = 0.44, $p < 0.001$). For *E. complanata*, buried individuals in drawdown lakes (n = 52) were smaller than buried mussels in control lakes (n = 301, D = 0.29, $p = 0.001$; Figure 5.6A). Sample sizes were too small for *P. cataracta* to test for size distribution differences between drawdown and control lakes.

Mussel Mortality

We surveyed a total of 336 dead *P. cataracta* and 48 dead *E. complanata* during stranding surveys in the nine drawdown lakes. Mussel mortality varied among and within lakes, with the highest densities of stranded mussels in Otis and Garfield. We found a significant negative correlation between median particle size and density of dead mussels, with consistently low mussel mortality at sites with larger particles and increasing variation in mussel mortality associated with relatively small particle sizes (Figure 5.7A, Table 5.3E). The next plausible model (i.e., $\Delta AIC_c<2$) included an insignificant positive effect of drawdown magnitude in addition to the positive effect of particle size. Drawdown magnitude showed a marginally insignificant positive correlation with mussel mortality as a single predictor model (beta = 0.47, *p* = 0.0614; Figure 5.7B), but was less plausible than sediment particle size alone. There were no correlations between mortality and drawdown rates (single predictor model mean: beta = 0.34, *p* = 0.174; max: beta = 0.33, *p* = 0.222), fetch (beta = -0.36, *p* = 0.201), and slope (beta = 0.26, *p* = 0.338; Table 5.2). Using surface and buried densities of live mussels from transects at 0.5-m depths, we estimated 0-2.1% mortality in Hamilton Reservoir and 0.15-7.2% mortality in Lake Wickaboag following drawdown. Mussel shell length distribution showed no difference between stranded mussels (n=71) and living buried mussels (n=58) when pooled across all drawdown lakes (D = 0.105, *p* = 0.882; Figure 5.6B). Of the dead mussels, 92.3% of *P. cataracta*, were ≤ 30mm (mean = 24.8mm, sd = 13.7mm) and 83.3% of *E. complanata* were ≤ 60mm (mean = 46.6mm, sd = 13.9mm).

Discussion

We provide evidence that annual winter water level drawdown regimes in lakes constrain mussel distributions below drawdown exposure zones during normal water levels in addition to causing stranding and mortality soon after drawdown exposure. When mussels were present in drawdown exposure zones during normal water levels, they were often buried in the substrate and smaller than buried mussels in control lakes. Mussel densities at unexposed depths may act as local sources for colonization into shallower depths. However, colonization is likely short-lived as suggested by the concordance of shell length distribution between living buried mussels during normal water levels and dead mussels in exposure zones.

Drawdown effects on mussel distributions, densities, and size

Annual winter drawdown regimes have lasted for >20 years in our study lakes, reducing water levels by 0.51–2.26 m for 1–4 months in winter. These winter drawdowns negatively impacted surface and buried mussel densities in areas annually exposed during winter even though these areas remain submerged from spring to fall. Winter drawdown presence was the most important predictor of mussel densities, suggesting that drawdowns are the primary factor constraining mussels to deeper depths. The negative effect of drawdown presence on surface mussel density was particularly stark and this effect persisted with buried mussels although to a lesser degree. We found an average of 1.1 mussels/m^2 (range = 0 to 5.3 mussels/m^2) in drawdown lakes compared to 10.1 mussels/m^2 in control lakes, composed mostly of *E. complanata*. These densities are consistent with Richardson et al. (2002) who documented declines of *P. cataracta* density from 14.2 to 0.2 mussels/m^2 over 3 years at exposed depths in the littoral zone. Below the drawdown exposure zone at the 1-m depth, we found evidence of higher mussel densities in drawdown lakes compared to control lakes. This supports other studies that found maximum densities of benthic invertebrates below the drawdown exposure zone (Kraft, 1988; Palomäki & Hellsten, 1996). This suggests drawdowns largely constrain and shift mussel densities to deeper unexposed depths, which seem relatively unaffected by drawdowns.

Winter drawdowns also negatively affected buried mussel size. While buried mussels are typically smaller than surface mussels (Amyot & Downing, 1991; Schwalb & Pusch, 2007) and likely represent younger cohorts, buried *E. complanata* in drawdown lakes had even smaller size distribution than buried mussels in control lakes. This suggests that larger individuals (e.g., >40 mm) are more susceptible to drawdown disturbance and/or smaller mussels in exposure zones represent colonizing juveniles between annual drawdown events that do not reach larger sizes because of mortality via stranding. Smaller mussels may be more capable of avoiding desiccation and freezing by burrowing to thermal and moisture substrate refugia compared to larger mussels. Alternatively, a smaller size distribution could suggest higher recruitment in our drawdown lakes compared to control lakes.

Landscape and habitat influences on mussel densities and distributions

At depths deeper than drawdown exposure zones (i.e., 1 m), mussel density was best explained by geographic region, with mussel densities 1-2 orders of magnitude higher in central MA than in western MA. Although we are uncertain of the main drivers for this effect, region-specific differences in watershed geomorphology (Arbuckle & Downing, 2002; Brainwood, Burgin, & Byrne, 2006), food availability (Kesler et al., 2007), and water temperature (Singer & Gangloff, 2011) may be key factors. Western MA has cooler temperatures and higher topographic relief than central MA, which could limit stream mussel densities because of flashy hydrology and consequent high bed mobility (Arbuckle & Downing, 2002; D. Strayer, 1983), further constraining potential sink populations in lakes.

Depth and slope interact to influence the effect of drawdowns on mussel densities. The positive effect of slope on mussel densities in drawdown lakes observed in this study aligns with findings from Newton et al. (2015) where high slopes tend to have lower mussel mortality under water level drawdown conditions. With steeper slopes, mussels may have an increased chance of colonizing the exposure zone during normal water levels and may more easily escape water emersion during water level decline (Howells et al., 2000). The use of systematic quadrat surveys enabled us to capture the edge of site-level mussel distributions in drawdown lakes. Several quadrats were randomly placed centimeters deeper than or shallower than mean drawdown magnitudes (i.e., minimum water levels), and the positive correlation of depth relative to the contour on mussel density highlights the fine scale importance of water levels on mussels (Bowers & De Szalay, 2004). Furthermore, we found that high mussel densities at deeper depths (e.g., 1 m) are related to high mussel densities in shallower depths (e.g., 0.5 m) during normal pool levels in drawdown lakes, providing further evidence of colonization into exposure zones.

Macrophyte cover has been positively associated with mussel *presence* (Bossenbroek et al., 2018) and negatively correlated with mussel *density* particularly in dense macrophyte stands (Burlakova & Karatayev, 2007; Cyr et al., 2017), suggesting a unimodal or nonlinear mussel density response. We found a weak positive effect of macrophyte cover on mussel abundance, which might indicate an indirect measure of suitable mussel habitat whereby macrophytes enhance fine sediment accumulation that encourages mussel colonization and persistence (Bossenbroek et al., 2018). Furthermore, we mostly sampled sparse to moderate macrophyte cover (e.g., <50%), uncharacteristic of dense macrophyte beds, which can limit mussel densities (Burlakova & Karatayev, 2007). Through substrate coarsening, annual winter drawdowns can reduce macrophyte densities (Carmignani & Roy, 2017), and may create less suitable mussel habitat over long time-scales. Further study is needed to better assess the interactive effects between mussel and macrophyte densities and water-level fluctuations. In contrast to previous studies, we found no significant correlations between mussel density and effective fetch, sediment depth, or substrate size class (e.g., Cyr, 2008; Cyr et al., 2012; Bossenbroek et al., 2018). We attribute the lack of these environment-density correlations to sampling limited gradients for our environmental covariates (e.g., effective fetch) and/or to winter drawdown outweighing other environmental effects.

Acute mortality in winter drawdown lakes

Mussel mortality varied within and among drawdown lakes. Surprisingly, mussel mortality was not correlated with drawdown rates. Our results match those of Galbraith et al. (2015) who found no difference in mussel mortality in experimental dewatering rates of 4 cm/day vs 8 cm/day and suggests that management strategies focused on altering drawdown rates is unlikely to reduce mortality. Similarly, drawdown magnitude had a negligible effect on mortality. We found a negative correlation between median particle size and dead mussel density, which in part, could reflect coarse substrates as poor habitat for living mussels and hence low densities exposed during drawdown. Accordingly, sites with finer substrates might harbor higher living mussel densities that represent sediment accumulation zones suitable for small/young individuals (Cyr et al., 2012) to colonize between drawdown events. Furthermore, given our pebble counts could not discriminate particles <1 mm, several sites with finer substrate could have been low in dissolved oxygen, unsuitable for juvenile growth and abundance (Polhill, V & Dimock, Jr., 1996; Sparks & Strayer, 1998). This in part could explain the higher variability of mortality at sites with finer substrates.

In two lakes (Wickaboag, Hamilton), we found low % mortality (0-7.2%) in the exposure zone despite having mussels in exposure zones during normal water levels, suggesting that mussels were largely able to find refuge to avoid mortality during dewatering and/or we underestimated mortality. Mussels can respond to drawdowns by tracking water levels via directed horizontal movement (Gough et al., 2012; Newton et al., 2015; Richardson et al., 2002) and permit survival during a drawdown event. We observed numerous sediment tracks roughly perpendicular to the waterline indicating attempted relocation during water recession. Our mortality estimates were lower than other studies (Samad and Stanley 1986, Gough et al. 2012, Galbraith et al. 2015) likely because of our survey design. For example, although we allowed >20 days after drawdown initiation, we may not have given enough time for mortality to occur at deeper depths in the exposure zone. Galbraith et al. (2015) found 25-35% mortality for *E. complanata* and *P. cataracta* after 10 days of exposure, but survival can drastically differ for longer stranding times (e.g., 15 weeks) as seen in other mussel species (Gough et al. 2012). Samad and Stanley (1986) observed 80% mortality of *E. complanata* after 25 days of exposure. Similarly, Howells et al. (2000) sampled zero live mussels burrowed in the exposure zone after 24 days. Therefore, winter drawdown durations in our study of >130 days may overwhelm burrowed mussels in the exposure zone, and may increase mortality at unexposed depths that experience lower water temperatures (Werner & Rothhaupt, 2008) and frozen sediment beneath ice cover associated with winter drawdowns. Finally, the size distribution of deceased mussels was similar to living buried mussels in drawdown zones (e.g., relatively small), suggesting a potential annual cycle of juvenile colonization into exposure zones during normal pool levels (i.e., peak activity) and subsequent susceptibility to stranding during drawdown.

Conclusions

Given the documented ecosystem services mussel populations provide including biofiltration, water-column and sediment nutrient coupling, and habitat structure for macroinvertebrates and primary producers (reviewed by Vaughn, 2018), the constraint of mussels deeper than the drawdown exposure zone may reduce these ecosystem services in the exposure zone. The extent of these potential functional losses relative to whole lake ecosystems may depend on winter drawdown regime character (e.g., magnitude, rate, timing, frequency) relative to mussel population density-depth distribution and population size. We encourage future research to examine the extent of potential ecosystem function loss in annual winter drawdown regimes. Any future increases in annual winter drawdown magnitude or rates in current drawdown regimes and application of winter drawdown to new lakes could expose relatively high mussel densities. Surveys that determine the lake-wide mussel distributions and the depth of maximum mussel density, as conducted elsewhere (e.g., Cyr, 2008; Cyr et al., 2017), may help to determine the drawdown magnitudes that will minimize impact upon areas of high mussel density in lake populations. Furthermore, estimating the rate and extent of mussel colonization into former exposure zones after reductions in magnitude or frequency would help in designing future winter drawdown regimes to minimize impacts; we might expect deep, infrequent drawdowns to cause mass mortalities after colonization. Developing sustainable winter drawdown regimes that meet stakeholder goals (e.g., macrophyte reduction, flood storage) while minimizing ecological integrity loss, as seen in hydro-economic models for hydropower reservoirs (Hirsch, Schillinger, Weigt, & Burkhardt-Holm, 2014), will help mitigate future threats to mussel populations and lake ecosystems.

Tables

Table 5.1. Study lake environmental characteristics.

Sample types include live surface mussels (S), live surface and buried mussels (SB), and mussel mortality (M). Lakes located in the Housatonic (H) River Basin are in the western region (w) of Massachusetts, and the Connecticut (C), and Thames (T) River Basins in the central region (c). Drawdown magnitude and duration are based on means for ≥2 annual drawdown events. Drawdowns are conducted at an annual frequency in drawdown lakes. NA = not applicable. Water chemistry (TP = total phosphorous, Chl-a = chlorophyll-a, secchi depth, and alkalinity) are averages based on 2-3 epilimnetic summer samples taken at the deepest point of the lake. Lakeshore development is the number of buildings within a 100m buffer from lake shorelines.

Lake	Treatment	Sample Type	River Basin/ Region	Drawdown Magnitude (m)†	Drawdown Duration (days)	Decade Drawdown Implemented	Surface Area (km^2)	Mean (Max) Depth (m)	TP (µg L^{-1})	Chl-a (µg L^{-1})	Secchi (m)	Alkalinity (CaCO$_3$ mg L^{-1})	Lakeshore Development (buildings km^{-2})
Buel	Control	S, SB	H/w	0.21	164	2010s	0.83	5.1 (14.4)	12.9	1.3	4.3	141.3	291.6
Congamond	Control	S, SB	C/c	0.13	NA	NA	1.93	5.6 (14.1)	22.3	3.1	3.1	49.2	376.7
Quacumquasit	Control	S, SB	C/c	0.12	NA	NA	0.94	7.6 (25.7)	13.5	1.3	4.9	11.7	325.2
Ashmere	Drawdown	S, SB, M	H/w	0.83	198	1950s	1.14	3.4 (8.3)	6.1	2.2	3.1	30.6	322.2
Greenwater	Drawdown	S, SB	H/w	0.51	155	1950s	0.38	5.0 (18.6)	4.1	0.6	6.5	24.8	178.2
Hamilton	Drawdown	S, SB, M	T/c	0.77	137	1990s	1.68	1.8 (6.4)	1.7	3.3	1.9	8.9	525.2
Richmond	Drawdown	S, SB, M	H/w	0.70	137	1960s	0.95	2.9 (17.2)	6.4	0.9	4.4	74.9	259.7
Stockbridge	Drawdown	S, SB, M	H/w	1.13	157	1980s	1.60	5.4 (15.9)	6	1.1	5.2	122.4	257.6
Wickaboag	Drawdown	S, SB, M	C/c	0.58	178	1960s	1.30	1.9 (3.8)	14.3	6.5	1.3	8.9	479.3
Garfield	Drawdown	M	H/w	1.91	178	1970s	1.11	3.8 (10.8)	23.1	2.2	4.2	49.0	217.3
Goose	Drawdown	M	H/w	1.50	188	1920s	1.30	5.0 (16.3)	8.7	0.7	5.0	18.2	194.0
Onota	Drawdown	M	H/w	1.25	156	1970s	2.66	4.1 (24.7)	10.0	1.1	5.2	72.2	237.6
Otis	Drawdown	M	C/c	2.26	240	1960s	4.21	4.5 (17.4)	4.8	2.7	3.3	9.7	289.3

†For control lakes, drawdown magnitude refers to natural, seasonal low water level (Congamond and Quacumquasit) or very minimal drawdown (e.g., <0.5m) at Buel.

Table 5.2. Model comparison of top mussel models.

Summary of the top models ($\Delta\text{AIC}_c<5$) and random intercept of lake models (for comparison) for each mussel response variable. K is the number of model parameters, which includes an area offset for mussel density models. Models for surface and buried abundance at the quadrat level are comprised of conditional predictor terms (Cond) including fixed and random effects, and zero-inflation predictors (ZI). Random intercepts are indicated in parentheses.

Mussel Response Model	K	AIC_c	ΔAIC_c
Surface Density, transect 0.5m			
Drawdown*slope	5	226	0
Drawdown + slope	4	228.7	2.6
Random (lake)	3	253.8	27.8
Surface Density, transect 1m			
Basin + drawdown	5	352.9	0
Basin + drawdown + effective fetch	5	355.1	2.2
Basin + drawdown + macrophyte cover	5	355.2	2.3
Basin + drawdown + slope	5	355.2	2.3
Basin	3	356.6	3.7
Basin + macrophyte cover	4	357.6	4.8
Random (lake)	3	377.3	24.5
Surface & Buried Density, transect			
Drawdown + 1-m surface mussel density	4	205.9	0
Drawdown	3	206.8	0.8
Drawdown + macrophyte cover	4	208.1	2.2
Drawdown + slope	4	209.3	3.4
Drawdown + depth to refusal	4	209.5	3.5
Drawdown + effective fetch	4	209.7	3.7
Random (lake)	3	210.9	5
Surface & Buried Abundance, quadrat			
Cond: Drawdown*relative depth + macrophyte cover + Random (site nested in lake); ZI: relative depth	9	786	0
Cond: Drawdown*relative depth + Random (site nested in lake); ZI: relative depth	8	787.8	1.9
Random (site nested in lake)	3	903.2	117.3
Surface Mortality Density			
Median pebble size	3	170.0	0
Median pebble size + mean drawdown amplitude	4	171.9	1.9
Median pebble size + mean drawdown rate	4	172.7	2.7
Random (lake)	3	178.1	8.1

Table 5.3. Parameter estimates of top mussel models.
Parameter estimates of the best performing models of mussel density and abundance. Predictor variables with DDYes, DDNo, (random), or (ZI) indicate the presence and absence of drawdown, random intercepts, and zero-inflated components of a model respectively. Random effect predictor estimates are variances.

Mussel Response	Predictor	Estimate (SE)	*p*-value
A) *Surface Density, transect 0.5m*	DDYes – DDNo	-7.62(1.2)	**<0.001**
	Slope	-0.12(0.31)	0.690
	Drawdown*Slope	1.07(0.45)	**0.020**
B) *Surface Density, transect 1m*	DDYes - DDNo	1.06(0.39)	**0.006**
	Western - Central	-4.63(0.39)	**<0.001**
C) *Surface + Buried Density, transect (based on quadrat sampling)*	Control (Intercept)	2.58(0.54)	**<0.001**
	Drawdown	-3.33(0.80)	**<0.001**
	Surface Mussel Density at 1m Depth	0.83(0.49)	0.091
D) *Surface + Buried Abundance, quadrat*	Control (Intercept)	0.25(0.97)	0.799
	Drawdown	-3.3(1.42)	**0.021**
	Relative Depth	0.17(0.06)	**0.003**
	Macrophyte Cover	0.19(0.09)	**0.042**
	Drawdown*Relative Depth	1.06(0.24)	**<0.001**
	Site:Lake (random)	2.01	-
	Lake (random)	2.06	-
	Intercept (ZI)	-3.84(0.92)	**<0.001**
	Relative Depth (ZI)	-1.88(0.62)	**0.003**
E) *Surface Mortality Density*	(Intercept)	-3.98(0.26)	**<0.001**
	Median Pebble Size	-0.96(0.29)	**<0.001**

Figures

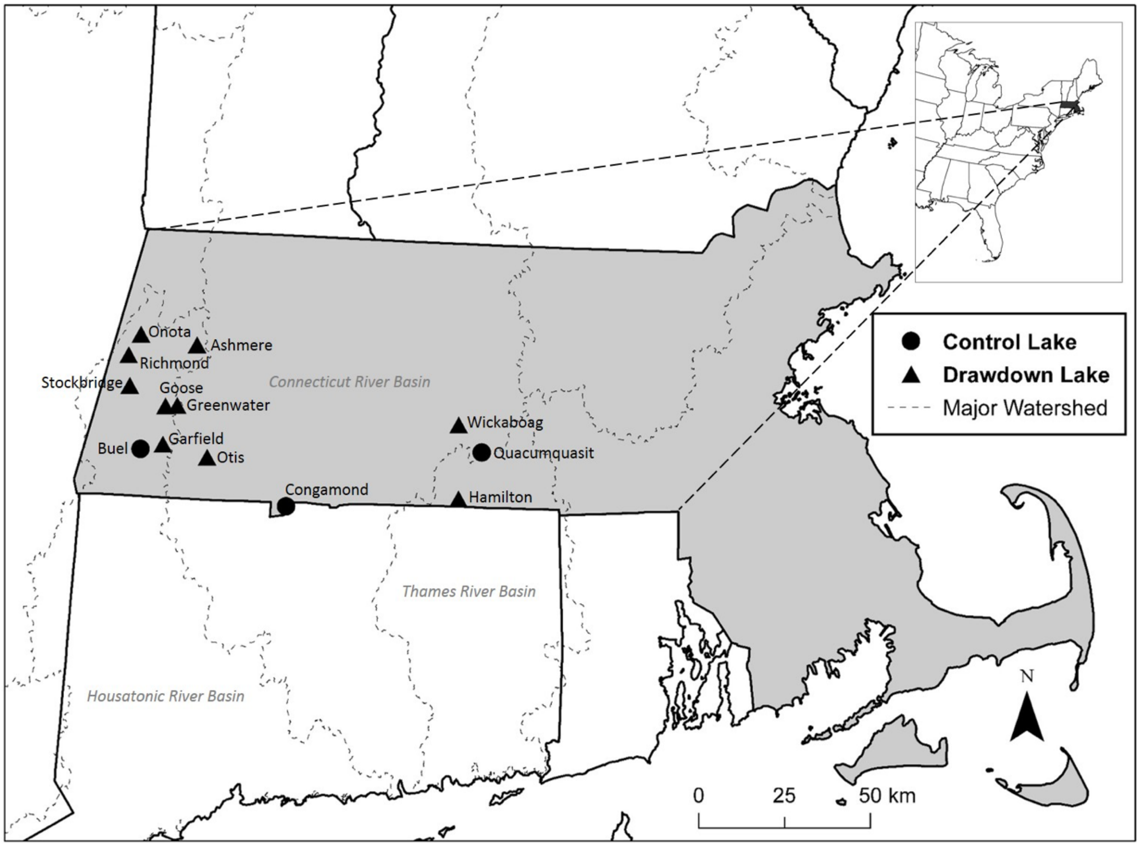

Figure 5.1. Map of study lakes.
Location of control (circle, n = 3) and drawdown (triangle, n = 10) study lakes in the Housatonic, Connecticut, and Thames River Basins in western and central Massachusetts, USA.

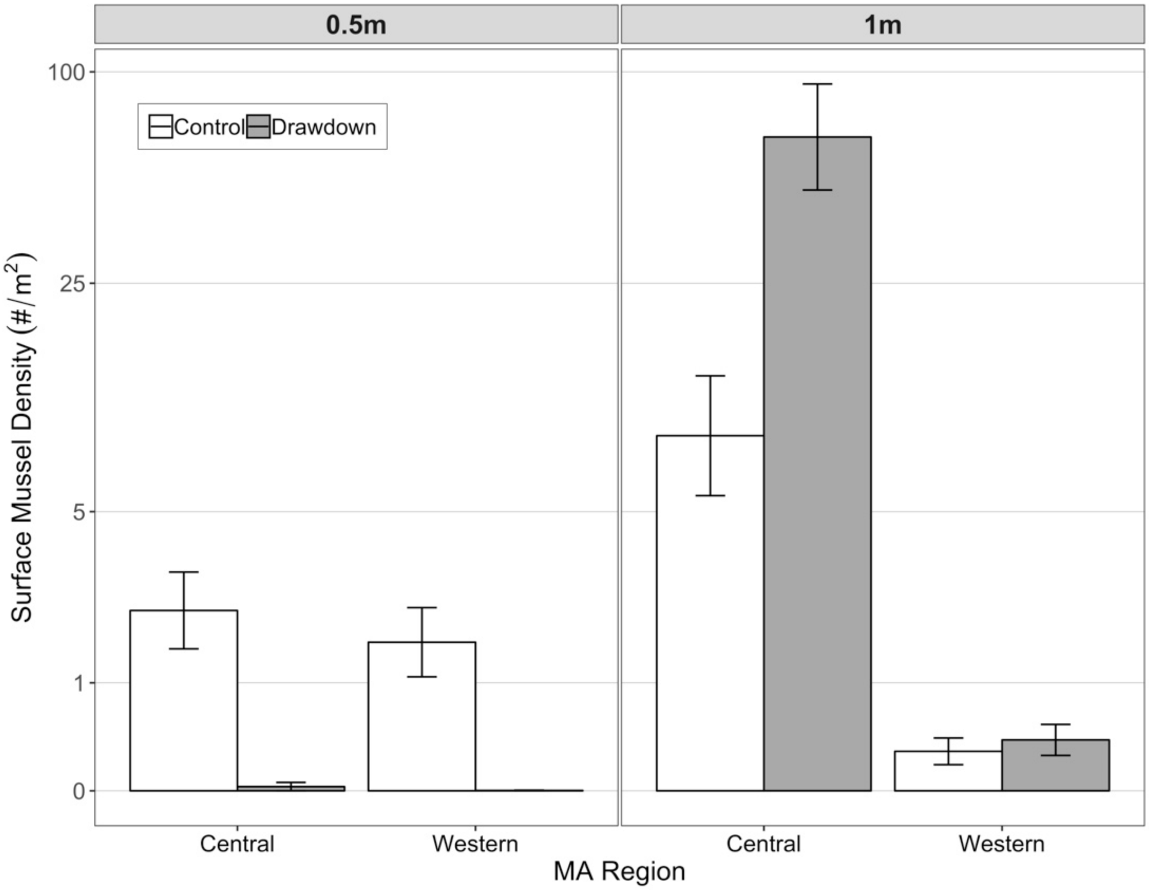

Figure 5.2. Surface mussel densities.
Mean surface mussel densities at 0.5-m (left panel) and 1-m transects (right panel) in drawdown (gray bars) and control lakes (white bars) across geographic area in MA (n_{site} = 36, n_{lake} = 9). Error bars represent one gaussian standard error. The x-axis is log(x+1) transformed.

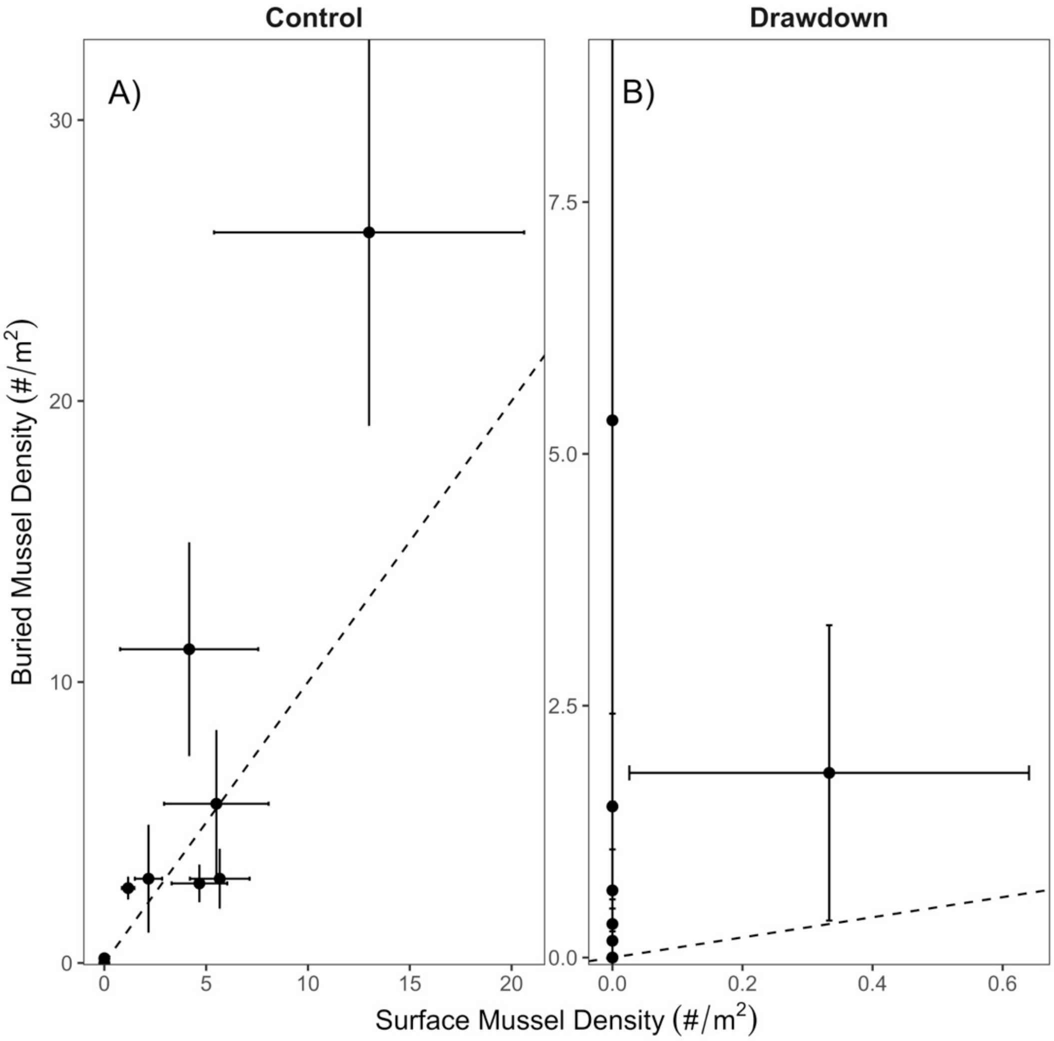

Figure 5.3. Surface versus buried mussel densities.
Mean site surface and buried mussel densities within A) 3 control (n_{site} = 9) and B) 3 drawdown lakes (n_{site} = 9) based on quadratic systematic sampling at the 0.5-m depth contour. Error bars represent 1 standard deviation. Points above 1:1 lines (dashed) indicate higher buried mussel density relative to surface mussel density. Note x- and y-scales differ between panels and 3 sites within drawdown lakes had zero mussels so are not shown.

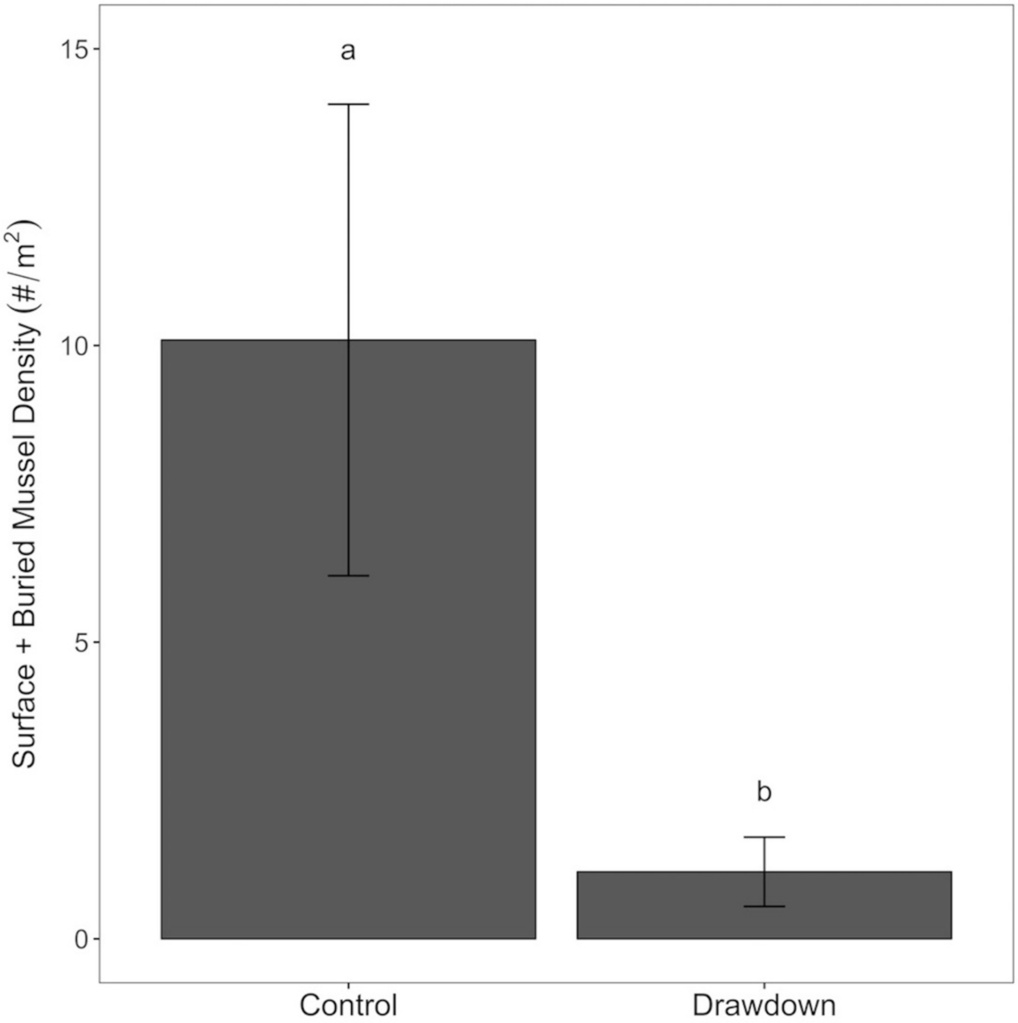

Figure 5.4. Mussel densities from systematic quadrat surveys.
Surface and buried mussel density from systematic quadrat surveys at 0.5-m (n_{site} = 18, n_{lake} = 6). Error bars represent 1 standard error based on a gaussian distribution. Different letters indicate statistically significant differences at the *p* = 0.05 level.

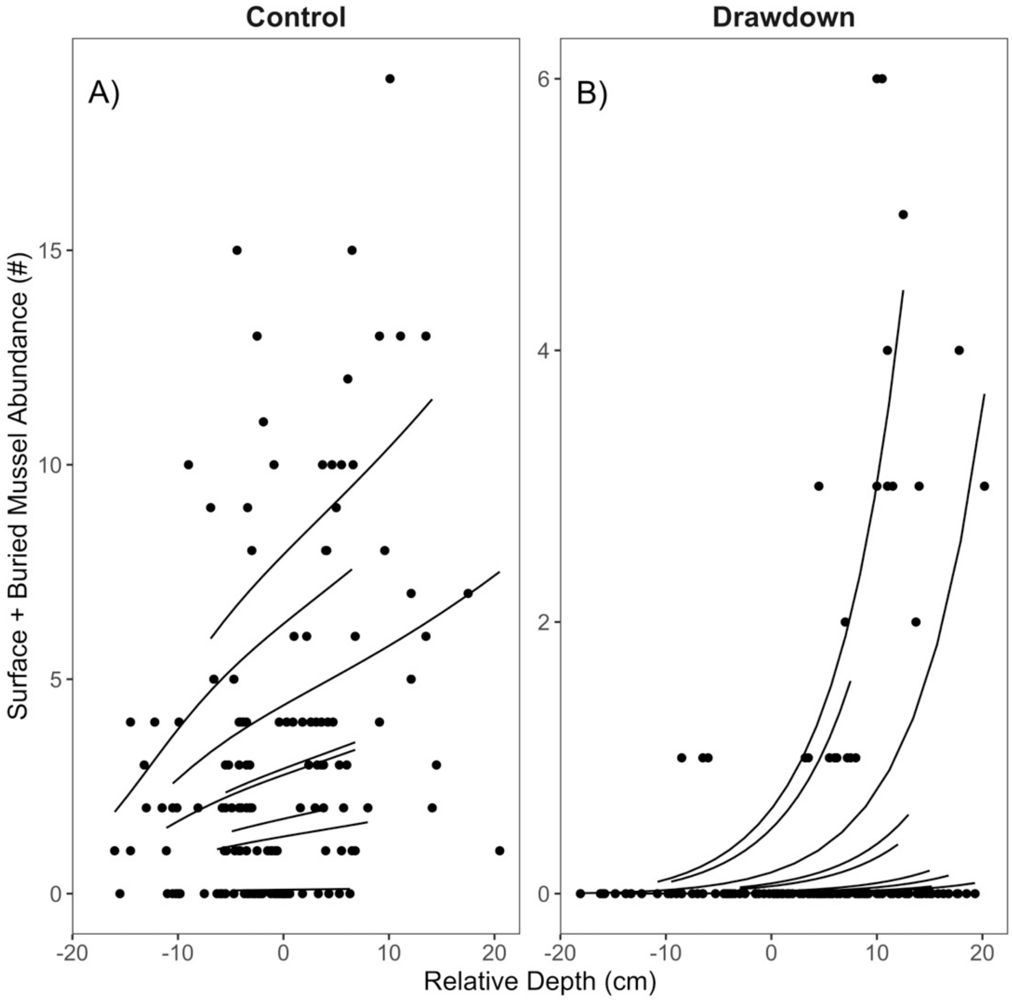

Figure 5.5. Mussel density versus relative depth.
Modeled relationship between relative depth and surface and buried mussel abundance at the quadrat-level for A) control and B) drawdown lakes ($n_{lake} = 6$). Relative depth is the difference between quadrat sampling depth and 0.5m depth contour such that 0 cm relative depth = 0.5-m contour and positive values indicate depths sampled deeper than the 0.5-m contour. Each line represents a single site ($n_{site} = 18$). Data derives from quadrat systematic sampling. Note difference in y-axis scales between panels.

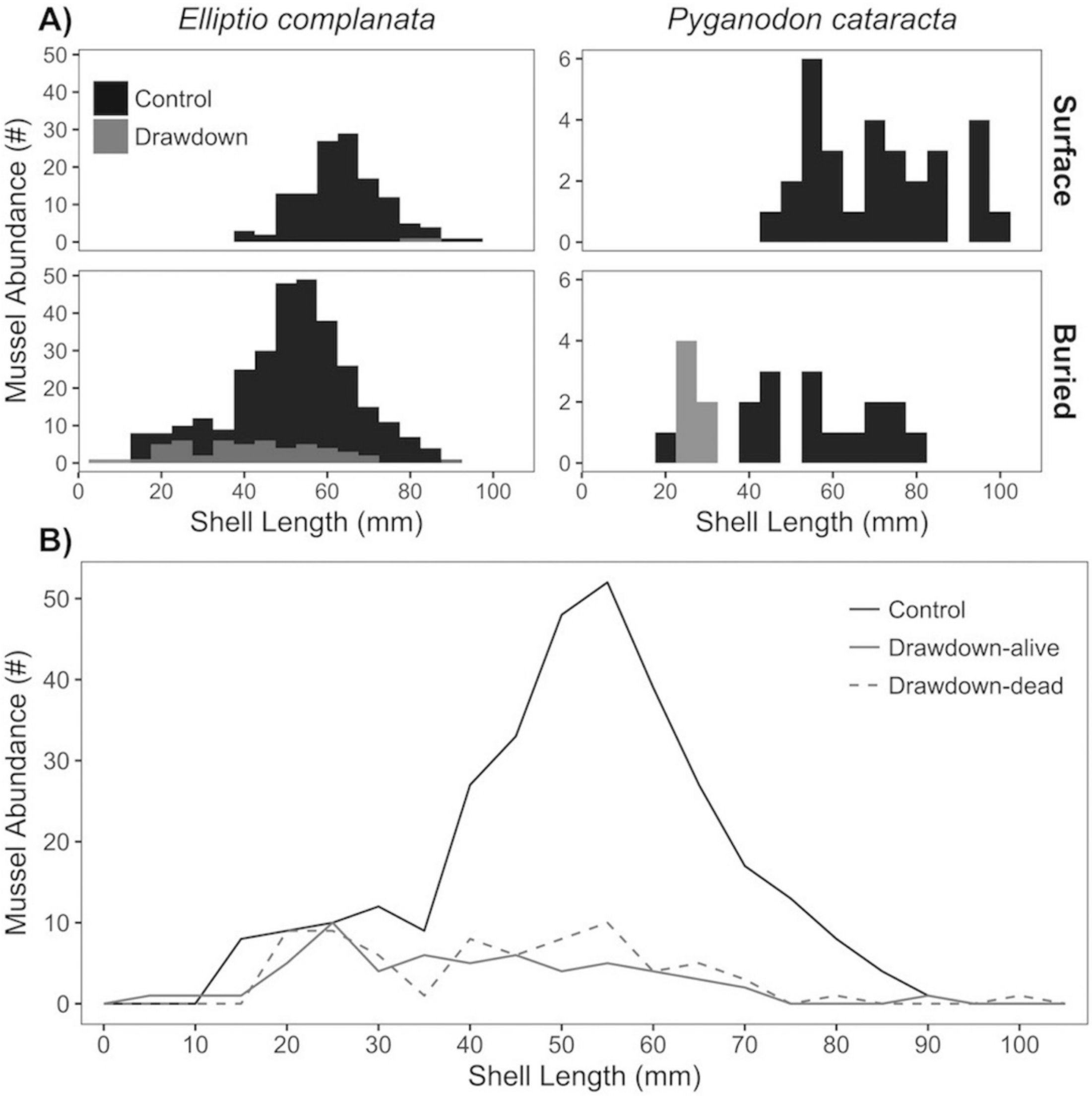

Figure 5.6. Shell-length frequency distributions.
Shell-length frequency distributions for **A)** *E. complanata* and *P. cataracta* at the sediment's surface and buried in control (black) and drawdown (gray) lakes. Data derived from quadrat systematic sampling at the 0.5-m depth contour ($n_{site} = 18$, $n_{lake} = 6$). Shell-length frequency distributions for **B)** buried mussels in control lakes (n = 3) and drawdown lakes (n = 3), and stranded mussels in drawdown lakes (n = 9) for pooled species.

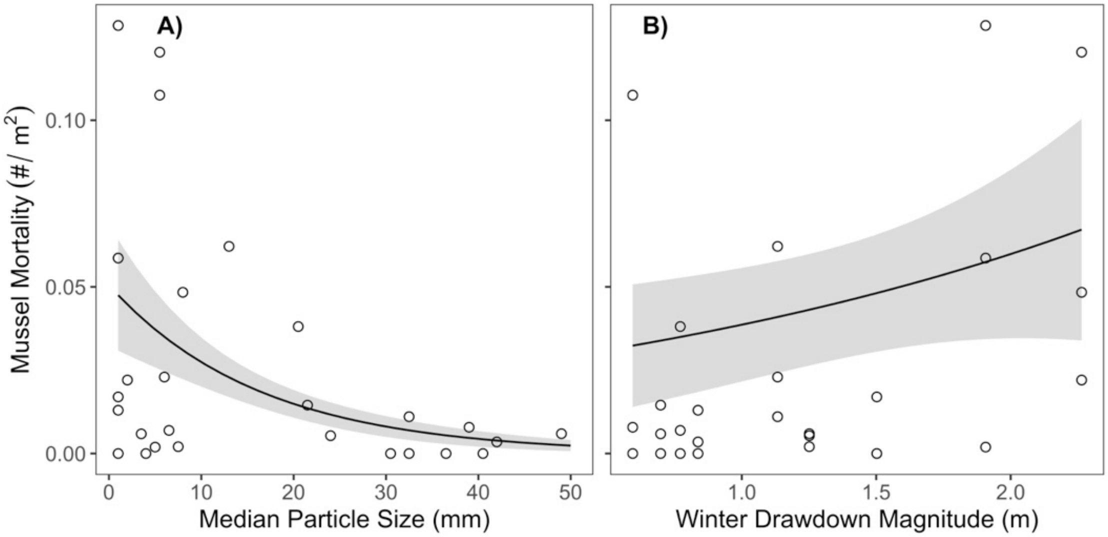

Figure 5.7. Mussel mortality versus sediment size and drawdown magnitude. Modeled relationship between site-level mussel mortality (n_{site} = 27, n_{lake} = 9) and median particle size A), abundance = $e^{(0.061x - 2.986)}$ + log(site area), $p < 0.001$) and drawdown amplitude B), $p = 0.343$), conditioned on median particle size. Error bands represent one standard error.

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CHAPTER 6

INFLUENCE OF ANNUAL WINTER WATER LEVEL DRAWDOWNS ON LITTORAL MACROINVERTEBRATE ASSEMBLAGES IN MASSACHUSETTS RECREATIONAL LAKES

Introduction

Lake water level fluctuations structure the habitat and resource heterogeneity that supports littoral biodiversity and productivity important for whole lake ecosystem functioning (Coops and Hosper 2002; Evtimova and Donohue 2015). This biodiversity is reflected in littoral macroinvertebrate communities that show distinct assemblages among physicochemical mesohabitats across macrophyte beds and inorganic substrate conditions (Tolonen et al. 2001; White and Irvine 2003; Heino 2008). While natural fluctuations can foster diverse communities, regulated water level fluctuations that exceed the natural variability of water level events across temporal scales are a major threat to littoral macroinvertebrate communities and hence to lake ecological integrity (Wantzen et al. 2008; Zohary and Ostrovsky 2011).

Among regulated water level regimes, annual wintertime drawdowns are practiced throughout boreal and temperate climate zones to achieve numerous anthropogenic goals including hydropower, flood storage, macrophyte control, and shoreline infrastructure protection (Cooke et al. 2005; Mjelde et al. 2012). Winter drawdowns can alter littoral macroinvertebrate assemblages through direct effects of desiccation and freezing, and indirectly through physicochemical resource change

(Carmignani and Roy 2017). With increases in winter drawdown magnitude, taxa richness tends to decline and taxonomic composition shifts (Kraft 1988; Aroviita and Hämäläinen 2008; McEwen and Butler 2010; White et al. 2011). Insect taxa from orders Ephemeroptera, Trichoptera, Coleoptera, and Megaloptera are generally reduced or absent from winter drawdown lakes (Aroviita and Hämäläinen 2008; White et al. 2011; Sutela et al. 2013). Taxa that are limited in mobility, such as Bivalvia, are particularly sensitive to drawdown and abundances decline across drawdown magnitudes (White et al. 2011; Carmignani et al. 2019). Furthermore, semivoltine taxa (e.g., *Hexagonia*, *Oulimnius*) may be sensitive to winter drawdowns because of the potential exposure to multiple annual drawdown events (Aroviita and Hämäläinen 2008; Carmignani and Roy 2017); however, this effect has not been explicitly quantified. In contrast, total macroinvertebrate abundance show mixed responses to winter drawdowns potentially because of differences in magnitude, sample timing relative to refill to normal pool levels, and community compositions dominated by r-selected taxa (Carmignani and Roy 2017).

Although littoral macroinvertebrates in annual winter drawdown regimes have received more study in recent years (e.g., Trottier et al. 2019), several research gaps exist where winter drawdown regimes differ in hydrological character and with different lake environmental settings. For example, in Massachusetts recreational lakes, winter drawdowns are implemented as a tool to maintain recreational value and consequently drawdown magnitudes are relatively mild (e.g., < 2.5 m) and have been conducted annually for several decades. Less research focus has been given to these relatively mild drawdown magnitudes. Furthermore, lakeshore residential development typically co-occurs with winter drawdown practice in recreational lakes, which has been well documented as a major stressor to littoral macroinvertebrates (Mcgoff et al. 2013). Increased human shoreline modification linked to degradation of habitat heterogeneity results in altered and less diverse littoral macroinvertebrate composition (Brauns et al. 2011) with declines in Bivalvia, Gastropoda, Ephemeroptera, Trichoptera, and Crustacea (Porst et al. 2019). Similarly, littoral macroinvertebrate functional trait composition is altered from development with reduction in semivoltine and shredding taxa and increases in multivoltine, herbivore, or detritivore taxa (Brauns et al. 2007; Francis et al. 2007; Twardochleb and Olden 2016). To our knowledge, no previous study has quantified the co-occurring relative influence of winter drawdowns and lakeshore residential development on littoral macroinvertebrates. Lastly, previous studies have primarily focused on macroinvertebrate responses to winter drawdown associated with cobble-dominated benthic habitat frequently observed in oligotrophic north temperate-boreal hydroelectric reservoirs (e.g., Aroviita and Hämäläinen 2008; White et al. 2011). Limited investigation exists that accounts for differences at littoral mesohabitat scales and across mesohabitat types more common in meso- to eutrophic lakes including macrophyte stands (Trottier et al. 2019).

We assess the relative influence of winter drawdown magnitude on the abundance, taxonomic composition, and functional trait composition of shallow littoral macroinvertebrate assemblages in Massachusetts recreational lakes. Specifically, we test the influence of winter drawdown magnitude on littoral macroinvertebrates associated with specific littoral mesohabitats (e.g., cobble, macrophyte beds) and estimate the effects of other environmental covariates at lake and mesohabitat scales including lakeshore residential development. We expect drawdown magnitude to significantly structure the taxonomic and functional trait composition of littoral macroinvertebrates in both cobble and macrophyte habitats. We further predict that taxa with semivoltine life cycles and taxa with low mobility, traits hypothesized to be sensitive to drawdown, decline with increasing drawdown magnitude in both cobble and macrophyte habitats.

Methods

Study area

We chose 14 study lakes from a predefined list of 21 lakes in Massachusetts generated through a stratified random selection process to capture a winter drawdown gradient for studies of drawdown hydrology and drawdown impacts to littoral physical habitat (Figure 6.1; see Chapter 4 for methods). Study lakes were in the Northeastern Highlands and Northeastern Coastal Zones (level 3 ecoregions) located in the Housatonic, Connecticut, and Thames River watersheds (Figure 6.1). Inland Massachusetts has a continental temperate climate with four seasons. Mean minimum and maximum July and January temperatures for ecoregions in the Northeastern Highlands tend to be 1-3°C degrees lower than in Northeastern Coastal Zone (Griffith et al. 2009). Winter precipitation averages 21.6–25.4 cm (1981-2010) across the study area (National Oceanic and Atmospheric Administration, 2018). Lake watersheds have mixed land use with variable urban development ranging from 2-27% (median = 9%) with a general increase from west to east, and relatively small proportions of pasture (0-15%) and agriculture (0-8%). Total watershed forest cover ranged from 20-83% (median = 63%) among lakes. Forests are primarily composed of mixed deciduous and conifer stands including northern, central, and transition hardwoods. Lakes located in the Northeast Highlands are characterized by coarse-loamy to loamy soils and metamorphic bedrock or limestone derived coarse-loamy soils and calcareous bedrock. In the Northeast Coastal Zone, lakes are underlain with sedimentary bedrock and alluvium soils, metamorphic bedrock with coarse-loamy soils, or coarse-loamy and sandy soils (see Griffiths et al. 2009 for more detail).

Macroinvertebrate sampling

We sampled macroinvertebrates once for each lake in July–August in 2015 (n=11) or 2016 (n=3) within a 30-day period at summer pool levels. For each lake, we randomly split shorelines into 5 equal sections to disperse our sampling effort lake-wide. Within each section, we targeted 2 littoral mesohabitats that typically occur in our study lakes: cobble-dominant substrate (cobble) and macrophyte or macroalgal beds (macrophyte). If a mesohabitat type was not present in a shoreline section, we collected a duplicate sample within another randomly selected section. We collected 136 total samples with 5 samples per habitat type for each lake except for cobble habitat at Wyola where we collected 1 sample because of cobble habitat scarcity. We performed mesohabitat-specific sampling to optimize macroinvertebrate collection. All cobble samples were collected at the 0.5-m depth contour, but macrophyte habitat samples were taken variably between 0.5 and 0.8 m because of inconsistent presence of macrophyte beds at the 0.5-m depth. Cobble-associated invertebrates were sampled by a single snorkeler gently placing three 0.25 m x 0.25 m replicate quadrats over cobble. Stones and associated debris were transferred underwater into a 500-µm mesh bag and hand-scrubbed in a bucket. For macrophyte beds, we placed a 1-m^2 quadrat and took 3 successive 1-m long sweeps using a D-frame dip net. In addition, we placed a 0.25-m^2 quadrat within the larger quadrat, harvested the encompassed macrophytes, and vigorously washed in a bucket to detach associated invertebrates. All samples were filtered through a 500-µm mesh sieve and preserved in 70% ethanol for later identification.

Environmental data collection

Within each mesohabitat type, we measured covariates that can influence macroinvertebrate abundance and composition. At cobble mesohabitats we estimated epilithic chlorophyll-*a* concentration from three stones adjacent to sampling quadrats. Stones were scrubbed in a prescribed area (11.4 cm^2), residue diluted in deionized water, filtered onto a pre-combusted 0.7-µm microfiber glass filter, put on ice, and brought back to the laboratory. We determined chlorophyll-*a* concentration using EPA method 445.0 in vitro determination of chlorophyll-*a* by fluorescence (Arar and Collins 1997). We visually estimated percent fine sediment embeddedness. In macrophyte mesohabitat, we visually estimated macrophyte cover within the 1-m^2 quadrat and determined wet biomass for harvested macrophytes using a salad spinner to remove freestanding water.

At all mesohabitats, we estimated effective fetch following methods from Cyr (1998), bed slope (i.e., ratio of sampling depth to the distance between the high waterline and sample location), and recorded the presence of shoreline attributes (dock, house, beach, retaining wall, lawn, woody vegetation) and in-water features (emergent vegetation, inlet). Canopy cover was estimated at the high-water mark using a spherical densiometer. We also estimated environmental covariates at the lake-level. We estimated drawdown magnitude following methods from Carmignani et al. (2019) (see Chapter 4 or

5) as the mean difference between summer pool levels (i.e., spillway height or median summer water level) and the lowest winter drawdown water level. We sampled water quality parameters and determined secchi depth at the deepest part of each lake for two years between 2014 and 2017. In June, July, and/or August we collected surface water samples for total phosphorous (TP), alkalinity, dissolved organic carbon (DOC), and chlorophyll-*a*. Water quality methods are outlined in Chapter 4 and Carmignani et al. (2019). Lastly, we determined lakeshore development density as the number of buildings within a 100-m buffer around shorelines using the 2011–2014 MassGIS Building Structures (2-D) data layer.

Macroinvertebrate identification and trait assignment

We identified macroinvertebrates to mixed levels of taxonomic resolution to maximize cost and time efficiency while meeting taxonomic sufficiency and functional trait assignment (Jones 2008). Orders from the Arthropoda phylum (Ephemeroptera, Coleoptera, Collembola, Plecoptera, Trichoptera, Odonata, Diptera, Lepidoptera, Hemiptera, Megaloptera, Neuroptera) were typically identified to genus or family, except for the order Acariformes. Within Diptera, we classified the Chironomidae into Tanypodinae or non-Tanypodinae subfamily groupings. Annelida were identified into Oligochaeta and Hirudinea classes. Gastropoda and Bivalvia were typically identified to family, genus, or species. Copepoda, Cladocera, and to classes or subclasses for Annelida. The Crustacea phylum was identified to genus for orders Amphipoda, Isopoda, and Decapoda, left at order for Cladocera, and identified to orders for the class Copepoda. Other identifications included Nematoda and Turbellaria. We used dissecting scopes (Nikon SMZ745T) and taxonomic keys from Peckarsky et al. (1990), Jokinen (1992), Smith (1991), and Merritt et al. (2008) to aid identification.

We assigned taxa to functional trait states according to their voltinism, habit, feeding guild, and swimming ability (Appendix P). We used primary trait states for each taxa based on the US EPA Freshwater Biological Traits database (US EPA 2012) and Vieira et al. (2006). If taxa-trait information was absent from these databases we used taxonomic key descriptions to assign trait states (Peckarsky et al. 1990; Jokinen 1992; Merritt et al. 2008; Thorp and Rogers 2014). Taxa without trait information (e.g., non-Tanypodinae Chironomids) were removed from functional trait analyses because of limited taxonomic resolution resulting in the removal of 32.5–42.5% and 18.6–31.3% of abundance data from cobble and macrophyte habitats respectively. Trait states for voltinism were multivoltine (>1 generation/year), univoltine (1 generation/yr), and semivoltine (<1 generation/yr). Habit integrates a taxa's relationship with the substrate and its locomotive ability. Habit trait states were defined as burrower, climber, clinger, skater, sprawler, and swimmer. Functional feeding groups were collector-filterer, collector-gatherer, herbivore, predator, and shredder. Lastly, we defined swimming ability as the presence or absence of swimming capacity.

Statistical analyses

We analyzed taxonomic and functional metrics using general and generalized linear mixed models to fit various statistical error distributions and to account for nonindependence inherent in our nested study design (Bolker et al. 2009). For all macroinvertebrate response metrics, we ran separate analyses for each habitat type ($n_{cobble} = 66$, $n_{macrophyte} = 70$). We used negative binomial and Poisson error distributions with a log link for macroinvertebrate abundance and richness respectively to match the discrete nature of the data. Overdispersion was checked to ensure values approximated to one. To model Shannon diversity, we used gaussian and gamma error distributions and we used beta error distributions with a logit link to model the variation in semivoltine and non-swimmer proportions. Lastly, we used negative binomial error distributions with a log link and offset of total site abundance to model the relative abundance of *Amnicola* (Gastropoda: Hydrobiidae). We also considered the addition of a zero-inflation term for *Amnicola* in cobble habitat because of the high-frequency of zeros (48.9%, Warton 2005). We checked for patterns in the residuals to ensure an appropriate model fit.

Before model generation, we checked for covariate collinearity using scatterplot matrices (e.g., Pearson $r \geq 0.7$) for continuous predictors, and generalized inflation factors (e.g., GVIF > 3) among covariates using the car package in R (Fox & Weisberg, 2011, version 2.1-5). We found surface water chlorophyll-a and lakeshore development were positively correlated ($r = 0.74$) and therefore kept lakeshore development as a surrogate for chlorophyll-a in addition to accounting for other disturbance from lakeshore development on macroinvertebrates. Log-transformation was applied to lake area, cobble chlorophyll-a, and macrophyte biomass to achieve evenly spread distributions. We started with full predictor sets of known covariates that could affect habitat response variables and iteratively removed single non-significant ($p > 0.05$) predictors using Chi-square tests to simplify models and isolate important predictors. We considered drawdown magnitude, TP, lakeshore development, lake area, alkalinity, fetch, slope as predictors within both mesohabitats with the addition of embeddedness, cobble chlorophyll-a, cobble B-length in cobble habitat, and macrophyte cover and biomass in macrophyte habitat. All predictor variables were Z-scored transformed before analyses. We compared models using corrected Akaike Information Criterion (AICc) to determine the most parsimonious and plausible models for each habitat response variable (Burnham and Anderson 2004). Models were validated examining residual plots at predictor and model levels to ensure no patterns existed. We detected an outlier in the macroinvertebrate abundance in cobble habitat which was the cause of overdispersion, and subsequently modeled abundance with the outlier removed. All regression models were performed using the glmmTMB package (Brooks et al., 2017, version 0.2.1.0) in R (R Core Team, 2017, version 3.4.2).

We used constrained analysis of principal coordinates (CAP) to determine whether environmental gradients significantly structured macroinvertebrate taxonomic and functional compositions. We ran separate analyses for cobble and macrophyte habitats using log-transformed macroinvertebrate abundances. For the taxonomic ordinations, we dropped taxa with fewer than 5 observations from each habitat reducing the datasets from 138 to 49 and 64 taxa for cobble and macrophyte habitat respectively. Using a preliminary detrended correspondence analysis, we found gradient lengths for taxonomic and functional compositions were ≤2, suggesting linear response models such as CAP were appropriate. We selected z-score standardized predictor variables using a stepwise forward selection procedure that minimizes AIC using the same predictor set from the univariate models described above. We performed Monte-Carlo permutational tests (n = 1000) to assess the significance of the entire ordination (i.e., 3 axes solution), for each axis, and the marginal effects for each constraining variable. CAP analyses and permutational tests for significance were performed using the vegan package in R (Oksanen et al. 2019, version 2.5-3).

Results

Mean winter drawdown magnitudes varied from 0.21–2.26 m including two non-drawdown lakes (Congamond, Quacumquasit) with low winter water levels <0.15 m (Table 6.1). Lakes varied in trophic state (oligotrophic to mesotrophic), alkalinity (acidic to alkaline), and lakeshore development density (Table 6.1).

Macroinvertebrate abundance varied from 49 to 4,249 individuals across the 66 cobble habitat samples and 68 to 6,266 individuals across the 70 macrophyte habitat samples (Table 6.2). We identified taxa from 23 orders, 66 families, and 67 genera (Appendix Q). Across lakes, richness varied from 8 to 32 taxa in cobble habitat and 10 to 41 taxa in macrophyte habitat. Non-Tanypodinae subfamilies from the Chironomidae family was the average dominant taxa by abundance in both habitats, followed by *Stenonema* (Ephemeroptera: Heptageniidae) and *Choroterpes* (Ephemeroptera: Leptophlebiidae), and *Amnicola* in cobble habitat (Appendix R), and Cladocerans, *Amnicola*, and oligochaetes in macrophytes (Appendix S).

Macroinvertebrate abundance in both cobble and macrophyte habitats was best explained by TP and lakeshore development with additional predictors exclusive to each habitat. In cobble, abundance had significant positive correlations with TP, lakeshore development, and epilithic chlorophyll-*a*. The top model also included lake area, which had a marginally nonsignificant negative effect (Table 6.3). The replacement of lake area with drawdown magnitude was also a plausible top model, such that magnitude also displayed a nonsignificant negative effect (β = -0.14, SE = 0.082, p = 0.083; Table 6.4). Models without magnitude and lake area were also plausible models (Table 6.4). In macrophytes, macroinvertebrate abundance was also positively correlated with TP and lakeshore development, although the TP effect was not significant. Macrophyte cover also had a significant positive effect on abundance (Table 6.3). Drawdown magnitude was not correlated with invertebrate abundance in macrophyte habitat (β = 0.10, SE = 0.12, *p* = 0.406) and was not in top plausible models.

Models of macroinvertebrate richness generally reflected the trends found with abundance. Within cobble habitat, TP and lakeshore development had significant positive correlations with richness. Slope and cobble embeddedness also displayed significant positive effects (Table 6.3). The next plausible model included a nonsignificant negative effect of drawdown magnitude (β = -0.049, SE = 0.034, *p* = 0.150; Table 6.4). Richness in macrophyte habitat was best explained by significant positive effects of TP, lakeshore development, macrophyte cover, and alkalinity. Drawdown magnitude was not correlated with richness in macrophyte habitat (β = 0.04, SE = 0.03, *p* = 0.273) and was not in plausible models.

In cobble habitat, macroinvertebrate Shannon diversity was best predicted by significant positive correlations with lake area and slope, and a significant negative effect of effective fetch (Table 6.3). The next plausible model included a nonsignificant negative effect of drawdown magnitude as seen in abundance and richness in cobble habitat (β = -0.047, SE = 0.039, *p* = 0.232; Table 6.4). Macroinvertebrate Shannon diversity in macrophyte habitat was positively correlated to TP and lakeshore development, with the next plausible models including a nonsignificant negative effect of lake area and a positive effect of alkalinity (Tables 6.3, 6.4).

Macroinvertebrate taxonomic composition was significantly structured by drawdown magnitude and other environmental covariates in both habitats (Figure 6.2). Cobble and macrophyte ordinations constrained a total of 37.0% and 27.1% respectively and each ordination was significant (Figure 6.2a; cobble – Pseudo-$F_{7,58}$ = 5.07, p = 0.001; Figure 6.2b, macrophyte – Pseudo-$F_{6,63}$ = 3.89, p = 0.001). The first four CAP axes explained significant proportion of variation in cobble habitat (CAP1 - Pseudo-$F_{1,58}$ = 21.68, p = 0.001; CAP2 - Pseudo-$F_{1,58}$ = 4.04, p = 0.001; CAP3 - Pseudo-$F_{1,58}$ = 3.12, p = 0.013; CAP4 - Pseudo-$F_{1,58}$ = 2.65, p = 0.029) with the first two axes explaining 23.2% and 4.3% of variation. Constraining variables also individually explained significant proportions of taxonomic variation including lakeshore development (Pseudo-$F_{1,58}$ = 8.20, p = 0.001), TP (Pseudo-$F_{1,58}$ = 6.12, p = 0.001), lake area (Pseudo-$F_{1,58}$ = 3.37, p = 0.002), cobble chlorophyll-*a* (Pseudo-$F_{1,58}$ = 3.35, p = 0.008), drawdown magnitude (Pseudo-$F_{1,58}$ = 2.12, p = 0.027) and effective fetch (Pseudo-$F_{1,58}$ = 1.97, p = 0.043). CAP1 was positively correlated with lakeshore development and TP, and negatively correlated with magnitude. CAP2 was negatively correlated with cobble chlorophyll-*a*. Also, the ordinations indicate associations between particular taxa and the at the extremes of environmental gradients. For example, in lakes with high drawdown magnitude, low TP, and low lakeshore development, we found relatively low abundances of *Amnicola* gastropods, *Crangonyx* amphipods, and non-Tanypodinae chironomids and relatively high abundances of *Choroterpes* (Ephemeroptera: Leptophlebiidae) and *Stenonema* (Ephemeroptera: Heptageniidae).

For macrophyte habitat, the first 3 CAP axes explained a significant proportion of taxa composition (CAP1 - Pseudo-$F_{1,63}$ = 9.24, p = 0.001; CAP2 - Pseudo-$F_{1,63}$ = 5.91, p = 0.001; CAP3 - Pseudo-$F_{1,63}$ = 3.84, p = 0.001), with the first two CAP axes explaining 10.7% and 6.8% respectively. All constraining variables significantly contributed to taxa composition variation including lakeshore development (Pseudo-$F_{1,63}$ = 5.47, p = 0.001), macrophyte cover (Pseudo-$F_{1,63}$ = 4.57, p = 0.001), drawdown magnitude (Pseudo-$F_{1,63}$ = 4.21, p = 0.001), alkalinity (Pseudo-$F_{1,63}$ = 2.95, p = 0.002), lake area (Pseudo-$F_{1,63}$ = 2.54, p = 0.004), and TP (Pseudo-$F_{1,63}$ = 2.33, p = 0.011). CAP1 was negatively correlated with lakeshore development, TP, macrophyte cover, and alkalinity. Lake area and drawdown magnitude were negatively correlated with CAP2. Similar to cobble habitat, we found relative associations between taxa and environmental correlate extremes. We found relatively low abundances of *Amnicola* gastropods, *Caecidotea* isopods, and *Nectopysche* (Trichoptera: Leptoceridae) in high drawdown magnitude, larger lake surface area, low macrophyte cover, low TP, and acidic conditions. In contrast, high abundances of *Caenis* (Ephemeroptera: Caenidae), Cyclopida copepods, and Cladocerans were associated with high drawdown magnitude, small lake surface area, and high lakeshore development.

Constrained ordinations also explained significant variation in macroinvertebrate functional trait composition in cobble (Pseudo-$F_{5,60}$ = 11.30, p = 0.001; Figure 6.3a) and macrophyte habitat (Pseudo-$F_{6,63}$ = 5.08, p = 0.001; Figure 6.3b). Constraining environmental variables captured 48.5% of the functional trait variation in cobble habitat and 32.6% in macrophyte habitat. For cobble, the first two CAP axes explained significant proportions of functional composition (CAP1 - Pseudo-$F_{1,60}$ = 44.35, p =

0.001; CAP2 - Pseudo-$F_{1,60}$ = 7.35, p = 0.001) with 38.1% and 6.3% respectively. Furthermore, lakeshore development (Pseudo-$F_{1,60}$ = 20.46, p = 0.001), TP (Pseudo-$F_{1,60}$ = 12.57, p = 0.001), cobble chlorophyll-*a* (Pseudo-$F_{1,60}$ = 6.35, p = 0.002), and magnitude (Pseudo-$F_{1,60}$ = 5.11, p = 0.003) were significantly correlated to functional composition. Lakeshore development and TP were positively correlated with CAP1. Drawdown magnitude was split between CAP axes, with a negative correlation with CAP1 and a positive correlation with CAP2. Semivoltine taxa, climbers, herbivores, and taxa with no swimming ability were positively correlated with CAP1 and negatively correlated with CAP2 indicating that taxa with these traits were less abundant in high drawdown magnitude lakes and more abundant in lakes with high lakeshore development and TP. Relatively high abundances of taxa that are swimmers, collector filterers, or possessed multivoltine life cycles were positively correlated along CAP1 and CAP2 axes, corresponding to higher drawdown magnitudes, lakeshore development densities and TP conditions (Figure 6.3a).

For macrophyte habitat, the first two axes explained significant proportions of the macroinvertebrate functional composition (CAP1 - Pseudo-$F_{1,63}$ = 19.61, p = 0.001; CAP2 - Pseudo-$F_{1,63}$ = 7.12, p = 0.001) with 21.0% and 7.6% respectively. Individually, lakeshore development (Pseudo-$F_{1,63}$ = 11.16, p = 0.001), macrophyte cover (Pseudo-$F_{1,63}$ = 7.04, p = 0.001), drawdown magnitude (Pseudo-$F_{1,63}$ = 4.40, p = 0.005), alkalinity (Pseudo-$F_{1,63}$ = 2.76, p = 0.037), and macrophyte richness (Pseudo-$F_{1,63}$ = 2.56, p = 0.038) explained a significant proportion of the functional trait variation. For constraining variables, TP, macrophyte richness, alkalinity, and macrophyte cover were negatively correlated with CAP1 and CAP2 axes. Lakeshore development was negatively correlated with CAP1 and positively correlated with CAP2. Drawdown magnitude was positively correlated with CAP1 and CAP2 axes. Taxa with univoltine life cycles, climbers, clingers, herbivores, and non-swimmers were negatively correlated with CAP1 and CAP2, corresponding to high abundances of these taxa in high macrophyte cover, high macrophyte richness, and high TP conditions. In contrast, low abundances with these traits are associated with lakes with high drawdown magnitudes. Taxa with multivoltine life cycles, swimmers, and collector-filterers were negatively correlated with CAP1 and positively correlated with CAP2 suggesting high abundances of these taxa are associated with high lakeshore development (Figure 6.3b).

Results from the CAP analysis for functional traits were supported by the beta regressions for semivoltine and non-swimming taxa. According to univariate beta regressions, drawdown magnitude had a significant negative effect on the proportion of semivoltine taxa in cobble habitat but not in macrophyte habitat (Figure 6.4a,b). The top model for cobble habitat included a negative effect of drawdown magnitude ($\beta = -0.41$, SE = 0.12, $p < 0.001$) and a positive effect of TP ($\beta = 0.29$, SE = 0.11, $p = 0.010$) with the next plausible model also including a nonsignificant positive effect of slope. The top model in macrophyte habitat included a positive effect of slope ($\beta = 0.16$, SE = 0.060, $p = 0.008$, $AIC_c = -536.5$), with the addition of nonsignificant negative effects of drawdown magnitude ($\beta = -0.088$, SE = 0.062, $p = 0.159$) and TP ($\beta = -0.094$, SE = 0.059, $p = 0.112$) as the next plausible model ($AIC_c = -535.6$). Drawdown magnitude had a negative effect on non-swimming taxa in both habitats (Figure6.4c, d). The top model for non-swimming taxa in cobble habitat included a significant negative effect of drawdown amplitude ($\beta = -0.23$, SE = 0.10, $p = 0.030$) and a significant positive effect of

TP ($\beta = 0.35$, SE = 0.10, $p < 0.001$, $AIC_c = -113.9$). The next plausible model included a nonsignificant negative effect of cobble chlorophyll-*a* ($\beta = -0.16$, SE = 0.093, $p = 0.094$, $AIC_c = -113.8$). We found the same pattern in macrophyte habitat with a significant negative effect of magnitude ($\beta = -0.38$, SE = 0.14, $p = 0.010$) and nonsignificant positive effect of TP ($\beta = 0.23$, SE = 0.14, $p = 0.100$) as the top model.

Drawdown magnitude was the strongest predictor of *Amnicola* relative abundances in both littoral mesohabitats. In the top model for cobble habitat, *Amnicola* had significant negative correlations with drawdown magnitude ($\beta = -1.19$, SE = 0.239, $p < 0.001$) and alkalinity ($\beta = -0.95$, SE = 0.170, $p < 0.001$), and significant positive correlations with TP ($\beta = 0.65$, SE = 0.158, $p < 0.001$), lakeshore residential development ($\beta = 0.83$, SE = 0.157, $p < 0.001$), and mean cobble size ($\beta = 0.79$, SE = 0.158, $p < 0.001$). Additionally, drawdown magnitude was correlated with *Amnicola* absence in cobble habitat, showing an increased chance of observing *Amnicola* absence with increasing drawdown magnitude ($\beta = 1.19$, SE = 0.493, $p = 0.016$). Declines in *Amnicola* were evident in lakes with drawdown magnitudes > 0.84 m where we observed a median ± SD of 0 ± 1 *Amnicola* individuals per sample in lakes compared to a median of 18 ± 137 individuals with magnitudes < 0.77 m (Figure 6.5a). *Amnicola* was best predicted in macrophyte habitat by a significant negative correlation with drawdown magnitude ($\beta = -1.22$, SE = 0.266, $p < 0.001$) and macrophyte cover ($\beta = -0.35$, SE = 0.121, $p = 0.003$). Declines in *Amnicola* were most evident at drawdown magnitudes >1.2 m with a median of 0 ± 7 individuals compared to 55 ± 235 individuals at magnitudes < 1.2 m (Figure 6.5b).

Discussion

We provide evidence that annual winter drawdowns significantly contribute in structuring macroinvertebrate assemblage composition in multiple littoral mesohabitats as drawdown magnitudes increase up to < 2.3 m. Abundance of semivoltine and non-swimming taxa displayed significant declines with increasing drawdown magnitude supporting previously untested hypotheses. Furthermore, we found *Amnicola* gastropods may be a potential sensitive indicator of drawdown disturbance in multiple mesohabitats. In contrast, drawdown magnitudes showed weak correlations with macroinvertebrate abundance, richness, and diversity. Other environmental factors at local (e.g., cobble chlorophyll-a, macrophyte cover) and lake-level (e.g., TP, lakeshore residential development) scales were equally or more important than drawdown magnitude in explaining macroinvertebrate abundance, richness, diversity, and compositional variation. Our results suggest that annual winter drawdowns are a selective disturbance agent on littoral macroinvertebrate assemblages. Winter drawdowns may further homogenize lake macroinvertebrate assemblage taxonomic and functional composition due to losses in macrophyte habitat associated with winter drawdowns.

Total abundance, richness, and diversity

Drawdown magnitude showed no to weak correlations with abundance, richness, and diversity. These results are in contrast to previous studies (e.g., White et al. 2011, Trottier et al. 2019), but may be explained by the timing of our sampling in combination with our relatively short magnitude gradient as compared to other studies. Our sampling in July, approximately 3-4 months after refill to summer pool levels, likely provided enough time for most invertebrates to recolonize even at the highest drawdown magnitudes. Similarly, Aroviita and Hämäläinen (2008) conducted sampling 4 months after refill and found no trend between abundance and magnitude even at a larger magnitude range (0.11 – 6.75 m). Although richness is a more responsive metric to drawdown magnitude (Aroviita and Hämäläinen 2008, White et al. 2011) compared to mixed abundance responses (Kaster and Jacobi 1978; Haxton and Findlay 2008; McEwen and Butler 2010), relatively mild drawdown magnitudes combined with our sampling 3-4 months after refill likely allowed for invertebrate recolonization of similar richness across magnitudes. White et al. (2011) found richness declines at magnitudes >2 m supporting our weak trends with magnitudes primarily < 2 m. Also, Kraft (1988) found taxa recovered after 2-3 months at exposed depths from a 2.5 m drawdown magnitude after refill, a similar magnitude and timeframe for potential recolonization in our study.

Although drawdown magnitude was not important in explaining macroinvertebrate abundance, richness, and diversity in both littoral mesohabitats, macroinvertebrates in cobble habitat were consistently negatively correlated with drawdown magnitude in contrast to macrophyte associated macroinvertebrates. Differences in physical mesohabitat conditions may explain the differences in macroinvertebrate responses to drawdown magnitude among habitats. Macroinvertebrates linked to macrophyte beds associated with fine sediments may be less susceptible to drawdown exposure compared to hard-bottom substrates. Higher survival rates are found in organic and silt-dominated substrates versus coarser bed textures when exposed to winter conditions likely because of increased water retainment and decreased freezing susceptibility (Palomäki and Koskenniemi 1993; Koskenniemi 1994). Furthermore, recolonization rates can be faster in organic-rich substrates (Kaster and Jacobi 1978).

This suggests that cobble associated macroinvertebrate assemblages are more sensitive to winter drawdown disturbance and therefore are best to sample to detect drawdown effects.

Environmental factors other than drawdown magnitude better predicted littoral macroinvertebrate metrics. At the lake-level, lakeshore residential development density and TP had consistent positive correlations with abundance and richness in both littoral mesohabitats. Since lakeshore development was positively correlated with surface water chlorophyll-*a*, it is likely that these predictors represent nutrient loading that supports phytoplankton, and, in turn, macroinvertebrates. Since our lakes ranged from oligotrophic to mesotrophic (e.g., TP < 23.1 μg L^{-1}), we likely captured levels of primary productivity along the ascending limb of a larger unimodal relationship between lake productivity and invertebrate biomass and richness (Jeppesen et al. 2000; Tolonen et al. 2005). At the mesohabitat scales, epilithic chlorophyll-*a* and macrophyte cover had a positive effect on macroinvertebrate abundance and richness. Higher macrophyte cover could be representative of more physical structural heterogeneity linked to higher abundances and richness (Cheruvelil et al. 2002; St. Pierre and Kovalenko 2014) and confers effective refuge from predation (Tolonen et al. 2003; Rennie and Jackson 2005; Sass et al. 2006) and supports more epiphytic algae and organic detritus as food resources (Weatherhead and James 2001).

Taxonomic and functional composition

Winter drawdown magnitude was significantly related to taxonomic and functional trait compositional shifts in macroinvertebrates. In particular, *Amnicola* gastropods were one of the most relatively abundant taxa in both habitats that also displayed significant negative correlations with drawdown magnitude according to CAP and regression analyses. Furthermore, drawdown magnitude was the strongest predictor of *Amnicola* relative abundance among a suite of environmental factors. This is consistent with White et al. (2011) who found no Hydrobiidae gastropods in hydroelectric reservoirs with magnitudes >3 m, but gastropods were present in most lakes with magnitudes <3 m. Often, drawdown magnitude structured macroinvertebrate composition in tandem with gradients of lakeshore development, TP, and macrophyte cover. For example, higher relative abundances of *Amnicola* were associated with higher TP and macrophyte cover conditions. Concordantly, we found higher abundances of herbivores in high TP and high macrophyte cover conditions, also seen found in previous studies (Twardochleb and Olden 2016). Further investigation is needed across a broader range of water chemistry and magnitude conditions to determine if *Amnicola* can be used as a widespread indicator of drawdown disturbance. This can further aid conservation efforts of rare and imperiled gastropod species under threat to lake management activities that have similar ecological niches as *Amnicola*.

Several functional trait states were associated with drawdown magnitude. As hypothesized by Aroviita and Hämäläinen (2008), proportion of semivoltine taxa were inversely correlated with drawdown magnitude. Semivoltine taxa included Coleopterans (Psephenidae: *Ectopria*, Elmidae: *Optioservus*, *Oulimnus*), Unionida species (*Elliptio complanata, Pyganodon cataracta*), and Plecopterans (Peltoperlidae), all of which had low abundances in winter drawdown regimes (White et al. 2011; Carmignani et al. 2019). The annual frequency of winter drawdowns likely prevents summer recolonization into winter-exposed depths because a single generation experiences multiple annual drawdown events. The lack of a relationship between semivoltine taxa and drawdown magnitude in macrophyte habitat might indicate a buffering effect to direct drawdown effects because of associated fine sediment and organic matter that could inhibit mortality from drying and freezing. Also, other factors could better explain this relationship including site and lake differences in predation rates and macrophyte structural complexity (Sass et al. 2006). Semivoltine taxa in cobble habitat were also positively associated with TP, likely because many of the semivoltine taxa are herbivores (e.g., Coleopterans) and herbivores increase with phosphorous nutrient loading (Tolonen et al. 2003), supporting the dual influence of drawdown magnitude and TP on macroinvertebrate composition.

Non-swimming taxa were inversely correlated with drawdown magnitude, a finding consistent with White et al. (2011). This suggests non-swimming taxa have lower probabilities of tracking receding water levels, become stranded, and die of exposure and/or have slower recolonization rates after refill. The common non-swimming taxa in our study included Gastropoda, Bivalvia, Trichoptera, Megaloptera, and Coleoptera. These taxa generally corresponded to climber, clinger, and burrower habitat states, which also showed general negative associations with high drawdown magnitudes. In particular, relatively attached taxa like *Polycentropus* (Trichoptera: Polycentropodidae) were among the non-swimming taxa previously identified as indicative of non-drawdown conditions (Aroviita and Hämäläinen 2008). Our findings extend that of White et al. (2011) to include drawdown magnitudes < 3 m and macroinvertebrates in macrophyte mesohabitat.

Multivoltine, swimming, collector-filtering, and collector-gatherer taxa were characteristic of lakes with high drawdown magnitudes, high lakeshore development, and high TP conditions. These traits are known indicators of anthropogenic pressure to littoral macroinvertebrate communities (White et al. 2011; Kovalenko et al. 2014; Twardochleb and Olden 2016). Generally, annual winter drawdowns promote r-selected life history strategies, which can rapidly reproduce during normal water levels (i.e., in between annual drawdown events) and consequently can have high relative abundances (McEwen and Butler 2010). Furthermore, previous studies show relative increases in more generalist feeding strategies like collector-filterers (e.g., Copepoda, Cladocera) linked to higher magnitude water level fluctuations potentially because of opportunistic food resource strategies based on food availability (Evtimova and Donohue 2015). These functional trait states are also characteristic of high lakeshore development across mesohabitats, which was positively collinear with surface water chlorophyll-*a* and associated with higher macrophyte cover. Twardochleb and Olden (2016) similarly found swimming and multivoltine taxa associated with high human development conditions and Heino (2008) found positive effects of macrophyte cover on collector gatherer-swimming and herbivore-swimming taxa as seen in the present study. Increases in surface water chlorophyll-*a*, potentially from nutrient leaching from shorefront property, support higher abundances of zooplankton (Canfield and Jones 1996) supporting our observations of higher abundances of Copepoda and Cladocera. Overall, higher nutrient status via TP and lakeshore development (i.e., cholorphyll-a) promotes specific functional traits and taxa, which as suggested from the literature, degrades functional diversity (Heino 2008; Kovalenko et al. 2014, Twardochleb 2016) and beta diversity or taxonomic heterogeneity (Donohue et al. 2009; Mcgoff et al. 2013).

Management implications and conclusions

Littoral macroinvertebrates are key components of food webs and energy flow in lakes (Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2002). Taxonomic and functional shifts in macroinvertebrate communities as a function of magnitude might have important implications for population dynamics and condition of fishes that feed predominantly on littoral macroinvertebrates. For example, population declines of insectivorous fish species are correlated with diminished littoral invertebrates in high magnitude drawdown lakes (Sutela et al. 2013). Consequently, fish species may rely more heavily on pelagic and profundal energy resources than littoral resources because of a diminished littoral macroinvertebrate community in drawdown lakes (Black et al. 2003).

Multiple anthropogenic stressors are often present and interacting in lake ecosystems across different spatial and temporal scales. More research is needed in a wider range and combination of water chemistry conditions (e.g., TP), lakeshore development, and magnitude conditions at several spatial scales to fully estimate anthropogenic impacts. Specifically, shoreline modification in the form of soft (recreational beaches, riparian deforestation) and hard (e.g., retaining walls, riprap) shore alterations significantly alter littoral macroinvertebrate composition and reduce richness through degradation of littoral habitat heterogeneity (Brauns et al. 2007; Porst et al. 2019). However, the multitude of stressors related to lakeshore development, including increased nutrient loading, may have contrasting effects on invertebrate communities as we generally observed higher macroinvertebrate richness presumably via increased trophic status.

Winter drawdowns are generally correlated with reduced macrophyte cover and biomass with concordant increases in coarser sediments (Chapter 4, Turner et al. 2005). Although we did not estimate relative mesohabitat availability along the drawdown gradient, the potential reduction or loss of macrophyte beds lake-wide likely will negatively impact epiphytic and associated macroinvertebrate assemblages. The decline or alteration of macrophyte habitat-specific macroinvertebrate assemblage composition may decrease whole-lake macroinvertebrate compositional heterogeneity, ultimately leading to a relatively homogenized community associated with increased coarse (e.g., cobble, pebble) and non-vegetated fine sediments (Figure 6.6). Careful consideration is needed to determine the relative extent of macrophyte bed habitat exposure for a given drawdown magnitude to maintain macrophyte beds and its macroinvertebrate assemblage.

Understanding the ecological impacts from winter drawdown regimes provides a basis for science-based lake management. Littoral macroinvertebrates are increasingly used as an assessment tool to measure lake ecological status because of the consistent responses to hydromorphological anthropogenic pressures across regions (e.g., Porst et al. 2019) and have been specifically used to determine the ecological status of lakes with annual winter drawdown regimes in hydroelectric reservoirs (Sutela et al. 2013). Our results support the use of littoral macroinvertebrate communities as a bioassessment tool to measure winter drawdown disturbance. Semivoltine and non-swimming taxa could be used as indicative functional traits to measure winter drawdown disturbance (e.g., Coleopterans and freshwater mussels). Further, *Amnicola* gastropods may be a potential indicator of drawdown disturbance across littoral mesohabitats and could act as surrogate for imperiled gastropod species. Even at relatively mild drawdown magnitudes (<2 m), our results suggest more consideration is needed towards littoral macroinvertebrate communities when first implementing annual winter drawdown regimes or increasing drawdown magnitudes to help maintain ecological integrity and promote resilience to emerging stressors.

Tables

Table 6.1. Study lake-level environmental characteristics.

Lake-level environmental characteristics potentially important for macroinvertebrate assemblages. Lakes are listed in ascending order according to drawdown magnitude. Values for drawdown magnitude, TP, alkalinity, chlorophyll-*a*, Secchi depth, and DOC are means from 2-4 years. See text for more detail. Variable codes are TP = total phosphorous, DOC = dissolved organic carbon.

Lake	Lake Code	Drawdown Magnitude (m)	Surface Area (km^2)	TP (μg L^{-1})	Alkalinity (CaCO$_3$ mg L^{-1})	Chlorophyll-*a* (mg L^{-1})	Lakeshore Development (buildings km^{-2})	Secchi Depth (m)	DOC (mg L^{-1})
Quacumquasit	QUA	0.115	0.94	13.5	11.7	1.3	325.2	4.85	2.7
Congamond	COG	0.135	1.93	22.3	49.2	2.1	376.7	3.04	3.4
Buel	BUL	0.21	0.83	16.3	141.3	1.3	291.6	4.25	3.5
Greenwater	GRN	0.508	0.38	4.1	24.8	0.6	178.2	6.45	3.0
Wickaboag	WIC	0.594	1.30	14.3	8.9	6.5	479.3	1.29	4.1
Richmond	RCH	0.698	0.95	6.4	68.3	0.9	259.7	4.39	3.1
Wyola	WYO	0.709	0.50	10.3	2.9	1.3	476.9	3.59	3.8
Hamilton	HAM	0.771	1.68	1.7	8.9	3.3	525.2	1.83	4.1
Ashmere	ASH	0.837	1.14	6.1	29.7	2.7	322.2	2.55	4.0
Stockbridge	STK	1.133	1.60	6.0	124.2	1.1	257.6	5.23	2.7
Onota	ONT	1.251	2.66	10.0	72.2	1.1	237.6	5.20	2.4
Goose	GOS	1.502	1.30	8.7	18.4	0.7	194.0	4.94	2.9
Garfield	GAR	1.907	1.11	23.1	49.0	2.2	217.3	4.25	3.3
Otis	OTS	2.264	4.21	4.8	9.7	2.7	289.3	3.30	4.3

Table 6.2. Summary of macroinvertebrate metrics.

Mean ± standard deviation of invertebrate metrics used in general and generalized mixed model regressions (abundance, richness, Shannon diversity) and constrained analysis of principal coordinates (functional trait states, collector – can't swim).

Invertebrate Metric	Cobble		Macrophyte	
	Mean	SD	Mean	SD
Abundance	410.8	548.3	1052.1	948.3
Richness	17.4	5.4	24.6	6.6
Shannon Diversity	2.0	0.3	2.1	0.5
Collector-Gatherer (%)	25.1	12.6	30.4	15.9
Collector-Filterer (%)	5.8	8.9	17.3	21.0
Predator (%)	12.6	7.5	10.2	7.8
Herbivore (%)	29.3	17.1	20.3	17.2
Shredder (%)	0.1	0.2	0.2	0.6
Burrower (%)	1.0	1.7	0.9	1.3
Climber (%)	8.4	12.5	20.0	16.9
Clinger (%)	40.8	24.1	5.5	6.9
Sprawler (%)	10.1	7.0	19.6	14.4
Swimmer (%)	9.2	9.3	19.8	21.0
Multivoltine (%)	11.2	10.9	35.2	22.2
Univoltine (%)	54.0	18.4	29.4	18.2
Semivoltine (%)	1.7	3.3	0.4	0.8
Can't swim (%)	20.3	14.1	24.9	17.9
Can swim (%)	47.4	20.0	40.6	22.6

Table 6.3. Parameter estimates of top macroinvertebrate models.
Top generalized and general linear mixed models for invertebrate response metrics as a function of environmental covariates. Random I (Lake) indicates a random intercept term for lake identity with the associated variance and *H'* = Shannon Diversity. Predictors in bold indicate significant estimates at the $\alpha = 0.05$ level.

Invertebrate Metric	*K*	Predictor	Estimate	*P* value	Overdispersion
Abundance					
Cobble	7	**Intercept**	**5.63**	**<0.001**	0.981
		Lake Area	-0.14	0.054	
		TP	**0.32**	**<0.001**	
		Cobble Chl-*a*	**0.24**	**0.001**	
		Lakeshore Development	**0.61**	**<0.001**	
		Random I (Lake)	0.03		
Macrophyte	6	**Intercept**	**6.81**	**<0.001**	1.007
		TP	0.21	0.064	
		Lakeshore Development	**0.29**	**0.010**	
		Macrophyte Cover	**0.43**	**<0.001**	
		Random I (Lake)	0.076		
Richness					
Cobble	6	**Intercept**	**2.83**	**<0.001**	0.840
		TP	**0.17**	**<0.001**	
		Lakeshore Development	**0.13**	**<0.001**	
		Slope	**0.06**	**0.044**	
		Embeddedness	**0.09**	**0.004**	
		Random I (Lake)	$1.04e^{-10}$		
Macrophyte	6	**Intercept**	**3.17**	**<0.001**	0.984
		TP	**0.07**	**0.007**	
		Lakeshore Development	**0.12**	**<0.001**	
		Macrophyte Cover	**0.10**	**<0.001**	
		Alkalinity	**0.07**	**0.014**	
		Random I (Lake)	0.002		
H'					
Cobble	6	**Intercept**	**2.00**	**<0.001**	NA
		Lake Area	**0.10**	**0.006**	
		Slope	**0.10**	**0.002**	
		Fetch	**-0.09**	**0.018**	
		Random I (Lake)	0.002		
Macrophyte	5	**Intercept**	**0.76**	**<0.001**	NA
		TP	**0.083**	**0.002**	
		Lakeshore Development	0.052	0.057	
		Random I (Lake)	$1.5e^{-11}$		

Table 6.4. Model comparison of top macroinvertebrate models.
Summary of the top models (ΔAICc <2) and for random intercept of lake -only models for comparison. *K* represents the number of parameters. Predictor abbreviations are TP = total phosphorous, CobbChl-*a* = chlorophyll-*a* from cobble, ShoreDev = lakeshore residential development, Magnitude = drawdown magnitude, LakeArea = lake surface area, Embedd = cobble embeddedness, MphyteCover = macrophyte cover, RandI(Lake) = random intercept of lake. and *H'* = Shannon Diversity.

Model	*K*	AIC_c	ΔAIC_c
Abundance – *Cobble*			
TP + CobbChl-*a* + ShoreDev + LakeArea + RandI(Lake)	7	808.6	0
TP + CobbChl-*a* + ShoreDev + Magnitude + RandI(Lake)	7	808.8	0.2
TP + CobbChl-*a* + ShoreDev + RandI(Lake)	6	809	0.4
TP + CobbChl-*a* + ShoreDev + LakeArea + Alkalinity + RandI(Lake)	8	810	1.4
RandI(Lake)	3	827.7	19.1
Abundance – *Macrophyte*			
TP +ShoreDev + Mphyte Cover + RandI(Lake)	6	1092.9	0
TP +ShoreDev + Mphyte Cover + Slope + RandI(Lake)	7	1093.9	1
RandI(Lake)	3	1110.6	17.7
Richness – *Cobble*			
TP + ShoreDev + Slope + Emdedd + RandI(Lake)	6	369.4	0
TP + ShoreDev + Slope + Embedd + Magnitude + RandI(Lake)	7	369.8	0.4
TP + ShoreDev + Slope + Embedd + Magnitude + CobbChl-*a* + RandI(Lake)	8	371.1	1.7
RandI(Lake)	2	389.9	20.5
Richness – *Macrophyte*			
TP + ShoreDev + Mphyte Cover + Alkalinity + RandI(Lake)	6	435.3	0
TP + ShoreDev + Mphyte Cover + Alkalinity + LakeArea + RandI(Lake)	7	436.2	0.9
RandI(Lake)	2	453.9	18.6
H' – Cobble			
LakeArea + Slope + Fetch + RandI(Lake)	6	23.1	0
LakeArea + Slope + Fetch + Magnitude + RandI(Lake)	7	24.2	1.2
RandI(Lake)	3	30.5	7.4
H' – Macrophyte			
TP + ShoreDev + RandI(Lake)	5	105.1	0
TP + ShoreDev + Alkalinity + RandI(Lake)	6	106.0	0.9
TP + ShoreDev + Alkalinity + LakeArea + RandI(Lake)	7	106.8	1.7
RandI(Lake)	3	111.9	6.8

Figures

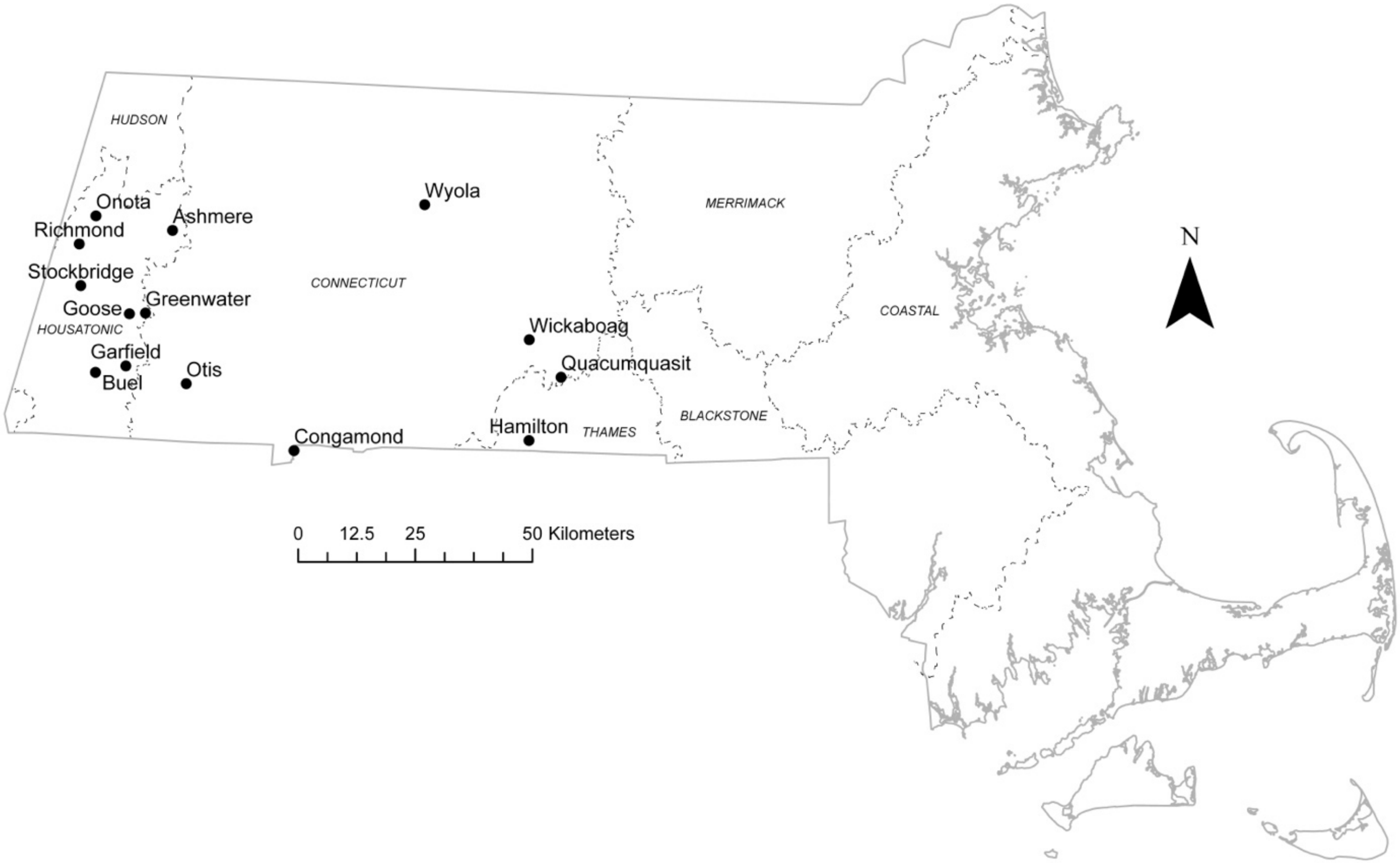

Figure 6.1. Map of study lakes.
Study lake locations in Massachusetts. Major watersheds are italicized.

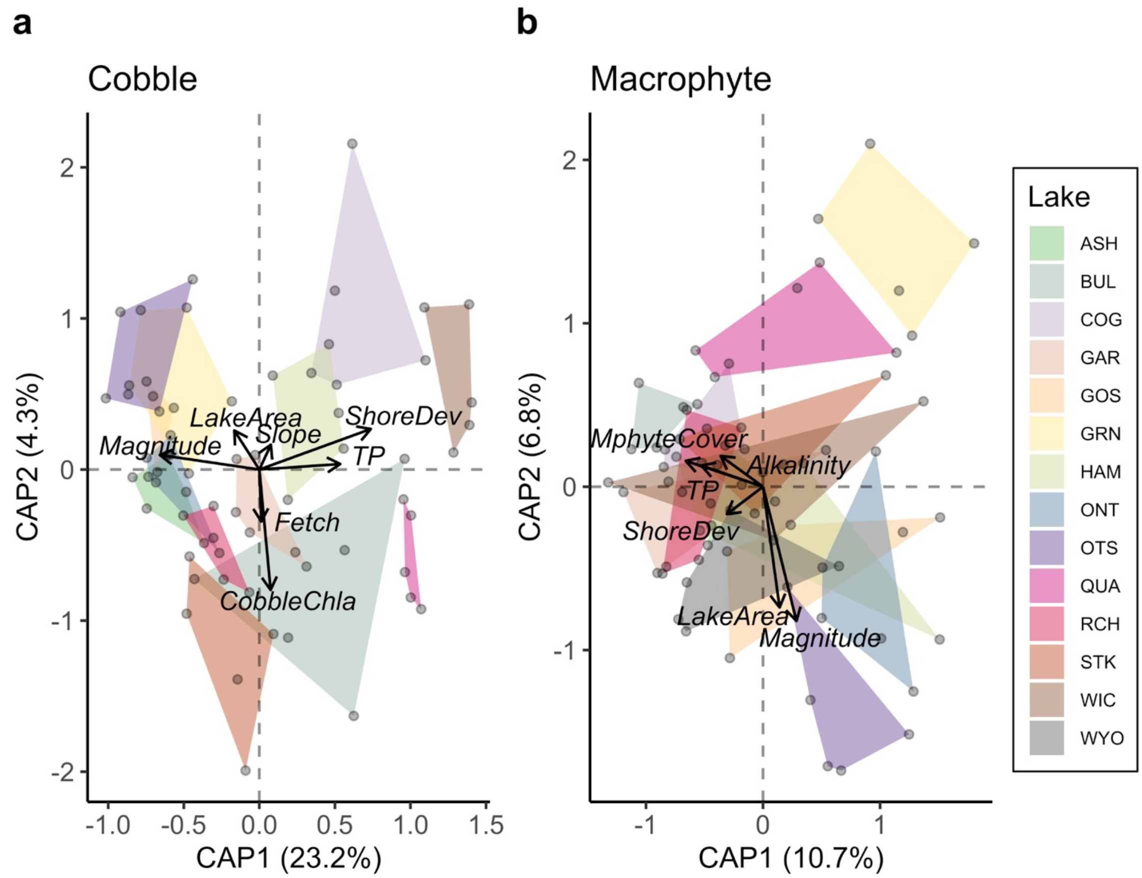

Figure 6.2. Ordination plots of macroinvertebrate taxonomic composition. Ordination plots from constrained analysis of principal coordinates (CAP) of littoral macroinvertebrate taxonomic composition from (a) cobble and (b) macrophyte mesohabitats. Points indicate intra-lake sites weighted by taxa scores. Polygons represent convex hulls color-coded by lake (see Table 1 for lake name codes) expect for WYO which had 1 sample in cobble habitat. Vectors represent constraining environmental predictors (see Table 4 for environmental vector name codes) that correlate with taxa composition and CAP1 and CAP2 axes. Vector directionality and length indicate the correlation to the axes and the importance to the ordination respectively. Percentages on axes represent percentage variation explained by CAP1 and CAP2 axes.

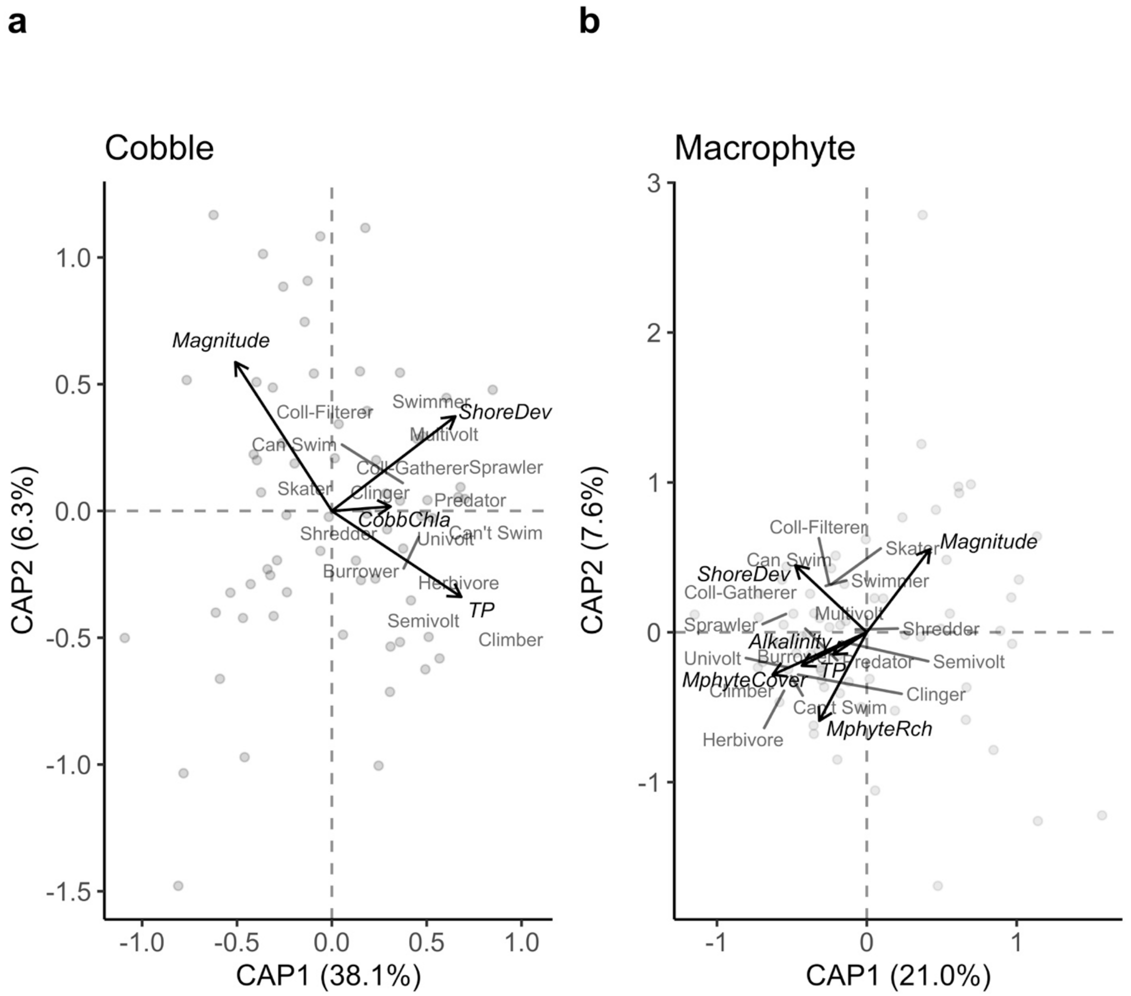

Figure 6.3. Ordination plots of macroinvertebrate functional trait composition. Ordination plots from constrained analysis of principal coordinates (CAP) of littoral macroinvertebrate functional trait composition from (a) cobble and (b) macrophyte mesohabitats. Points indicate intra-lake sites weighted by taxa scores. Vectors represent constraining environmental predictors that correlate with taxa composition and CAP1 and CAP2 axes. Vectors are TP = total phosphorous, CobbChl-*a* = epilithic chlorophyll-*a*, ShoreDev = lakeshore residential development, Magnitude = drawdown magnitude, LakeArea = lake surface area, MphyteCover = macrophyte cover, and MphyteRch = macrophyte richness. Percentages on axes represent percentage variation explained by CAP1 and CAP2 axes. Functional trait codes are functional feeding states: coll-gatherer = collector-gatherer =, coll-filterer = collector-filterer, predator, herbivore, shredder; voltinism: multivolt = multivoltine, univolt = univoltine, semivolt = semivoltine; habit: burrower, climber, clinger, sprawler, swimmer; presence of swimming ability: can swim or can't swim. Lines directed from functional trait states indicate true location in ordination space.

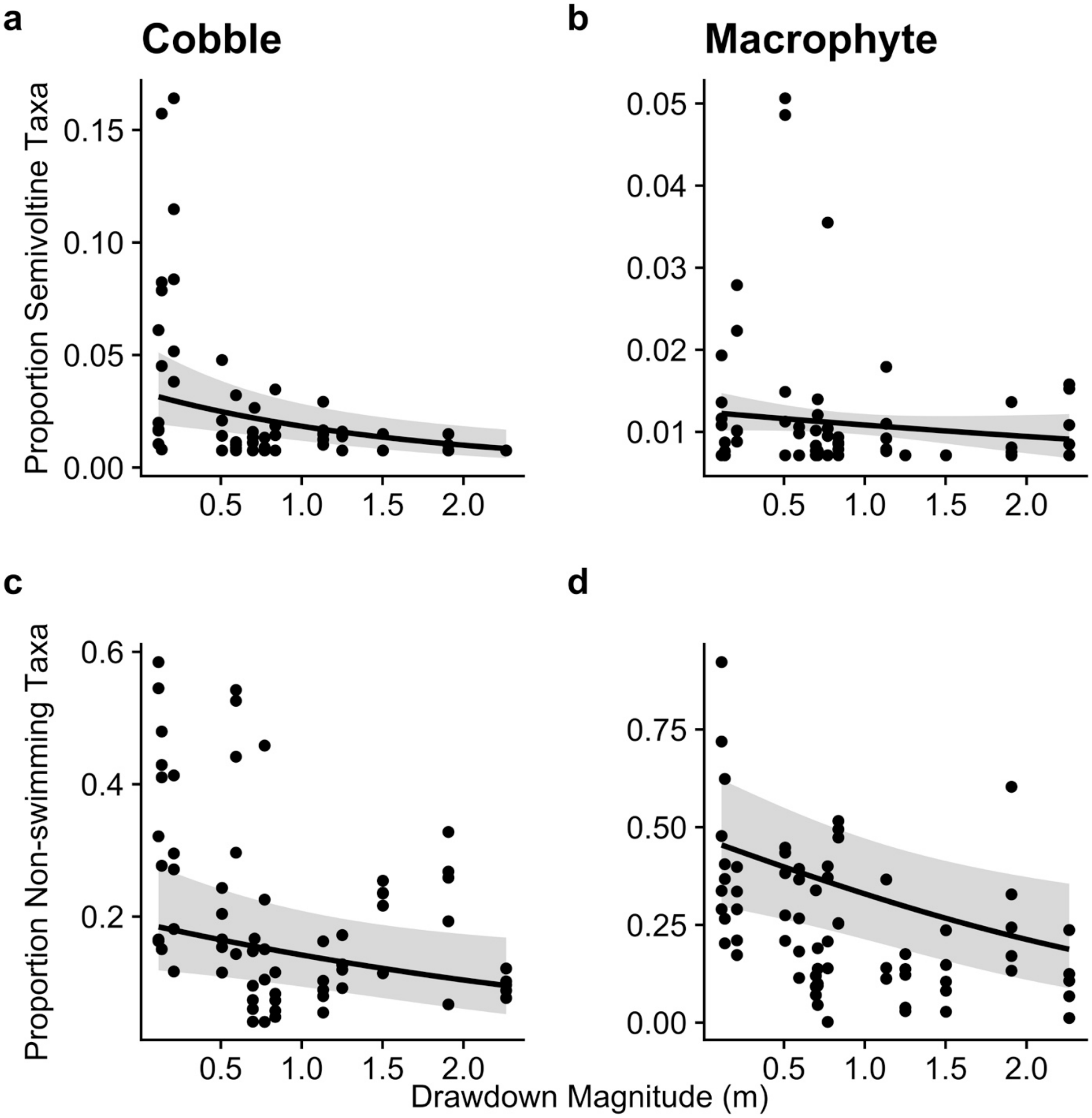

Figure 6.4. Semivoltine and non-swimming trait proportions versus drawdown magnitude.

Modeled relationship between drawdown magnitude and proportions of semivoltine taxa (a,b) and non-swimming taxa (c,d) in cobble (a,c) and macrophyte (b,d) habitat. Points represent raw values from intra-lake sites. Lines are model predictions with 95% confidence bands with other predictors held constant. Note differences in y-axis scales.

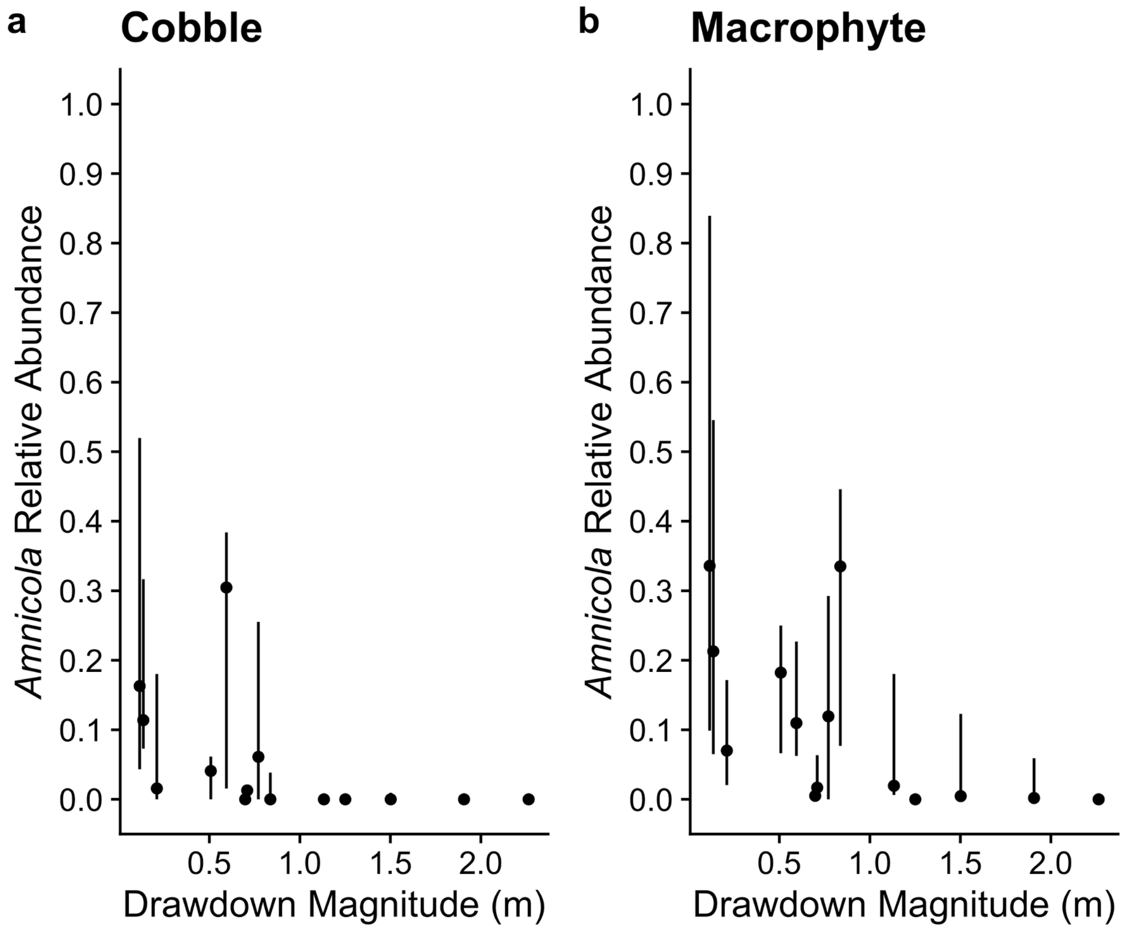

Figure 6.5. *Amnicola* relative abundance versus drawdown magnitude in cobble and macrophyte habitats.
Relative abundance of *Amnicola* gastropods in cobble (a) and macrophyte (b) littoral mesohabitats. Points represent lake medians and error bars represent lake ranges.

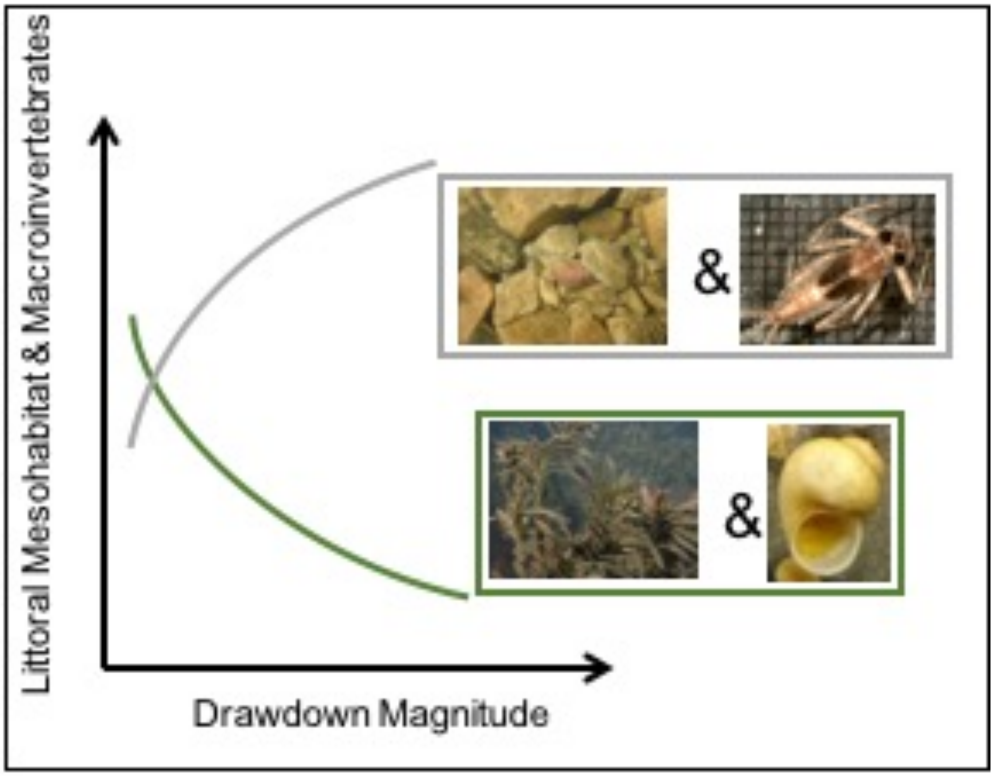

Figure 6.6. Conceptual diagram of littoral mesohabitat and associated macroinvertebrate assemblage as a function of drawdown magnitude. Potential relationship between littoral mesohabitat abundance (coarse substrate, macrophyte beds) and its associated macroinvertebrate assemblages as a function of drawdown magnitude. Winter drawdowns reduce macrophyte biomass and coarsen substrates (Chapter 4), potentially leading to lake-wide losses of macrophyte-associated macroinvertebrates and concurrent increases in cobble or coarse substrate-associated macroinvertebrates. *Stenonema* (Ephemeroptera: Heptageniidae) picture courtesy of Walters et al. (2017).

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CHAPTER 7

CONCLUSIONS

Effects of winter drawdowns

Annual winter water level drawdowns have been conducted for decades in many lakes in Massachusetts to maintain and enhance recreational value. In recent years, multiple environmental state agencies (e.g., MADEP, MassWildlife) have provided lake managers guidance to implement and practice winter drawdowns; however, scarce empirical data on winter drawdown hydrological regimes and estimates of impacts to non-target biota impedes regulating entities and lake managers from making ecologically-sustainable decisions. Therefore, this dissertation was designed to: (1) review the winter drawdown literature and identify knowledge gaps (Chapter 2), (2) monitor and characterize winter drawdown hydrological regimes (Chapter 3), and (3) identify the relative effect of winter drawdown on the physicochemical habitat and potentially susceptible biotic assemblages of lake littoral areas (Chapters 4–6, Figure 7.1).

In Chapter 2, I synthesized the varied and significant impacts of winter drawdowns to macrophyte, macroinvertebrate, and fish assemblages reported in previous literature. Winter drawdowns drive changes in assemblage composition and total abundance directly through exposure (e.g., desiccation, freezing) and indirectly through changes in littoral zone resources (e.g., habitat condition, water quality, food resources). Which species decline or increase depend on life history traits (e.g., voltinism, propagation strategy), mobility, and the degree of littoral zone resource use (e.g., food, spawning habitat). Additionally, increases in drawdown magnitude (e.g., ≥2-3 m) significantly alter littoral assemblage composition and reduce species richness (e.g., macrophytes, macroinvertebrates). However, the role of winter drawdown disturbance in whole-lake and cross-ecosystem nutrient and energy dynamics (i.e., food webs), the interaction with co-occurring anthropogenic pressures, and in pelagic compartment of lakes (e.g., algae) remains uncertain. Studies primarily derive from winter drawdown regimes from hydroelectric reservoirs, with little study from recreational lakes, which may have nuanced drawdown regimes. Magnitude is often the indicator of related disturbance, but the importance of other hydrological features (e.g., rate, duration, timing) on ecological response have received little attention (Carmignani and Roy 2017).

In Chapter 3, I continuously measured water level from 18 winter drawdown lakes and 3 non-drawdown lakes. I captured a gradient of drawdown magnitude across lakes (0.07–2.66 m), while intra-lake magnitudes were relatively consistent among years (over 2–4 annual events). These magnitudes translated into lakebed exposures of 1.3–37.6% and littoral zone exposures of 9.2–71.1%, which are highly dependent on lake-specific bathymetry and environmental factors that affect water transparency. Compared to magnitude, percent exposure metrics are likely more relevant in predicting ecological impacts to benthic communities and should be estimated for newly proposed magnitudes. I found high inter- and intra-lake variability of the timing and duration of whole drawdown events along with their recession, drawdown, and refill phases suggesting a strong influence of precipitation and melting events. Drawdown events consistently did not meet state-issued refill timing guidelines, with 70.6% of events refilled to summer pool levels after the recommended April 1st date. These results will help lake managers and regulating authorities identify and resolve obstacles to meet drawdown hydrological guidelines.

Many Massachusetts lakes are anthropogenically derived through impoundment with their current ecological state representing a suite of historical and ongoing anthropogenic disturbances from impoundment to eutrophication to water level manipulations. Among this set of stressors, annual winter drawdowns contribute to observed littoral zone ecological patterns. Winter drawdowns can alter physicochemical benthic habitat (Turner et al. 2005; Cooley and Franzin 2008), but little study has quantified its effects in recreational lakes with developed shorelines and drawdown regimes with relatively mild magnitudes. In Chapter 4, I found that drawdown magnitude significantly influenced littoral zone physicochemical habitat represented as sediment texture and macrophyte assemblages. Significant drawdown effects were detected for habitat components at exposed depths even at relatively mild magnitudes (<1 m). Specifically, sediments became coarser and macrophyte biomass and biovolume decreased with increasing magnitudes. Drawdowns select for species with annual longevity strategies and amphibious growth forms. The results further suggest the importance of ambient water quality conditions (e.g., alkalinity, water transparency) and bathymetry that influence macrophyte community assembly and likely shape the response to winter drawdown regimes including the development of tolerant macrophyte assemblages. Overall, winter drawdowns, combined with lakeshore development, degrade littoral habitat, with the extent of habitat alteration varying by lake.

Freshwater mussels tend to be absent or in relatively low densities in water level fluctuation zones (e.g., Bowers and De Szalay 2004; Richardson, Hanson, and Locke

2002); however, it is uncertain if winter drawdowns can limit mussel density and distribution during early fall after months of normal water levels. Results from snorkel and excavation surveys (Chapter 5) revealed significantly lower mussel densities in between annual drawdown events (Sept-Oct.) in drawdown lakes compared to control lakes, specifically at depths exposed during drawdown. The mussels present in drawdown exposure zones were mostly buried and relatively small which suggests colonization attempts of younger cohorts into exposure zones between drawdown events. However, colonization is short-lived until the next annual drawdown event as suggested by mortality data. This study confirmed the notion that annual winter drawdowns negatively impact mussel assemblages and justified taking mussel populations into serious consideration when implementing a new winter drawdown regime (Mattson et al. 2004), as mussels provide important ecosystem services (Vaughn 2017).

Winter drawdown magnitude can significantly reduce littoral macroinvertebrate abundance, richness, and alter taxonomic and functional compositions (Aroviita and Hämäläinen 2008, White et al. 2011, Trottier et al. 2019); however, few studies measure the drawdown magnitude impact to multiple littoral mesohabitats at magnitudes < 2–3 m and with co-occurring anthropogenic pressures (e.g., lakeshore development). Along a gradient of drawdown magnitude < 2.3 m across 14 lakes, I did not detect significant effects of drawdown on macroinvertebrate abundance, richness, and diversity in cobble and macrophyte habitat. Instead, these metrics were better explained by lake-scale nutrient-related variables (e.g., phosphorous, lakeshore development) and mesohabitat-scale factors (e.g., macrophyte cover, epilithic chlorophyll-*a*). Macroinvertebrates likely recolonized from unexposed littoral depths during normal water levels throughout the summer. In contrast, drawdown magnitude significantly structured the macroinvertebrate taxonomic and functional trait compositions. Relative abundance of *Amnicola* gastropods and proportions of semivoltine taxa and/or taxa with no swimming capacity (e.g., Coleoptera, Unionoida) significantly declined with drawdown magnitude (Figure 7.1). More investigation is required on macroinvertebrate colonization rates post-refill from spring through fall months and how that influences seasonal temporal patterns of littoral food webs.

The results from this project support previous winter drawdown research, but also highlight new relationships within a nuanced winter drawdown regime context of MA recreational lakes (Figure 7.1). Generally, the winter drawdowns under study possess relatively mild magnitudes (e.g., <2 m) compared to the predominance of relatively large magnitudes in previous research associated with hydroelectric reservoirs. Even at these relatively shallow magnitudes, I found drawdowns as a significant driver of littoral ecological patterns consistent with previous research. As a function of drawdown magnitude or lakebed exposure, winter drawdowns coarsen bed texture, reduce macrophyte biomass and mussel densities, and structure macrophyte and macroinvertebrate composition. Among these patterns, I identified mussels, *Amnicola* gastropods, non-swimming macroinvertebrate taxa in general, and semivoltine macroinvertebrate taxa are particularly sensitive to winter drawdown regimes. Additionally, I quantified winter drawdown hydrological metrics (e.g., rate, duration, timing) in addition to magnitude and integrated bathymetry with water level data to produce percent exposure estimations of whole lake beds and littoral zones. Although these metrics were not used extensively in modeling ecological responses, I expect these metrics to better predict ecological responses (e.g., food web energy flow, population density, individual growth) than drawdown magnitude alone. Further modeling efforts are needed to test the strength of individual and potentially pluralistic effects of winter drawdown hydrological metrics.

Winter drawdowns can also impact fish and semi-aquatic organisms (Carmignani et al. 2017), which were not addressed in this project. Fish species that spawn in littoral zones in the fall (e.g., *Coregonus*, Mills et al. 2002) or spring (e.g., *Esox*, Kalleymeyn 1987), depend on littoral zone derived food sources and habitat refuge (e.g., *Lota lota*, Sutela et al. 2011), and/or are insectivorous consumers (e.g., *Lepomis gibbosus*, Haxton and Findlay 2009) are likely to experience population declines. Fish population responses to drawdowns are further modified by a lake's environmental and biological context including lake morphometry (e.g., mean/max depth, area, shoreline complexity) and fish assemblage composition that determine the quantity of littoral food and habitat resources, the strength of resource competition, and trophic niche availability (Eloranta et al. 2016a, McMeans et al. 2016). For example, drawdown magnitude in smaller lakes with co-occuring fish species can show stronger negative impacts on fish population density compared to larger lakes with single fish species assemblages as seen in brown trout (*Salmo trutta*) populations in Norwegian hydroelectric reservoirs (Eloranta et al. 2018). However, more research is needed to understand the interactive effects of fish population density and inter- and intraspecific littoral zone food resource use in response to mild winter drawdown magnitudes for a diversity of fish species in the northeastern United States. Utilization of ecological tracers such as bulk and compound-specific stable isotopes (McMeans et al. 2016) will help to detect annual winter drawdown impacts on lake food web structure and function as seen in other water level regulation conditions (e.g., Eloranta et al. 2016b). Lastly, few studies have examined the likely negative impacts of winter drawdowns for many semi-aquatic fauna (Carmignani et al. 2017). Specifically, beaver, muskrat, frog and turtle species that inhabit shallow lakes, ponds, and hydrologically connected wetlands may experience stressful conditions (e.g., exposure to freezing and predation) and larger winterkill events during low winter water levels (Smith and Peterson 1991, Thurber et al. 1991, Tattersall and Ultsch 2008, Edge et al. 2009). More research is needed to understand the relative effect of annual winter drawdowns on these populations and how it may limit their distributions across the landscape.

Placing drawdowns in an environmental and management context

Along with drawdown hydrology, other environmental factors often contributed in explaining variation in ecological responses, including bathymetry (e.g., slope, depth) and water quality (e.g., alkalinity, total phosphorous, water transparency), and lakeshore residential development. These covariates were often stronger predictors at perennially submerged depths (i.e., not exposed by drawdowns) as observed with mussel densities and macrophyte biomass and were also more influential on macroinvertebrate assemblages than drawdown magnitude. Furthermore, although interactions were not directly tested between drawdown and other environmental factors, drawdown effects likely vary with lake environmental context. For example, my data suggests that water quality factors (e.g., alkalinity, transparency) that influence macrophyte composition likely shape the response to winter drawdowns such that lake-specific macrophyte assemblages in low alkaline and low water clarity are more susceptible to biomass loss compared to high alkaline and high clarity water conditions. In addition, total phosphorous, lakeshore residential development, and chlorophyll-*a* strongly influence macroinvertebrate composition that is further shaped by winter drawdowns. Therefore, a lake's specific bathymetry, water quality, and biological community composition may modify the ecological responses to winter drawdown regimes.

A potential caveat of this research is not capturing interannual variability of measured physical habitat and biotic responses to winter drawdowns. Potential sources of interannual variation include other lake management practices including herbicide use to control macrophytes. For example, abundant macrophytes were sampled at one site, but were largely absent at the same site the following year because of herbicide treatment. Additionally, the interannual variability of ice and snow cover and depth and the timing of refill were not accounted for in this project and would likely help explain variability in littoral zone communities. Winter weather conditions that cause relatively thick ice cover and deep snow cover could create extensive anoxic conditions for invertebrates and fish, which are already exacerbated by low winter water levels from drawdowns (Cott et al. 2008). The interannual variability of refill timing to normal lake levels may also influence recolonization timing of invertebrates into exposure zones, but this relationship has not been previously examined. However, as shown through this research, winter drawdown exposure or drawdown magnitude is a major predictor of habitat and biological patterns. Since winter drawdowns have been conducted annually at consistent magnitudes for several years, the biological patterns I measured represent cumulative effects of prior annual drawdowns. The annual frequency of winter drawdowns is enough to prevent recolonization at exposed depths for several taxa across assemblages and prevent recovery to a more natural state (Richardson et al. 2002). Other winter drawdown studies monitoring littoral zone communities over several annual winter drawdowns show relatively little change in biotic responses after the introduction of the first winter drawdown, which can cause dramatic ecological changes (e.g., macrophyte biomass declines, Turner et al. 2005). Therefore, we likely captured a new ecological drawdown state sustained by the annual frequencies of winter drawdowns.

Drawdowns are a short-term macrophyte control technique conducted annually to prevent macrophyte regrowth and colonization within exposure zones. Although this project was not designed to assess the efficacy of winter drawdowns on specific macrophyte taxa often targeted for macrophyte control (e.g., *Myriophyllum spicatum*), I found a general decrease in total macrophyte biomass supporting the use of winter drawdowns as a macrophyte control tool. However, I also found considerable variation in macrophyte biomass likely because of interlake differences in macrophyte taxa tolerance to exposure (annuals are favored), local morphometry that effects water drainage (i.e., slope), and variable winter precipitation and temperature conditions. Future monitoring efforts could determine the composition and abundance of seed and vegetative propagule banks in drawdown exposure zones (Liu et al. 2006), which may help to predict the development of a drawdown-tolerant macrophyte assemblage. Predicted warmer and wetter winters associated with climate change will need to be incorporated in future winter drawdown implementation to reassess its efficacy as a tool for macrophyte control.

Classification of lake vulnerability to drawdowns

Although ecological responses to winter drawdowns vary by lake, management and regulation of winter drawdowns would benefit from a lake classification scheme to develop ecological predictions in unstudied lakes and guide implementation of monitoring and management. Lake classification across Massachusetts should include environmental drivers on multiple spatial scales from lake to watershed scales to sufficiently capture the hierarchal structure of lake ecosystem dynamics and its connectivity to the landscape (Soranno et al. 2010; Martin et al. 2011). In particular, lake hydromorphological processes at multiple spatial scales are essential in understanding lake biogeochemical patterns and biological conditions (Tranvik et al. 2009) and have been applied in predictive lake classification models for water chemistry variables (e.g., Soranno et al. 2010, Martin et al. 2011). Similarly, I propose the use of hydromorphological variables at lake and watershed scales to help classify lake winter drawdown sensitivity because hydromorphological conditions determine lake water level fluctuations, winter drawdowns alter lake water levels, and hydromorphological variables set constraints on winter drawdown regimes (e.g., magnitude, rates). Potential variables to use for lake classification include lake morphometry (e.g., shape, mean/max depth), water residence time, connectivity to groundwater inputs, lake watershed position (i.e., watershed area to lake area ratios) and watershed land use/cover that are major drivers of lake water quality and biotic assemblages (Figure 7.2; Martin and Soranno 2006; Bremigan et al. 2008; Vadeboncoeur et al. 2008; Zwart et al. 2017). In addition to hydromorphological variables, lakes that support relatively high biodiversity and extremely rare and sensitive species in Massachusetts should be prioritized for protection from winter drawdowns.

Fine-scale estimation of depth distributions are currently available across many lakes in MA, which integrates information on lake shape, surface area, volume, mean and maximum depths that can help determine relative lakebed and littoral zone exposure during winter drawdowns. Shallow lakes and lakes consisting mostly of large benthic shelves (low mean-max depth ratios) are most susceptible to lakebed exposure for a given drawdown magnitude compared to a relatively deep or steeply sloped lake (Beklioglu et al. 2006). Additionally, environmental factors that drive light attenuation that determine littoral zone depth distribution would be important to consider for lake classification. Shallow, polymictic, and eutrophic lakes that promote sediment resuspension and algae-dominance or lakes with naturally high dissolved organic carbon inputs have limited littoral zone primary production. This suggests even a relatively mild drawdown magnitude exposes a large proportion of littoral zone. Oligotrophic lakes with low mean/max depth ratios (i.e., mostly shallow depth distribution) and high water clarity may also be susceptible to winter drawdowns, as benthic primary production can support a significant portion of lake food web (Vadeboncoeur et al. 2008).

Other lake-scale factors that might be important for assessing lake susceptibility to winter drawdowns are water residence time and direct groundwater inputs. Water residence time is generally a function of water inflows, outflows, and lake volume that regulates lake biogeochemical processing (Brett and Benjamin 2008; Brooks et al. 2014; Zwart et al. 2017). Winter drawdowns likely alter water residency times by shortening water retention during water level recession and increasing retention during refill phases.

Lakes with longer water residence times tend to have less water level fluctuations (Keto et al. 2008) suggesting greater ecological impact of winter drawdowns. Lakes dominated by groundwater inputs may be less susceptible to winter drawdowns. Refill would be less dependent on climate variability and surface water inflow and could buffer potential ecological impacts on drawdown exposed sediments. However, the extent of groundwater inflow will determine if refill to full pool level is realistic.

Lastly, watershed scale factors that regulate lake hydrology should be integrated into a lake classification scheme. The watershed area relative to lake surface area is a typical environmental correlate relating watershed and lake patterns in water and associated nutrient flow (Soranno et al. 2015). This ratio can determine the magnitude of lake water level fluctuations and can constrain winter drawdown magnitude (Keto et al. 2008). Also, watershed-lake area ratios can be tightly linked with water residence time, whereby longer residence times are correlated to low watershed-lake area ratios (Soranno et al. 2015). Lakes with relatively low watershed-lake area ratios are more hydrologically constrained to perform winter drawdowns and would require more time to achieve refill to full pool levels. Thus, these lakes are likely more susceptible to winter drawdown impacts on lake physical, chemical, and biological components.

Watershed and lakeshore land use/cover will also be important to consider in conjunction to managing winter drawdowns because of its strong influence on lake ecosystem patterns and functioning. For example watershed and lakeshore land use alter lake water quality, including increased nutrient inputs, (Fraterrigo and Downing 2006, Soranno et al. 2015), increased road salt and sedimentation (Stoler et al. 2018), degrade littoral zone physical habitat (e.g., coarse wood loss, Czarnecka 2016 and references therein), which altogether influence lake biological community dynamics (e.g., Vanni et al. 2005). Since lakeshores and watersheds are moderately to heavily developed (e.g., impervious cover, agriculture, pasture) for many lakes across Massachusetts, the protection of relatively undeveloped lakes from winter drawdown regimes should be a primary conservation target. Furthermore, implementation of new drawdown regimes should be considered with co-occurring land use stressors to minimize impacts to already degraded physical, chemical, and biological conditions of a given lake.

Further investigation is needed to determine the covariation of these hydromorphological, watershed and lakeshore land use parameters in Massachusetts lakes and how they might interact with future climate variability to determine lake water level fluctuations (Boon et al. 2019). Once lake classes have been identified as sensitive to annual winter drawdowns, local and state-level regulating authorities can prioritize biological monitoring and assessments and make more effective decisions on current and proposed winter drawdown management.

Policy and management implications

The results from this project will help inform regulating authorities on the potential impacts of winter drawdowns and be used to update regulation policies. Currently, local conservation commissions rely on several documents (Langley et al. 2004; MassWildlife 2002; Mattson et al. 2004) for guidance to review and issue an Order of Conditions for a proposed winter drawdown project. However, a major shortcoming of these documents, as highlighted in Mattson et al. (2004), is limited empirical research on the impacts to non-target biota specific to MA lakes. This project begins to fill this knowledge gap and offers MA-specific research for conservation commissions to reference. Additionally, regulating authorities can use the winter drawdown hydrology metrics (Chapter 3) to improve hydrological metric (e.g., timing, rate, magnitude) standards. The prevalent incongruency between the timing of observed winter drawdown events and the recommended timing standards (MassWildlife 2002) suggests the need to reevaluate the practice of current drawdown regimes and amend drawdown performance guidelines. I recommend applying hydrological budget models to estimate the probability of meeting water level target (e.g., normal pool levels, drawdown levels) and MA timing guidelines under hypothetical precipitation and drawdown magnitude scenarios. This will help set realistic drawdown management goals given the water budget of a given lake and its watershed. If macrophyte control is the primary reason for winter drawdown implementation, it is possible to adjust drawdown durations based on the lethal soil temperature and moisture conditions needed to kill targeted macrophyte taxa (Lonergan et al. 2014). Once these conditions are met for a sufficient duration, water level refill can begin. However, this strategy would require careful monitoring of water levels and soil conditions and would need to balance with other management goals achieved by the drawdown like ice damage prevention to shoreline infrastructure.

Our data suggests increases in drawdown magnitude will result in significant impacts to littoral zones and may have lake-wide consequences. Magnitude increases will expose more littoral zone area and likely delay the timing of refill to normal pool levels. Consequently, this could result in significant population declines, biodiversity loss, and overall ecosystem functioning. Incorporation of lake-specific ecological knowledge (e.g., biological community composition, water quality, morphometry) and watershed characteristics (e.g., land use) will improve the ecological sustainability of drawdown management. This knowledge will help estimate the hydrological feasibility of winter drawdown regimes, the potential impacts to non-target biota and associated habitat, and the efficacy of meeting management goals particularly for macrophyte control. Regular monitoring efforts are needed to document water level fluctuation, water quality (e.g., nutrients, dissolved oxygen), and taxa that are at risk to winter drawdown disturbance. In addition, impacts of winter lake drawdowns on downstream habitat and biological assemblages have yet to be investigated. Given that lake outflow is restricted typically when streamflows are high during spring and lake outflow is increased when streamflows are typically low to moderate in the fall, there are potential significant impacts to stream ecosystems. Therefore, emphasis should also be given to potential impacts to downstream ecosystems when considering lake management strategies that include winter drawdown. Ultimately, because of the heterogenous conditions of watershed, lake, and shoreline environmental factors that regulate lake ecology, management of winter drawdown regimes will require lake-specific strategies to minimize impacts to non-target biota while still meeting recreational goals.

Figures

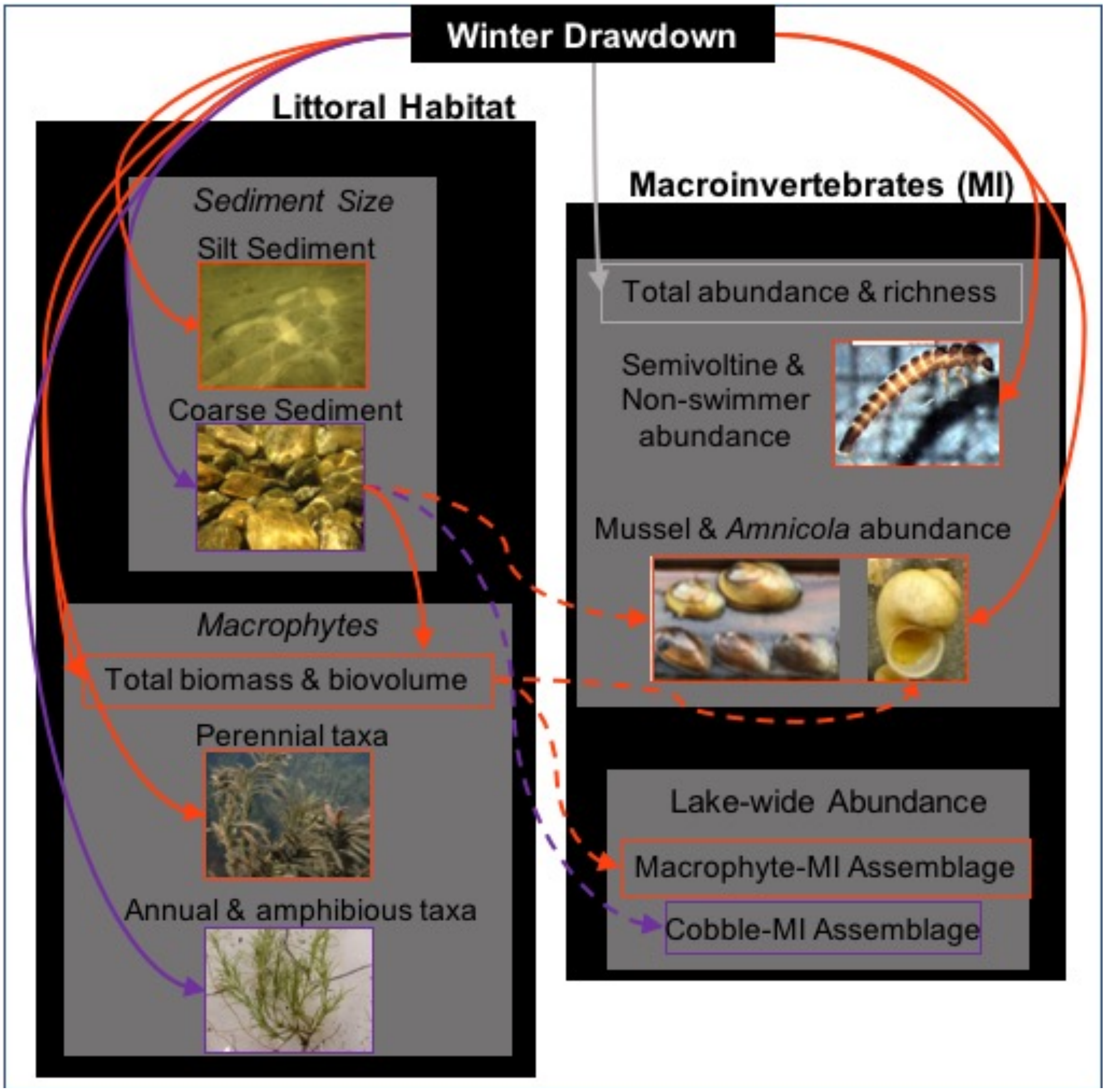

Figure 7.1. Observed ecological impacts of winter drawdowns.
Flow diagram of measured and hypothesized winter drawdown effects on littoral habitat and littoral biota. Solid lines represent measured negative (red), positive (purple), or no effect (gray) of winter drawdown magnitude or exposure. Dashed lines represent hypothesized indirect relationships of winter drawdown effects. Lake-wide abundance of macroinvertebrates refers to the relative abundance of habitat specific (macrophyte, cobble) macroinvertebrate assemblages in the littoral zone. Picture of *Oulimnus* (Coleoptera: Elmidae) courtesy of Walters et al. (2017).

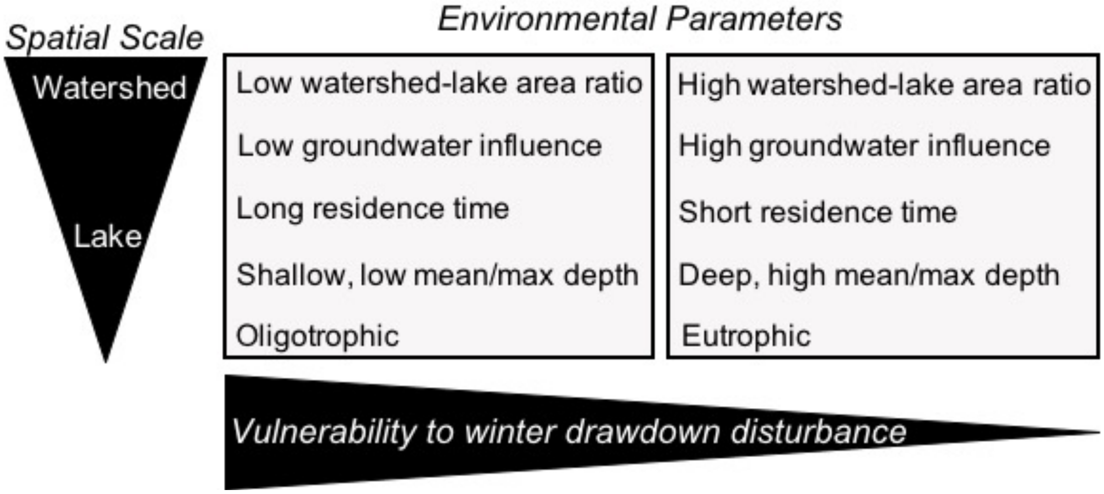

Figure 7.2. Hydromorphological conditions that influence sensitivity to winter drawdowns.
Hydromorphological variables at watershed and lake scales that may be used to classify lakes in New England based on their potential susceptibility to winter drawdown disturbance.

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APPENDICES

APPENDIX A

WINTER DRAWDOWN EMAIL SURVEY

Email survey questions sent to municipal conservation commissions and lake and pond associations to collect historical and current winter drawdown information.

QUESTIONS

1)Does the waterbody have a history of winter drawdowns? If so, approximately for how many years?

2)How frequent are winter drawdowns conducted and at what level is the water lowered (e.g. 2-3ft every year and 6 ft every third year)?

3)Is a winter drawdown planned for the 2013-2014 winter and for future winter seasons?

4) Why were winter drawdowns conducted (i.e. aquatic vegetation removal, prevent dock and impoundment damage, dam repair) in the past or for coming years?

APPENDIX B

RESULTS OF WINTER DRAWDOWN EMAIL SURVEY

Winter drawdown information by waterbody collected from an email survey (2013-2014) to municipal conservation commissions and lake and pond associations in Massachusetts (MA). PALIS Code refers to the Pond and Lakes Inventory System identification for MA waterbodies derived from the MassDEP Hydrography (1:25,000) GIS layer via MassGIS (https://www.mass.gov/orgs/massgis-bureau-of-geographic-information). Winter drawdown (WD) information are historical presence of winter drawdowns (History), number of years WD's have been practiced (Years Conducted), WD magnitudes of ongoing winter drawdown regimes (Magnitude), frequency of WD's (Frequency), whereby multiple magnitudes correspond to a multiple magnitude WD. and purposes for WD's (Purposes). Magnitudes are reported as single values, ranges, or multiple values (e.g., 1.06/1.52), whereby multiple magnitude values represent a multiple WD magnitude regime if it has a corresponding multiple WD frequency values (e.g., annual/triennial). Frequency coded as 'isolated' refers to single drawdown events. Codes for WD purposes are AV = aquatic vegetation control, IM = infrastructure maintenance (e.g., dams, docks, retaining walls), SM = shoreline maintenance (i.e., shoreline cleanup), FC = flood control, IP = infrastructure protection from ice erosion, ZM = zebra mussel control, EU = nutrient control, DR = drinking water demand.

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Hamilton Reservoir	41019	Holland	Quinebaug	Yes	154	0.61	annual	AV, IM, SM
Greenwood/Bungay Lake	52017	North Attleboro	Ten Mile	Yes	12	1.2	annual	AV, SM, IM
Lake Maspenock/North Pond	51112	Upton	Blackstone	Yes		1.52-2.13	annual	AV
Lake Quannapowitt	93067	Wakefield	North Coastal	Yes	114	0.3	annual	DM, FC
Goose Pond	21043	Lee	Housatonic	Yes	94	1.83	annual	AV, IM
Bourn-Hadley Pond	35008	Templeton	Millers	Yes	47			
Otis Reservoir	31027	Otis	Farmington	Yes	45	2.44	annual	IM
Big Pond	31004	Otis	Farmington	Yes	45	0.76	annual	AV, IM, SM
Stodge Meadow Pond	84095	Ashburnham	Merrimack	Yes	45	0.61	annual	
Brookhaven Lake	36021	West Brookfield	Chicopee	Yes	45			

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Falls Pond	52014	North Attleboro	Ten Mile	Yes	44	1.82-2.13	annual	FC, IM
Whiting Pond	52042	North Attleboro	Ten Mile	Yes	44	0.91	annual	FC, IM
Onota Lake	21078	Pittsfield	Housatonic	Yes	40	1.06/1.82	annual/triennial	
Pontoosuc Lake	21083	Pittsfield	Housatonic	Yes	40	1.06/1.52	annual/triennial	AV, FC, IM
Inner Little Harbor	94180	Cohasset	South Coastal	Yes	39	0.76	annual	IM
Lake Massapoag	84087	Dunstable	Merrimack	Yes	30	1.67-1.83	annual	AV, IM, SM
Laurel Lake	21057	Lee	Housatonic	Yes	30	0.91	annual	AV, IM, ZM
Town River Reservoir	62196	West Bridgewater	Taunton	Yes	25	0.61-0.91	annual	IP
Wyman Pond	81161	Westminster	Nashua	Yes	25	0.61	annual	SM, IM
Lake Samoset	81116	Leominster	Nashua	Yes	22	0.91	annual	AV, SM
Silver Lake Reservoir	34084	Agawam	Connecticut	Yes	18		annual	AV
Ellis Pond	73018	Norwood	Boston Harbor	Yes	15	0.45	annual	FC
Silver Lake/Hoag Lake	51150	Bellingham	Blackstone	Yes	14	0.3	annual	IM, AV, SM
Indian Lake	51073	Worcester	Blackstone	Yes	12	1.22	annual	AV
Bare Hill Pond	81007	Harvard	Nashua	Yes	10	0.61-1.83	annual	AV
Watson Pond	31009	Otis	Farmington	Yes	10	0.91	annual	AV
Dean Pond	36049	Monson	Chicopee	Yes	1		isolated	SM
Ice House Pond	82066	Acton	SuAsCo	Yes	1		isolated	EU
Country Club Pond	97107	Longmeadow	Connecticut	Yes	1		isolated	AV
Neponset Reservoir	73034	Foxborough	Boston Harbor	Yes		0.61-0.91		
Stockbrigde Bowl	21105	Stockbridge	Housatonic	Yes		0.61-0.91	annual	
Cohasse Brook Reservoir	41012	Southbridge	Quinebaug	Yes		0.3-0.45	annual	IM

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Number Five Reservoir	41040	Southbridge	Quinebaug	Yes		0.3-0.45	annual	IM
Number Four Reservoir	41039	Southbridge	Quinebaug	Yes		0.3-0.45	annual	IM
Number Three Reservoir	41038	Southbridge	Quinebaug	Yes		0.3-0.45	annual	IM
Noyes Pond	31026	Tolland	Farmington	Yes		<1.07	annual	
Fort Meadow Reservoir	82042	Marlborough	SuAsCo	Yes		1.22	biennial/triennial	
Lower Naukeag Lake	35041	Ashburnham	Millers	Yes		1.22		
Cedar Pond	41008	Sturbridge	Quinebaug	Yes		1.06	annual	AV, SM
Sunset Lake	35086	Ashburnham	Millers	Yes		0.91	annual	IM
Beaumont Pond	62009	Foxborough	Taunton	Yes		0.91	annual	
Lake Watatic	35095	Ashburnham	Millers	Yes		0.35	annual	AV
Baker Pond	51005	Upton	Blackstone	Yes		0		
Davidson Pond	51037	Upton	Blackstone	Yes		0		
Forge Pond	62071	East Bridgewater	Taunton	Yes		0		
Goss Pond	51054	Upton	Blackstone	Yes		0		
Mill Pond	51104	Upton	Blackstone	Yes		0		
Pratt Pond	51123	Upton	Blackstone	Yes		0		
Taft Pond	51165	Upton	Blackstone	Yes		0		
West River Reservoir/Lake Wildwood	51181	Upton	Blackstone	Yes		0		
Zachary Pond	51187	Upton	Blackstone	Yes		0		
Sunset Lake	74020	Braintree	Boston Harbor	Yes				AV
Lake Boon/Boon Pond	82011	Stow	SuAsCo	Yes			annual	SM, AV
Lake Wyola	34103	Shutesbury	Connecticut	Yes			annual	IP, IM
Ward Pond	62203	Easton	Taunton	Yes			isolated	FC

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Payson Park Reservoir	71034	Cambridge	Boston Harbor	Yes				DR
Little Alum Pond	41029	Brimfield	Quinebaug	Yes				AV, SM, IM
Foundry Lake	97106	Foxborough	Taunton	Yes				AV
Lake Sabbatia	62166	Taunton	Taunton	Yes				AV
Ashmere Lake	21005	Hinsdale	Housatonic	Yes				
Baker Pond/Gore Pond	42018	Dudley	French	Yes				
Cedar Meadow Pond	42009	Leicester	French	Yes				
Cocasset Lake	62043	Foxborough	Taunton	Yes			isolated	
Dunn Pond	35021	Gardner	Millers	Yes				
Forge Pond	84015	Westford	Merrimack	Yes				
Glen Echo Lake	41017	Charlton	Quinebaug	Yes				
Greenwater Pond	21044	Becket	Housatonic	Yes				
Hobbs Brook Pond	72048	Weston	Charles	Yes			isolated	
Knops Pond	84084	Groton	Merrimack	Yes				
Lake Attitash	84002	Amesbury	Merrimack	Yes				
Lake Buel	21014		Housatonic	Yes				
Lake Garfield	21040	Monterey	Housatonic	Yes				
Lake Hiawatha	51062	Bellingham	Blackstone	Yes				
Lake Lashaway	36079	East Brookfield	Chicopee	Yes				
Lake Shirley	81122	Shirley	Nashua	Yes				
Lake Whittemore	36165	Spencer	Chicopee	Yes				
Long Pond	32049	Blandford	Westfield	Yes				
Longwater Pond	62109	Easton	Taunton	Yes			isolated	

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Lost Lake	41030	Groton	Quinebaug	Yes				
Manchaug Pond	51091	Sutton	Blackstone	Yes				
Mausert's Pond	11009	Clarksburg	Hudson	Yes				
Nashawannuck Pond	34057	Easthampton	Connecticut	Yes				
Packard Pond	35053	Orange	Millers	Yes				
Palmer Brook Reservoir	97104	Becket	Farmington	Yes				
Pearl Hill Brook Pond	97108	Townsend	Nashua	Yes				
Pine Island Lake	34069	Westhampton	Connecticut	Yes				
Plunkett Reservoir	21082	Hinsdale	Housatonic	Yes				
Ramshorn Pond	51126	Sutton	Blackstone	Yes				
Reservoir Number Two/Secret Lake	35064	Athol	Millers	Yes				
Richmond Pond	21088	Richmond	Housatonic	Yes				
Sherman Lake	41046	Brimfield	Quinebaug	Yes				
Singletary Pond	51152	Sutton	Blackstone	Yes			annual	
Stevens Pond	51159	Sutton	Blackstone	Yes				
Stiles Reservoir	42055	Leicester	French	Yes				
Sugden Reservoir	36150	Spencer	Chicopee	Yes				
Tully Pond	35089	Orange	Millers	Yes				
Wachusett Reservoir	81147	West Boylston	Nashua	Yes				
Watershops Pond/Lake Massasoit	34099	Springfield	Connecticut	Yes				
White Pond	35098	Athol	Millers	Yes				
Stagecoach Lake/Calkins Pond	36027	Monson	Chicopee	No	1	0.91	isolated	AV
Aaron River Reservoir	94178	Cohasset	South Coastal	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Accord Pond	94002	Norwell	Boston Harbor	No				
Arlington Reservoir	71003	Arlington	Boston Harbor	No				
Artichoke Reservoir	84034	Newburyport	Merrimack	No				
Ashland Reservoir	82003	Ashland	SuAsCo	No				
Baldwin Pond	36007	Monson	Chicopee	No				
Barkers Pond	82006	Acton	SuAsCo	No				
Barstows Pond	62008	Taunton	Taunton	No				
Bartholomew Pond	93002	Peabody	North Coastal	No				
Beaver Pond	97119	Leverett	Connecticut	No				
Beaver Pond	72004	Bellingham	Charles	No				
Berkley Street Pond	62010	Taunton	Taunton	No				
Bixby Reservoir	81010	Townsend	Nashua	No				
Black Pond	62016	Taunton	Taunton	No				
Black Pond	84076	Harvard	Merrimack	No				
Blacks Nook	71005	Cambridge	Boston Harbor	No				
Blood Pond	41004	Dudley	Quinebaug	No				
Bogastow Pond	72007	Millis	Charles	No				
Boulder Hill Pond	34010	Monson	Connecticut	No				
Bound Brook Pond	94017	Norwell	South Coastal	No				
Bow Brook Reservoir	81013	Shirley	Nashua	No				
Box Pond	72008	Bellingham	Charles	No				
Bradford Pond	92005	North Reading	Ipswich	No				
Bradley Pond	97122	Monson	Connecticut	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Brookline Reservoir	72010	Brookline	Charles	No				
Brooks Pond	36022	Spencer	Chicopee	No				
Browning Pond	36025	Spencer	Chicopee	No				
Browns Pond	93008	Peabody	North Coastal	No				
Bruces Pond	82012	Hudson	SuAsCo	No				
Buckhill Pond	36174	Spencer	Chicopee	No				
Buffom Pond	42004	Oxford	French	No				
Bugs Swamp	42006	Oxford	French	No				
Burncoat Pond	42007	Spencer	French	No				
Butler Road Pond	34012	Monson	Connecticut	No				
Buttery Brook Tributary Reservoir	97127	South Hadley	Connecticut	No				
Cain Pond	62030	Taunton	Taunton	No				
Carbuncle Pond	42008	Oxford	French	No				
Cargill Pond	52004	Plainville	Ten Mile	No				
Carpenter Pond	62032	Foxborough	Taunton	No				
Carpenter Road Pond	42026	Dudley	French	No				
Cedar Pond	93013	Peabody	North Coastal	No				
Cedar Pond	92007	Wenham	Ipswich	No				
Center Pond	32015	Becket	Westfield	No				
Charles River Pond	72019	Bellingham	Charles	No				
Chestnut Street Pond	52007	Plainville	Ten Mile	No				
Chicopee River Reservoir	36171	Ludlow	Chicopee	No				
Chimney Pond	42011	Oxford	French	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Cider Millpond	36034	Spencer	Chicopee	No				
Clay Pit Pond	71011	Belmont	Boston Harbor	No				
Colburns Reservoir/Chestnut Street Pond	81162	Leominster	Nashua	No				
Cold Spring Pond	97111	Ashland	SuAsCo	No				
Conant Brook Reservoir	36038	Monson	Chicopee	No				
Conant Pond	41013	Dudley	Quinebaug	No				
Congamond Lake	32021	Southwick	Westfield	No				
Congamond Lake	32023	Southwick	Westfield	No				
Congamond Lake	32022	Southwick	Westfield	No				
Craig Pond	97125	Peabody	North Coastal	No				
Cranberry Bog Pond	73011	Foxborough	Boston Harbor	No				
Cranberry Bog/Lubber Pond East	92035	Wilmington	Ipswich	No				
Cranberry Bog/Lubber Pond West	92036	Wilmington	Ipswich	No				
Cranberry Meadow Pond	36040	Spencer	Chicopee	No				
Cranberry Pond	36041	Brookfield	Chicopee	No				
Cranberry Pond	74007	Braintree	Boston Harbor	No				
Crystal Lake	97112	Bellingham	Blackstone	No				
Crystal Lake	92013	Peabody	Ipswich	No				
Curtis Pond	97115	Bellingham	Blackstone	No				
Dead Pond	36048	Hardwick	Chicopee	No				
Dead Pond	81030	Shirley	Nashua	No				
Deep Pond	62058	Taunton	Taunton	No				
Devils Dishfull Pond	92015	Peabody	Ipswich	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Distributing Reservoir	81032	Leominster	Nashua	No				
Duck Pond	36055	Monson	Chicopee	No				
Dudley Pond	82029	Wayland	SuAsCo	No				
Dudleys Pond	34020	Leverett	Connecticut	No				
Eames Pond	42016	Oxford	French	No				
East Fuller Street Pond	52012	Plainville	Ten Mile	No				
East Hill Road Pond	36059	Monson	Chicopee	No				
Easterbrook Pond	42017	Dudley	French	No				
Eatons Pond	97117	Braintree	Boston Harbor	No				
Eisenhaures Pond	92016	North Reading	Ipswich	No				
Elginwood Pond	92017	Peabody	Ipswich	No				
Fairhaven Bay	82033	Lincoln	SuAsCo	No				
Fall Brook Reservoir	81038	Leominster	Nashua	No				
Fisk Pond	36060	Hardwick	Chicopee	No				
Flagg Hill Pond	97129	Stow	SuAsCo	No				
Fletchers Pond	82040	Stow	SuAsCo	No				
Florence Pond	34108	Northampton	Connecticut	No				
Fort Pond Brook Reservoir/Merriam's Pond	82076	Acton	SuAsCo	No				
Freitag Pond	36064	Monson	Chicopee	No				
Frog Pond	97124	Newburyport	Merrimack	No				
Fuller Pond	52016	Plainville	Ten Mile	No				
Furnace Lake	62076	Foxborough	Taunton	No				
Gales Pond	35024	Warwick	Millers	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Goodfellow Pond	81049	Leominster	Nashua	No				
Goodrich Pond	21042	Pittsfield	Housatonic	No				
Grassy Pond	82050	Acton	SuAsCo	No				
Graves Pond	81050	Townsend	Nashua	No				
Great Pond/Great Pond Upper Reservoir	74012	Braintree	Boston Harbor	No				
Halls Pond	72043	Brookline	Charles	No				
Harbor Pond	81054	Townsend	Nashua	No				
Hardwick Pond	36066	Hardwick	Chicopee	No				
Hardy Pond	72045	Waltham	Charles	No				
Harris Pond	36067	Ludlow	Chicopee	No				
Hastings Pond	35028	Warwick	Millers	No				
Hatch Pond	97132	Norwell	Boston Harbor	No				
Haviland Pond	36069	Ludlow	Chicopee	No				
Hayden Pond	42024	Dudley	French	No				
Haynes Reservoir	81055	Leominster	Nashua	No				
Hersey Pond	62087	Foxborough	Taunton	No				
Heywood Reservoir	81057	Leominster	Nashua	No				
Hollingsworth Pond	74014	Braintree	Boston Harbor	No				
Horse Meadows Reservoir	81059	Harvard	SuAsCo	No				
Howe Pond	36073	Spencer	Chicopee	No				
Hubbards Pond	35031	Warwick	Millers	No				
Hudson Pond	42029	Oxford	French	No				
Jenks Reservoir	51075	Bellingham	Blackstone	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Jerrys Pond	71020	Cambridge	Boston Harbor	No				
Johnsonian Pond	35032	Warwick	Millers	No				
Jones Pond	42030	Spencer	French	No				
Jones Pond	62098	East Bridgewater	Taunton	No				
Kittredge Dam Reservoir	36076	Spencer	Chicopee	No				
Lake Holbrook	74013	Holbrook	Boston Harbor	No				
Lake Mirimichi	62118	Plainville	Taunton	No				
Lake Nagog	82082	Acton	SuAsCo	No				
Lake Paradise	36116	Monson	Chicopee	No				
Lake Rico/Furnace Pond/Middle pond	62115	Taunton	Taunton	No				
Lake Rico/King's Pond	62102	Taunton	Taunton	No				
Lakeview Pond	51084	Bellingham	Blackstone	No				
Larner Pond	42068	Dudley	French	No				
Laurel Lake	35035	Warwick	Millers	No				
Leaping Well Reservoir	34040	South Hadley	Connecticut	No				
Lenox Reservoirs/Lower Root	21059	Lenox	Housatonic	No				
Lenox Reservoirs/Upper Root	21111	Lenox	Housatonic	No				
Leverett Pond	72060	Brookline	Charles	No				
Leverett Pond	34042	Leverett	Connecticut	No				
Lily Hole	97114	Bellingham	Blackstone	No				
Lily Pond/Scituate Pond	94179	Cohasset	South Coastal	No				
Lithia Springs Reservoir	34109	South Hadley	Connecticut	No				
Little Bearhole Pond	62105	Taunton	Taunton	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Little Fresh Pond	71023	Cambridge	Boston Harbor	No				
Little Harbor Reservoir	97105	Cohasset	South Coastal	No				
Little Pond	71024	Belmont	Boston Harbor	No				
Long Pond	97113	Bellingham	Blackstone	No				
Longham Reservoir	92030	Wenham	Ipswich	No				
Lost Pond	72067	Brookline	Charles	No				
Low Pond	42033	Dudley	French	No				
Lower Mill Pond	91008	Rowley	Parker	No				
Lower Mystic Lake	71027	Arlington	Boston Harbor	No				
Lowes Pond	42034	Oxford	French	No				
Lyman Pond	72069	Waltham	Charles	No				
Lyons Pond	36087	Ludlow	Chicopee	No				
Magnolia Pond	34034	Northampton	Connecticut	No				
Mann Pond	73027	Foxborough	Boston Harbor	No				
Mansfield Pond	21065	Great Barrington	Housatonic	No				
Martins Pond	92038	North Reading	Ipswich	No				
Mcavoy/Vandy's Pond	62112	Foxborough	Taunton	No				
McCarthy Pond	72072	Millis	Charles	No				
McKinstry Pond	42035	Oxford	French	No				
Merino Pond	42036	Dudley	French	No				
Mile Brook Reservoir	92040	Topsfield	Ipswich	No				
Milk Pond	72074	Medway	Charles	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Mill Pond	62116	West Bridgewater	Taunton	No				
Mill Pond	94099	Norwell	South Coastal	No				
Mill River Reservoir	62228	Taunton	Taunton	No				
Minechoag Pond	36093	Ludlow	Chicopee	No				
Ministers Pond	82020	Stow	SuAsCo	No				
Monson Reservoir	36095	Monson	Chicopee	No				
Moores Pond	35048	Warwick	Millers	No				
Morewood Lake	21071	Pittsfield	Housatonic	No				
Morse Reservoir	81086	Leominster	Nashua	No				
Mud Pond	21073	Pittsfield	Housatonic	No				
Muddy Brook Pond	36100	Hardwick	Chicopee	No				
Murphy Pond	36103	Ludlow	Chicopee	No				
Nara Pond	97109	Acton	SuAsCo	No				
Nash Hill Reservoir	36104	Ludlow	Chicopee	No				
New Pond	42037	Dudley	French	No				
Nipmuc Pond/Lake Nipmuc	51111	Mendon	Blackstone	No				
Nonesuch Pond	72085	Weston	Charles	No				
Norroway Pond	74016	Randolph	Boston Harbor	No				
Notown Reservoir	81092	Leominster	Nashua	No				
Oakland Pond/Sheppards Factory Pond	62136	Taunton	Taunton	No				
Old Millpond	81095	Harvard	Nashua	No				
Old Quincy Reservoir	74017	Braintree	Boston Harbor	No				
Packard Pond	42040	Dudley	French	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Park Pond	72091	Medway	Charles	No				
Patches Pond	97131	Wilmington	Ipswich	No				
Pearl City Pond	34113	South Hadley	Connecticut	No				
Peck's Pond	21080	Pittsfield	Housatonic	No				
Peter Pond	42042	Dudley	French	No				
Peterson Pond	94118	Norwell	South Coastal	No				
Phoenix Pond	81100	Shirley	Nashua	No				
Pickerel Pond/Bliss Pond	36018	Ludlow	Chicopee	No				
Pierce Pond	81101	Leominster	Nashua	No				
Pierces Pond	97126	Peabody	Ipswich	No				
Pierpont Meadow Pond	42043	Dudley	French	No				
Pine Hill Brook Pond	36124	Hardwick	Chicopee	No				
Pintail Pond	97130	Topsfield	Ipswich	No				
Plainville Pond	52033	Plainville	Ten Mile	No				
Pleasant Pond	92049	Wenham	Ipswich	No				
Pond Meadow Pond/Smelt Brook Pond	74018	Braintree	Boston Harbor	No				
Ponkapoag Pond	73043	Randolph	Boston Harbor	No				
Precinct Street Pond	62148	Taunton	Taunton	No				
Prospect Hill Pond	62149	Taunton	Taunton	No				
Puffer's Pond	34021	Amherst	Connecticut	No				
Pulpit Rock Pond	36127	Monson	Chicopee	No				
Quaboag Pond	36130	Brookfield	Chicopee	No				
Quinebaug River Reservoir	41054	Dudley	Quinebaug	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Reservoir Number Two	82045	Ashland	SuAsCo	No				
Reservoir Pond	73048	Ashland	Boston Harbor	No				
Reynolds Pond	97121	Ludlow	Chicopee	No				
Rice Pond	36135	Brookfield	Chicopee	No				
Richardi Reservoir	97116	Braintree	Boston Harbor	No				
Richards Mill Pond	35066	Warwick	Millers	No				
Richards Reservoir	35067	Warwick	Millers	No				
Richardsons Pond	72100	Millis	Charles	No				
Richmond Pond	62159	Taunton	Taunton	No				
Robbins Pond	62162	East Bridgewater	Taunton	No				
Roberts Meadow Reservoir	97133	Northampton	Connecticut	No				
Robinson Pond	42047	Oxford	French	No				
Rockery Pond	92056	Topsfield	Ipswich	No				
Rockwell Pond	81112	Leominster	Nashua	No				
Rocky Hill Pond	34114	Northampton	Connecticut	No				
Rocky Pond	81113	Leominster	Nashua	No				
Russell Cove	34077	South Hadley	Connecticut	No				
Sacrarrappa Pond/Slater's Pond	42053	Oxford	French	No				
Sanctuary Pond	94181	Cohasset	South Coastal	No				
Sargent Pond	72106	Brookline	Charles	No				
Satsuit Meadow Pond	94134	Norwell	South Coastal	No				
Satucket River Reservoir/Cotton Gin Dam	97118	East Bridgewater	Taunton	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Second Pond	34081	Ludlow	Connecticut	No				
Seekell Street Pond	62168	Taunton	Taunton	No				
Segreganset River Reservoir	62169	Taunton	Taunton	No				
Sheomet Lake	35074	Warwick	Millers	No				
Shepherd Pond	42051	Dudley	French	No				
Sidneys Pond	93069	Peabody	North Coastal	No				
Sigourney Pond/Thayer's Pond	42059	Oxford	French	No				
Silver Lake	92059	Wilmington	Ipswich	No				
Silver Lake	21097	Pittsfield	Housatonic	No				
Simonds Pond	81138	Leominster	Nashua	No				
Slyvestri Pond	41049	Dudley	Quinebaug	No				
Smith Pond	97123	Monson	Chicopee	No				
South End Pond	72109	Millis	Charles	No				
Spring Lake	93073	Salem	North Coastal	No				
Spring Pond	93074	Peabody	North Coastal	No				
Spring Street Pond	62177	Holbrook	Taunton	No				
Springfield Reservoir	36145	Ludlow	Chicopee	No				
Spy Pond	71040	Arlington	Boston Harbor	No				
Squire Pond	36146	Monson	Chicopee	No				
Staples Street Pond	62179	Taunton	Taunton	No				
Stump Pond	51162	Oxford	Blackstone	No				
Stumpy Pond	42056	Oxford	French	No				
Sudbury River Reservoir	97110	Ashland	SuAsCo	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Sunset Lake	62184	Foxborough	Taunton	No				
Suntaug Lake	92065	Peabody	Ipswich	No				
Swan Pond	92066	North Reading	Ipswich	No				
Taylor Pond	34064	South Hadley	Connecticut	No				
Texas Pond	42058	Oxford	French	No				
The Oxbow	34066	Easthampton	Connecticut	No				
Thompson Pond	51166	Spencer	Blackstone	No				
Titus Pond	97128	South Hadley	Connecticut	No				
Torrey Pond	95149	Norwell	Buzzards Bay	No				
Tripp Pond	82107	Hudson	SuAsCo	No				
Turner Park Pond	34090	Longmeadow	Connecticut	No				
Turner Pond	94163	Norwell	South Coastal	No				
Turnpike Lake	62198	Plainville	Taunton	No				
Upper Dam Pond	62199	Foxborough	Taunton	No				
Upper Leeds Reservoir	34094	Northampton	Connecticut	No				
Upper Mill Pond	91015	Rowley	Parker	No				
Upper Mystic Lake	71043	Arlington	Boston Harbor	No				
Upper Reservoir	21112	Lee	Housatonic	No				
Valley Pond	72123	Weston	Charles	No				
Vinton Pond	81145	Townsend	Nashua	No				
Vose Pond	82108	Maynard	SuAsCo	No				
Wade Pond	97120	Ludlow	Connecticut	No				
Walker Pond	72126	Millis	Charles	No				

Waterbody	PALIS Code	Town	Major Basin	WD History	WD Years Conducted	Current WD Magnitude (m)	WD Frequency	WD Purpose
Wallis Pond	42062	Dudley	French	No				
Watson Millpond	42063	Spencer	French	No				
Waushakum Pond	82112	Ashland	SuAsCo	No				
Weir Village North Pond	62206	Taunton	Taunton	No				
Weir Village South Pond	62207	Taunton	Taunton	No				
Wenham Lake	92073	Wenham	Ipswich	No				
West Meadow Brook Pond	62208	West Bridgewater	Taunton	No				
Weston Station Pond/Duck Pond	72135	Weston	Charles	No				
Wetherells Pond	52041	Plainville	Ten Mile	No				
Wheeler Pond	82116	Stow	SuAsCo	No				
Wheelers Pond	35097	Warwick	Millers	No				
White Pond	82119	Hudson	SuAsCo	No				
Wielock Pond	41056	Dudley	Quinebaug	No				
Willett Pond/New Pond	73062	Norwood	Boston Harbor	No				
Willis Pond	62212	Taunton	Taunton	No				
Wilson Pond	91017	Rowley	Parker	No				
Winona Pond	92077	Peabody	Ipswich	No				
Witch Pond	62215	Plainville	Ten Mile	No				
Wood Pond	36168	Ludlow	Chicopee	No				
Zero Mill Pond	36170	Monson	Chicopee	No				
Quacumquasit Pond	36131	Brookfield	Chicopee	No				

APPENDIX C

STUDY APPROACHES AND BIOTIC RESPONSES OF WINTER DRAWDOWN STUDIES

Winter drawdown studies covering biotic responses. Data includes study location, purpose of winter drawdown(s), study approach, number of study lakes, drawdown amplitude, drawdown timing and duration, whether winter drawdowns are annually conducted (A) or are novel to a lake system (N), number of study years, target assemblage and corresponding metrics per assemblage. Study approach codes are R-E=reference-experimental, B-A=before-after. Number of lakes are coded by study approach, (R)=reference lakes, (E)=experimental lakes, and if it's a gradient study approach, (R) and (E) refer to natural and regulated lakes respectively. Amplitude is coded similarly for reference-experimental approach, and if numerous lakes exist, the range of amplitude is given. Number of study years are coded for before-after study approaches, with (B)=before drawdown was conducted, (D)=during drawdown, (A)=after drawdown was completed (i.e., after refill).

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
Aroviita & Hämäläinen 2008	Finland	Power production	R-E	11(R)-12(E)	0.11-0.55(R),1.19-6.75(E)	Winter-Spring	6-7	A	3	Invertebrates	Abundance Composition Richness
Beard 1973	Wisconsin	Aquatic plant control	B-A	1	1.5	Fall-Winter	6	N	1(B)-1(D)-1(A)	Macrophytes	Abundance Frequency
Benejam et al. 2008	Spain	Water quality enhancement	B-A	1	11.6	Fall	2	N	1	Fish	Abundance Composition Condition
Benson & Hudson 1975	South Dakota	Power production	B-A	1	7-12	Fall		A	5(B)-3(A)	Invertebrates	Density
Black et al. 2003	Washington	Flood control	B-A	1	17, 23	Winter-Summer	6	A	2	Phytoplankton	Biotracer
									2	Benthic Algae	Biotracer
									2	Invertebrates	Biotracer
									2	Fish	Biotracer
Cott et al. 2008	Northwest Territories	Experimental (winter road construction)	R-E	2(R)-2(E)	10%, 20% volume	Winter	1	N	2	Fish	Abundance

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
Delong & Mundahl 1995	Wisconsin	Power production	B-A	1	2.9	Winter	3	A	1(B)-1(A)	Invertebrates	Density Composition
Fillion 1967	Alberta	Power production	B-A	3	10.4, 13.1, 15.8	Winter-Summer	3-5	A	3	Invertebrates	Density Composition
Fischer & Öhl 2005	Germany	Experimental	Mesocosm							Fish	Size Habitat selection Movement
Fiske 1989	Vermont	Aquatic plant control	B-A	1	1.15	Fall-Winter	8	N	1(B)-1(A)	Invertebrates	Density Richness Diversity Composition
Gaboury & Patalas 1984	Manitoba	Power production	B-A	1	1.7	Winter-Fall	7-8	A	2-11	Fish	Abundance Age Growth
Godshalk & Barko 1988	Wisconsin	Impoundment repair	B-A	1	1.25	Fall-Winter	4	A	1(B)-2(A)	Macrophytes	Biomass Composition
Goldsby & Sanders 1977	Louisiana	Aquatic plant control	B-A	1	2.1, 2.6	Fall-Winter	5-6	N	1(B)-1(D)-1(A)	Macrophytes	Biomass
Grimås 1961	Sweden	Power production	R-E	1(R)-1(E)	6(E)	Winter-Spring	6-7	A	2	Invertebrates	Density Composition
Grimås 1962	Sweden	Power Production	B-A	1	13	Winter-Spring	6-7	A	2(B)-1(A)	Invertebrates	Density Abundance
Grimås 1965	Sweden	Power Production	B-A	1	5	Winter	5-6	A	1(B)-1(A)	Invertebrates	Abundance Biomass Density
Hall & Cuthbert 2000	Minnesota	Waterfowl management	B-A	1	75% drainage	Fall-Summer	8-9	N	1	Turtles	Abundance Movement
Haxton & Findlay 2009	Quebec, Ontario	Power production	R-E	3(R)-2(E)	3-4(E)	Winter-Spring	5	A	1	Fish	Abundance Age Growth Condition
Hellsten & Riihimäki 1996	Finland	Power production	R-E	1(R)-1(E)	<1(R), 3.4(E)	Winter	5-6	A	5	Macrophytes	Composition Richness Abundance
Hellsten 2002	Finland	Power production	R-E, B-A	1(R)-1(E), 1	<1(R), 3.4(E), 7	Winter	5-6	A	6	Macrophytes	Frequency
Heman et al. 1969	Missouri	Fish habitat & growth enhancement	B-A	1	2.4	Summer	1	N	2(B)-1(A)	Fish	Abundance Growth

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
											Diet (largemouth bass)
Hestand & Carter 1974	Florida	Aquatic plant control	B-A	1	1.5	Fall-Winter	5	N	2(B)-1(A)	Macrophytes	Frequency Cover Density
Hulsey 1957	Arkansas	Flood control	B-A	1	3.7	Fall-Winter	4	N	4(B)-1(A)	Fish	Abundance Biomass
Hynes 1961	Wales	Flood control	B-A	1	5	Winter		A	2(B)-1(D)-1(A)	Invertebrates	Density Composition
Kallemeyn 1987a	Minnesota	Power production	R-E	1(R)-1(E)	1.1(R), 2.7(E)	Winter-Spring	4-5	A	5	Fish	Abundance (YOY)
Kallemeyn 1987b	Minnesota	Power Production	B-A	1	2.7	Winter-Spring	4-5	A	3	Fish	Abundance (YOY)
Kaster & Jacobi 1978	Wisconsin	Power production	B-A	1	7.7	Summer-Spring	9-10	A	1(B)-1(A) (monthly)	Invertebrates	Abundance Biomass Density
Keto et al. 2006	Finland	Power production and flood control	R-E	11(R)-8(E)	0.04-0.55(R), 2.27-6.75(E)	Winter	5-6	A	8	Macrophytes	Composition Richness Abundance
Koskenniemi 1994	Finland	Power production and flood control	B-A	1	2	Winter	5-7	A	5	Invertebrates	Biomass Density Composition Richness
Kraft 1988	Minnesota	Power production	R-E	1(R)-3(E)	1.1-1.3(R), 2.3-2.7(E)	Winter-Spring	7-8	A	3	Invertebrates	Density Diversity Frequency Richness Equitability Distribution
Manning & Johnson 1975	Louisiana	Aquatic plant control	B-A	1	2.1	Fall-Winter	3	N	1(B)-1(A)	Macrophytes	Biomass
Manning & Sanders 1975	Louisiana	Aquatic plant control	B-A	1	2.1	Summer-Winter	6	N	1(B)-1(A)	Macrophytes	Biomass
Mathis 1965	Arkansas	Aquatic plant control	B-A	1	0.9, 1.5, 2.1	Fall-Winter	5	N		Macrophytes	Qualitative
McAfee 1980	Colorado	Fish management	R-E	2(R)-2(E)	Complete drainage	Fall-Spring	7-8	N	2	Invertebrates	Density

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
										Fish	Abundance Composition Condition
McDowell 2012	Connecticut	Experimental/ recreational	R-E	1(R)-4(E)	0.91, 1.82	Fall-Winter	6-7	A,N	3	Fish	Growth (YOY) Spawning timing
McEwen & Butler 2010	Minnesota	Power production	BACI	1(R)-1(E)	1.5 (R), 1.5-2.5(E)	Winter-Spring	5-6	A	2	Invertebrates	Density Composition Richness
McGowan et al. 2005	Saskatchewan	Experimental	BACI	1(R)-1(E)	1(E)	Fall-Winter	6-7	N	2(B)-2(D)-2(A)	Phytoplankton	Abundance (pigments)
									2(B)-2(D)-2(A)	Zooplankton	Abundance
									1(B)-2(D)	Macrophytes	Diversity Biomass Composition
Mills et al. 2002	Ontario	Experimental	B-A	1	2, 3	Winter	3	N	10(B)-2(D)-3(A)	Fish	Abundance
Mjelde et al. 2012	Finland, Sweden, Norway	Power production, drinking water	Gradient	73	0.1-2.95(R) 0.05-6.8(E)	Winter	5-6	A	9, 28	Macrophytes	Composition Richness Frequency
Nichols 1975	Wisconsin	Aquatic plant control	B-A	1	1.5, 1.8	Fall-Winter	6-7	N	1(B)-2(D)-1(A)	Macrophytes	Frequency Density Abundance
Nilsson 1964	Sweden	Power production	B-A	2		Winter	5-7	A	6	Fish	Diet
Nordhaus 1989	Florida	Fish habitat & growth enhancement	B-A	1	6	Fall-Summer	10	N	2(B)-4(A)	Fish	Abundance
Olson et al. 2012	Wisconsin	Aquatic plant control	B-A	1	1.3	Winter	-	A	2	Macrophytes	Abundance Frequency
Palomäki & Koskenniemi 1993	Finland	Power production and flood control	B-A	1	0.35	Winter	5-6	A	4	Invertebrates	Abundance Biomass Richness
Palomäki 1994	Finland, Sweden	Power production	Gradient	14		Variable	Variable	A	1	Invertebrates	Biomass
Paterson & Fernando 1969	Ontario		B-A	1	Complete drainage	Fall-Winter	6-7	A	1(B)-1(A)	Invertebrates	Density

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
Peverly & Kopka 1991	New York	Aquatic plant control	B-A	1	2.5	Winter	4-5	N	1(B)-1(A)	Macrophytes	Density Biomass
Pierce et al. 1963	Georgia	Fish population manipulation	B-A	15	10-75% Volume	Fall-Winter	4	N	1(B)-1(A)	Fish	Biomass Abundance
			B-A						1(B)-1(A)	Invertebrates	Density
Reiser 1988	Minnesota	Power production	R-E	5(R)-2(E)	<1(R), 0.5(E), 2.5(E)	Winter-Spring		A	4	Waterbirds	Abundance
Rogers & Bergersen 1995	Colorado	Dam repair	R-E	1(R)-1(E)	1(E)	Fall	3	N	1	Fish	Movement
Samad & Stanley 1986	Maine	Reduce internal phosphorous	B-A	1	4	Summer-Spring	7-8	N	2	Invertebrates	Density Abundance Movement
Siver et al. 1986	Connecticut	Aquatic plant control	B-A	1	2, 2.7	Fall-Winter		N	1(B)-1(D)-1(A)	Macrophytes	Density Biomass
Smagula & Connor 2008	New Hampshire	Aquatic plant control	B-A	1	1.1, 1.8	Fall-Winter	5-6	A	4	Macrophytes	Abundance Cover
									4	Invertebrates	Abundance
									4	Fish	Cover Abundance Size
			B-A						3	Frogs	Abundance
Smith & Petersen 1991	Minnesota	Power production	R-E	1(R)-1(E)	0.3-1(R), 2.3(E)	Winter-Spring	4-5	A	3	Beavers	Density Condition Movement
Sutela & Huusko 1995	Finland	Power production	R-E	1(R)-1(E)	4.4(E)	Winter		A	3	Zooplankton	Biomass
									3	Fish	Diet
Sutela & Vehanen 2008	Finland	Power production	R-E	5(R)-8(E)	0.22-0.43(R), 1.54-6.75(E)	Winter	5-6	A	3	Fish	Density Composition Richness
Sutela et al. 2011	Finland	Power production	Gradient	9(R)-14(E)	0.09–0.48(R),	Winter	5-6	A	5	Fish	Richness Density

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
					1.18–6.75(E)						Biomass Frequency
Sutela et al. 2013	Finland	Power production	Gradient	14(R)-16(E)	0.9-0.55 (R), 1.19-6.75(E)	Winter	5-6	A	7	Macrophytes	Abundance Frequency
									3	Invertebrates	Composition
									5	Fish	Density Biomass Frequency
Swanson 2010	Wisconsin	Power production	B-A	1	0.9	Winter	4-5	A	1(B)-1(A)	Invertebrates	Density Abundance
Tarver 1980	Florida	Aquatic plant control	B-A	1	7	Winter-Winter	14	N	2(B)-2(A)	Macrophytes	Frequency Cover
Tazik et al. 1982	Pennsylvania	Aquatic plant control	B-A	1	2	Fall-Winter		N	1(B)-1(A)	Macrophytes	Biomass Productivity
Thurber et al. 1991	Minnesota	Power production	R-E	1(R)-1(E)	0.5-1(R), 2.5(E)	Winter-Spring	4-5	A	3	Muskrats	Density Condition Movement
Turner et al. 2005	Ontario	Experimental	BACI	1(R)-4(E)	2-3(E)	Winter-Spring	6	N	4-6	Benthic Algae	Biomass Composition Metabolism
									6	Phytoplankton	Biomass, Productivity Composition
									4	Macrophytes	Biomass Frequency Cover
Crosson 1990	Vermont	Aquatic plant control	B-A	1	1.15	Fall-Winter	8	N	1(B)-1(A)	Macrophytes	Cover Richness
										Fish	Abundance
Verrill & Berry Jr. 1995	Minnesota	Remove undesired fish species via winterkill, waterfowl management	B-A	2	<1	Winter		A	2	Fish	Abundance Movement
Vuorio et al. 2015	Finland	Power production	R-E	2(R)-1(E)	1(E)	Winter		A	21 and 1	Phytoplankton	Biomass Frequency
Wagner & Falter 2002	Idaho	Power Production & flood control	B-A	1	3.5, 2.1	Winter	6	A	2(B)-1(A)	Macrophytes	Biomass Abundance Composition

Study	Location	Purpose	Approach	No. of Lakes	Amplitude (m)	Timing of Drawdown	Drawdown Duration (months)	Annual or Novel Drawdown	No. of Study Years	Target Assemblage	Metric
Wegener & Williams 1975	Florida	Fish habitat enhancement	B-A	1	2.1	Spring-Spring	12	N	1(B)-3(A)	Fish	Density
Wegener et al. 1974	Florida	Fish habitat & growth enhancement	B-A	1	2.1	Winter-Winter	12	N	1(B)-4(A)	Invertebrates	Density Abundance
White et al. 2011	Ontario	Power production	Gradient	20(R)-28(E)	0-1.5(R), 0.8-10(E)	Winter-Spring	4	A	1	Invertebrates	Composition, Richness (taxa, functional feeding, mobile groups)
Wilcox & Meeker 1991	Minnesota	Power production	R-E	1(R)-2(E)	1.8(R), 1.1(E), 2.7(E)	Fall-Winter	5-6	A	1	Macrophytes	Frequency Cover Composition (taxon & physical structure)
WRS 2011	Massachusetts	Aquatic plant control	B-A	1	0.9	Winter	4	N	2	Macrophytes	Cover
									2	Invertebrates	Abundance Density

APPENDIX D

SUPPLEMENTARY REFERENCES FOR APPENDIX C

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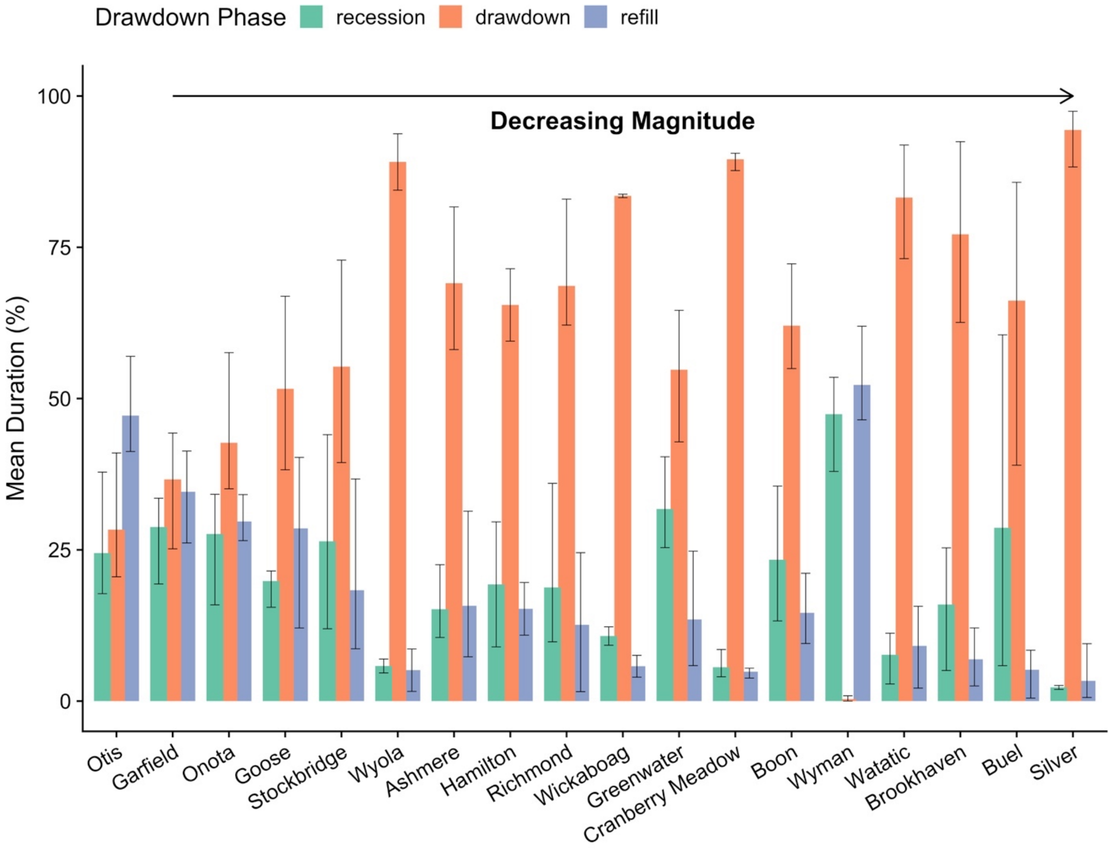
APPENDIX E

PERECENT DRAWDOWN PHASE DURATIONS

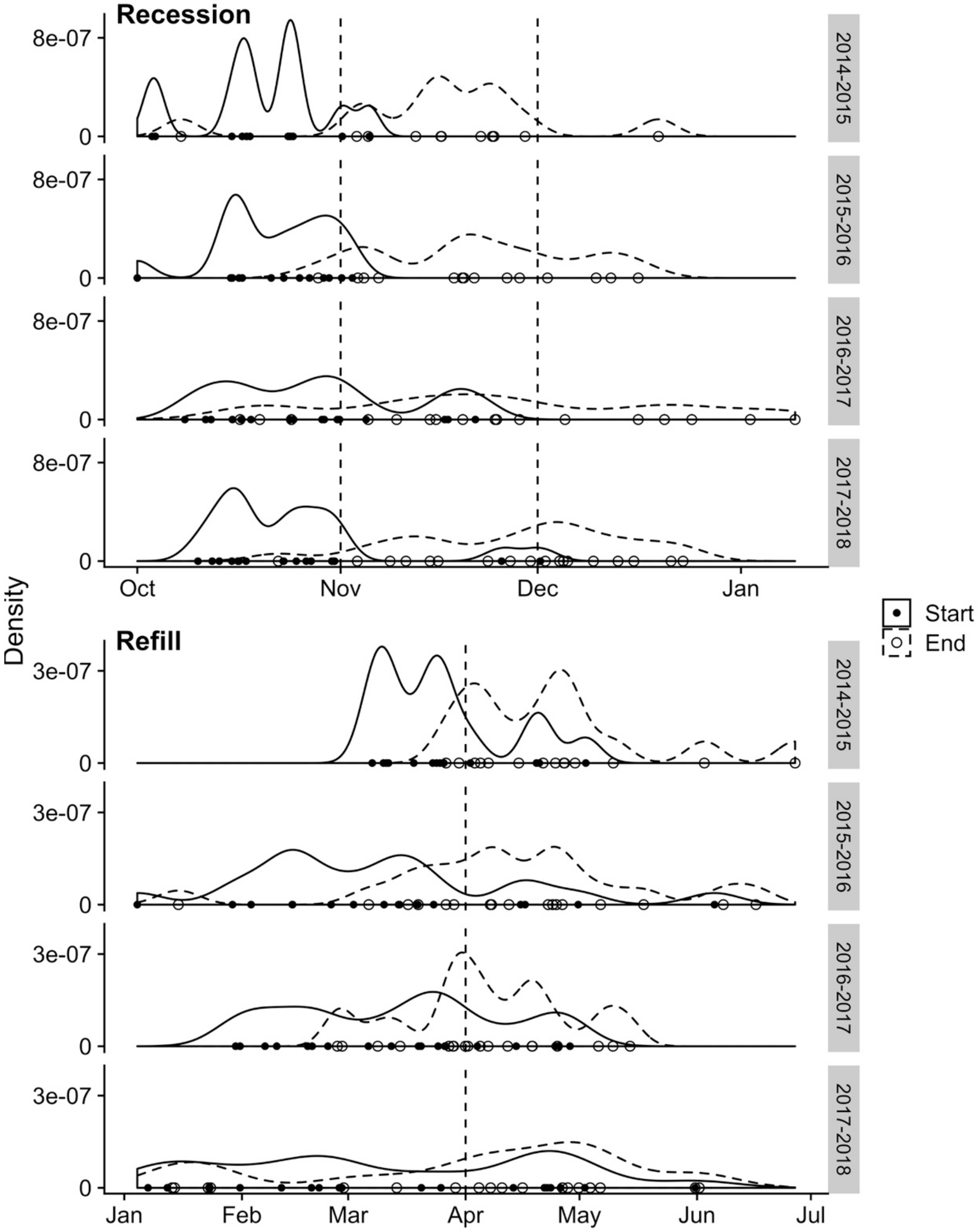
Interannual mean (± range) percentage of WD duration phases (color-coded) along a decreasing magnitude gradient.



APPENDIX F

PROBABILITY OF ANNUAL PHASE TIMING

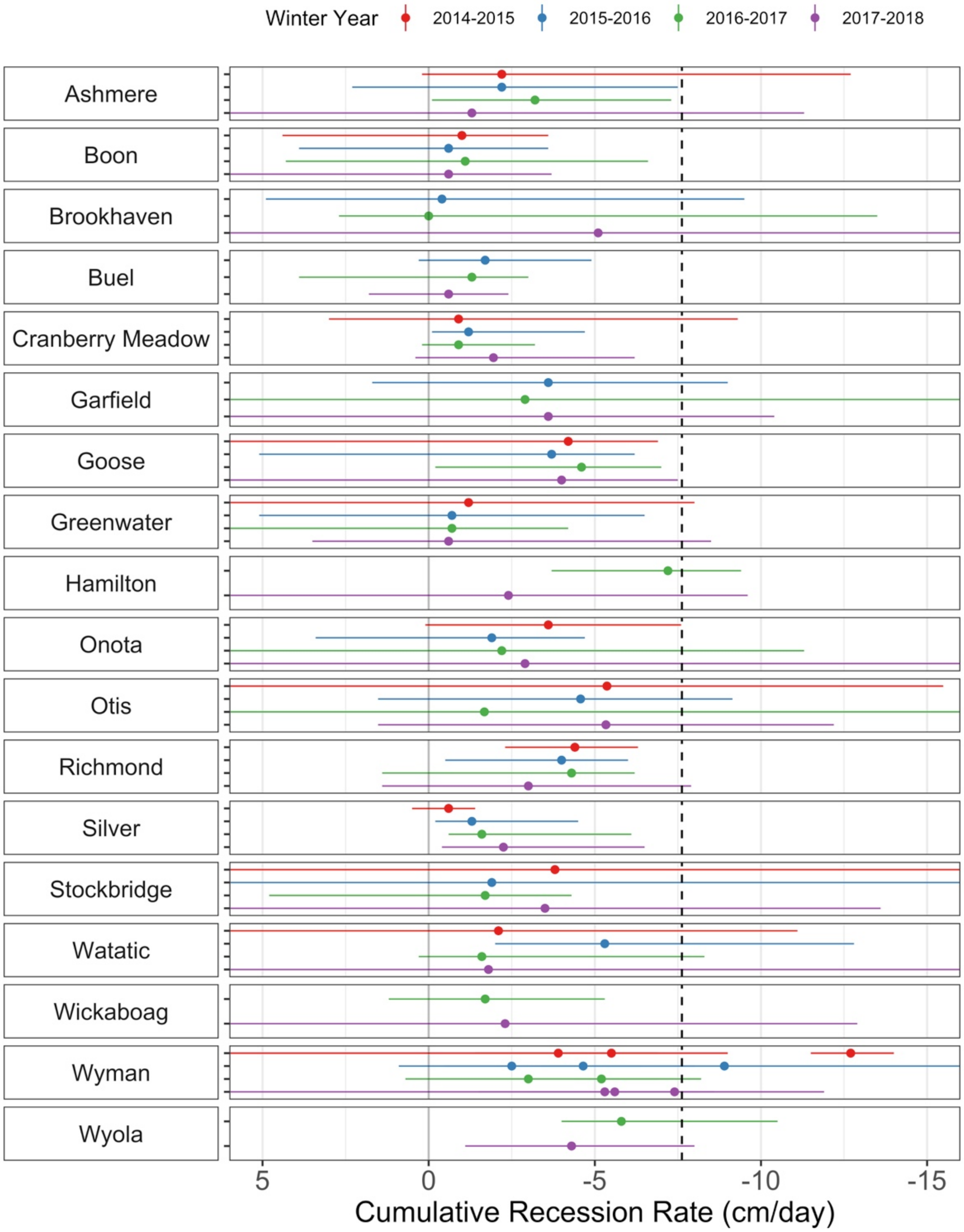
Density of recession (top) and refill (bottom) start and end dates (solid, dashed) aggregated by lake and paneled by winter-year (e.g., 2014-2015). Points along the x-axis correspond to start (filled) and end (open) dates. Dashed vertical lines represent MassWildlife (2002) recommendations for WD initiation start (Nov. 1st) and recession end dates (Dec. 1st) and refill end date (Apr. 1st). Note difference in x-axis time scale between recession and refill graphs. Phase dates from late winter-spring WD periods in Wyman are not included.



APPENDIX G

CUMULATIVE RECESSION RATES

Median cumulative recession rates (± range) per WD period for each lake. WD periods are color-coded by winter-year and only complete recession are included. Rate ranges exceed the recession rate scale where bars reach margins. Dashed black lines are the lower (-5.08cm/day) and upper (-7.62 cm/day) recession rate guidelines from Mattson et al. (2004).



APPENDIX H

CORRELATION MATRIX OF DRAWDOWN METRICS

Values represent Pearson *r* correlation coefficients determined from WD periods across lakes. Bolded values indicate $r \geq 0.4$. WD metric categories are for magnitude, mean = average water levels during drawdown phase, max. = lowest water level during WD period, Exp. = maximum lake or littoral area exposed during WD periods; duration, WD = full WD period duration, and recession, drawdown, refill represent phase durations; rate is divided into recession and refill rates with summary statistics (mean, median, min., max, SD-standard deviation) per WD period.

		Magnitude				**Duration**				**Duration Exposed**							
		Mean	Max.	Lake Exp.	Littoral Exp.	WD	Recession	Drawdown	Refill	0.25m	0.5m	0.75m	1m	1.25m	1.5m	1.75m	2m
Magnitude	Mean	1.00	**0.93**	**0.56**	**0.74**	**0.41**	**0.61**	-0.21	**0.89**	**0.61**	**0.81**	**0.92**	**0.92**	**0.91**	**0.83**	**0.77**	**0.65**
	Max.	**0.93**	1.00	**0.65**	**0.80**	**0.45**	**0.61**	-0.12	**0.82**	**0.64**	**0.84**	**0.90**	**0.86**	**0.82**	**0.72**	**0.66**	**0.55**
	Lake Exp.	**0.56**	**0.65**	1.00	**0.77**	0.24	0.23	-0.05	**0.45**	0.21	**0.54**	**0.59**	**0.54**	**0.53**	**0.52**	**0.41**	0.23
	Littoral Exp.	**0.74**	**0.80**	**0.77**	1.00	**0.45**	**0.40**	0.02	**0.65**	**0.45**	**0.60**	**0.72**	**0.71**	**0.71**	**0.70**	**0.61**	**0.45**
Duration	WD	**0.41**	**0.45**	0.24	**0.45**	1.00	0.40	**0.75**	**0.50**	**0.71**	**0.48**	**0.46**	**0.43**	**0.42**	0.37	0.36	0.34
	Recession	**0.61**	**0.61**	0.23	**0.40**	0.40	1.00	-0.15	**0.58**	**0.53**	**0.44**	**0.56**	**0.54**	**0.53**	**0.48**	**0.42**	0.34
	Drawdown	-0.21	-0.12	-0.05	0.02	**0.75**	-0.15	1.00	-0.15	0.34	0.04	-0.10	-0.13	-0.14	-0.13	-0.10	-0.07
	Refill	**0.89**	**0.82**	**0.45**	**0.65**	**0.50**	**0.58**	-0.15	1.00	**0.56**	**0.68**	**0.81**	**0.81**	**0.82**	**0.74**	**0.70**	**0.65**
Duration Exposed	0.25m	**0.61**	**0.64**	0.21	**0.45**	**0.71**	**0.53**	0.34	**0.56**	1.00	**0.75**	**0.60**	**0.53**	**0.49**	**0.41**	0.39	0.36
	0.5m	**0.81**	**0.84**	**0.54**	**0.60**	**0.48**	**0.44**	0.04	**0.68**	**0.75**	1.00	**0.85**	**0.74**	**0.69**	**0.58**	**0.55**	**0.48**
	0.75m	**0.92**	**0.90**	**0.59**	**0.72**	**0.46**	**0.56**	-0.10	**0.81**	**0.60**	**0.85**	1.00	**0.96**	**0.90**	**0.76**	**0.71**	**0.62**
	1m	**0.92**	**0.86**	**0.54**	**0.71**	**0.43**	**0.54**	-0.13	**0.81**	**0.53**	**0.74**	**0.96**	1.00	**0.96**	**0.83**	**0.77**	**0.67**

		Magnitude				**Duration**				**Duration Exposed**							
		Mean	Max.	Lake Exp.	Littoral Exp.	WD	Recession	Drawdown	Refill	0.25m	0.5m	0.75m	1m	1.25m	1.5m	1.75m	2m
	1.25m	**0.91**	**0.82**	**0.53**	**0.71**	**0.42**	**0.53**	-0.14	**0.82**	**0.49**	**0.69**	**0.90**	**0.96**	1.00	**0.92**	**0.87**	**0.76**
	1.5m	**0.83**	**0.72**	**0.52**	**0.70**	0.37	**0.48**	-0.13	**0.74**	**0.41**	**0.58**	**0.76**	**0.83**	**0.92**	1.00	**0.96**	**0.85**
	1.75m	**0.77**	**0.66**	**0.41**	**0.61**	0.36	**0.42**	-0.10	**0.70**	0.39	**0.55**	**0.71**	**0.77**	**0.87**	**0.96**	1.00	**0.93**
	2m	**0.65**	**0.55**	0.23	**0.45**	0.34	0.34	-0.07	**0.65**	0.36	**0.48**	**0.62**	**0.67**	**0.76**	**0.85**	**0.93**	1.00
Recession Rate	Mean	-0.22	-0.21	-0.18	-0.17	0.31	**0.43**	0.32	-0.15	0.03	-0.22	-0.18	-0.19	-0.18	-0.17	-0.18	-0.18
	Median	-0.17	-0.17	-0.19	-0.10	0.40	0.38	0.40	-0.09	0.12	-0.15	-0.11	-0.11	-0.09	-0.06	-0.06	-0.03
	Max.	-0.25	**-0.46**	**-0.42**	-0.41	-0.11	-0.31	0.07	-0.18	-0.25	-0.26	-0.30	-0.26	-0.24	-0.20	-0.16	-0.12
	Min.	0.15	0.39	0.39	0.34	0.06	0.28	-0.09	0.11	0.11	0.15	0.19	0.13	0.13	0.08	0.02	0.00
	SD	0.17	0.39	0.39	0.37	0.01	0.22	-0.13	0.12	0.09	0.14	0.20	0.16	0.15	0.10	0.06	0.04
Refill Rate	Mean	-0.10	-0.09	-0.16	-0.18	-0.32	-0.11	-0.17	-0.30	-0.13	-0.03	-0.16	-0.15	-0.15	-0.12	-0.11	-0.09
	Median	-0.12	-0.12	-0.15	-0.22	-0.31	**-0.16**	-0.14	-0.30	-0.14	-0.04	-0.16	-0.15	-0.15	-0.12	-0.11	-0.09
	Min.	-0.33	**-0.45**	-0.26	-0.41	-0.26	-0.29	0.01	**-0.41**	-0.35	-0.39	**-0.41**	-0.37	-0.28	-0.21	-0.23	-0.24
	Max.	0.28	0.37	0.25	0.36	0.10	0.29	-0.10	0.26	0.25	0.29	0.23	0.19	0.12	0.09	0.06	-0.04
	SD	0.21	0.31	0.08	0.23	-0.02	0.23	-0.13	0.08	0.23	0.30	0.19	0.14	0.08	0.04	0.06	0.02

APPENDIX H (CONTINUED)

		Recession Rate					Refill Rate				
		Mean	Median	Max.	Min.	SD	Mean	Median	Min.	Max.	SD
Magnitude	Mean	-0.22	-0.17	-0.25	0.15	0.17	-0.10	-0.12	-0.33	0.28	0.21
	Max.	-0.21	-0.17	**-0.46**	0.39	0.39	-0.09	-0.12	**-0.45**	0.37	0.31
	Lake Exp.	-0.18	-0.19	**-0.42**	0.39	0.39	-0.16	-0.15	-0.26	0.25	0.08
	Littoral Exp.	-0.17	-0.10	**-0.41**	0.34	0.37	-0.18	-0.22	**-0.41**	0.36	0.23
Duration	WD	0.31	0.40	-0.11	0.06	0.01	-0.32	-0.31	-0.26	0.10	-0.02
	Recession	**0.43**	0.38	-0.31	0.28	0.22	-0.11	-0.16	-0.29	0.29	0.23
	Drawdown	0.32	0.40	0.07	-0.09	-0.13	-0.17	-0.14	0.01	-0.10	-0.13
	Refill	-0.15	-0.09	-0.18	0.11	0.12	-0.30	-0.30	**-0.41**	0.26	0.08
Duration Exposed	0.25m	0.03	0.12	-0.25	0.11	0.09	-0.13	-0.14	-0.35	0.25	0.23
	0.5m	-0.22	-0.15	-0.26	0.15	0.14	-0.03	-0.04	-0.39	0.29	0.30
	0.75m	-0.18	-0.11	-0.30	0.19	0.20	-0.16	-0.16	**-0.41**	0.23	0.19
	1m	-0.19	-0.11	-0.26	0.13	0.16	-0.15	-0.15	-0.37	0.19	0.14
	1.25m	-0.18	-0.09	-0.24	0.13	0.15	-0.15	-0.15	-0.28	0.12	0.08
	1.5m	-0.17	-0.06	-0.20	0.08	0.10	-0.12	-0.12	-0.21	0.09	0.04
	1.75m	-0.18	-0.06	-0.16	0.02	0.06	-0.11	-0.11	-0.23	0.06	0.06
	2m	-0.18	-0.03	-0.12	0.00	0.04	-0.09	-0.09	-0.24	-0.04	0.02
Rec	Mean	1.00	**0.91**	0.02	0.03	-0.07	-0.15	-0.18	0.07	-0.04	-0.06

		Recession Rate					Refill Rate				
		Mean	Median	Max.	Min.	SD	Mean	Median	Min.	Max.	SD
	Median	**0.91**	1.00	0.02	-0.05	-0.16	-0.12	-0.15	0.02	0.00	-0.01
	Max.	0.02	0.02	1.00	**-0.87**	**-0.90**	0.07	0.07	0.27	-0.24	-0.22
	Min.	0.03	-0.05	**-0.87**	1.00	**0.96**	-0.06	-0.04	-0.15	0.17	0.10
	SD	-0.07	-0.16	**-0.90**	**0.96**	1.00	-0.08	-0.07	-0.23	0.19	0.14
Refill Rate	Mean	-0.15	-0.12	0.07	-0.06	-0.08	1.00	**0.98**	0.26	0.09	**0.51**
	Median	-0.18	-0.15	0.07	-0.04	-0.07	**0.98**	1.00	0.29	0.02	**0.40**
	Min.	0.07	0.02	0.27	-0.15	-0.23	0.26	0.29	1.00	**-0.70**	**-0.56**
	Max.	-0.04	0.00	-0.24	0.17	0.19	0.09	0.02	**-0.70**	1.00	**0.74**
	SD	-0.06	-0.01	-0.22	0.10	0.14	**0.51**	**0.40**	**-0.56**	**0.74**	1.00

APPENDIX I

SELECTION PROCESS FOR STUDY LAKES

We selected lakes using a stratified random approach to primarily capture a winter drawdown magnitude gradient. Lakes were selected from local conservation commissions and lake associations that responded to a statewide email survey in 2013-2014 where we requested information about lake management (i.e., 397 out of 2080 waterbodies). We targeted lakes in the Northeastern Highlands (e.g., Western New England Marble Valleys/Berkshire Valley/Housatonic and Hoosic Valleys) and two ecoregions in the Northeastern Coastal Zone (e.g., Connecticut River Valley, Lower Worcester Plateau) to help reduce water quality variation among waterbodies based on watershed land cover and geology (Griffiths et al. 2009) for a related project on physical habitat (e.g., macrophytes). We first removed waterbodies with lake surface area < 0.035 km^2 producing 271 lakes remaining for selection. Where we received reported drawdown magnitude information ($n = 21$ lakes), we selected two lakes each from four drawdown magnitude classes (<0.5 m, 0.5–1 m, 1–1.5 m, >1.5 m) to ensure a drawdown magnitude gradient. We then selected 8 additional lakes with a history of WD but without magnitude information, which were further stratified into four lakeshore development density classes (e.g., 0–155, >155–284, >284–395, 412–536 buildings km^{-2} within a 100 m buffer) determined by natural breaks in the data distribution. The final four lakes had no history of annual winter drawdowns, and these lakes were randomly selected from survey respondents based on natural breaks in lake area (2 in each of 0.035–0.186 km^2, 0.272–2.20 km^2) and lakeshore development density (2 in each of <78 km^{-2}, >105 km^{-2}), which corresponded with lake size and development of selected drawdown lakes. Where waterbodies were exhausted within a stratification (low drawdown magnitude class: <0.5 m), we extended our selection area to include the New England Coastal Plains and Hills in eastern MA. We were unable to sample five of the original 20 selected lakes (4 WD, 1 non-drawdown) due to access issues; and therefore, replaced those with 6 additional lakes within our existing study area and criteria. Ultimately, we selected 18 lakes with current WD regimes (Table 1) and 3 lakes (Quacumquasit, Congamond, Leverett) with no history of annual winter drawdowns (Figure 1).

APPENDIX J

LAKE DEPTH INTERPOLATION METHODOLOGY

Sample points were imported into ArcGIS 10.3 and inspected for local outliers using the cluster classification of Voronoi polygons and subsequently removed (0–242 removed points per lake). Sonar depth estimates can be inaccurate because of shallow depths, unconsolidated lake bottom, and dense beds of vegetation. From the remaining sampled depths, we used empirical Bayesian kriging (EBK) models in ArcGIS 10.3 to interpolate unsampled depths for each lake. EBK model parameters were set as: subset size = 200, overlap factor = 2, simulation number = 200, power semivariogram, max. neighbors = 15, min. neighbors = 10, 1 sector, and angle = 0. For a subset of 3 lakes (Ashmere, Garfield, Silver) that encompass a range of magnitude and sample points, we varied subset size (25, 50, 100, 200), overlap factor (1, 2), and simulation number (100, 200) to assess differences in resulting bathymetry-related WD metrics (e.g., exposure areas) based on parameters selected. We found small differences in estimated percent lake exposure area (0.25–1.25%) and littoral exposure area (0.091–1.57%) with the different parameters, and thus determined that the single parameters selected were adequate.

We evaluated EBK model performance with cross-validation 95% confidence intervals to assess single-point predictions and average continuous ranked probability score (CRPS) to assess full distribution predictions. Greater than 95% of cross-validated points fell within 95% confidence intervals for all lake models except Brookhaven (93.6%). CPRS values ranged from 0.043–0.149. We further identified potential outliers from cross-validation, removed these points, and updated models. From the EBK model output, we generated 1-m^2 raster grids of predicted depths and predicted standard errors. Negative depth values were predicted from every lake bathymetry model (21–970 cells). These occurred at or adjacent to shorelines where observed depths were 0 m (i.e., shoreline) or where depth sampling was relatively distant from shore because of boat inaccessibility in shallow shelves. Despite these negative values, they were included in exposure area calculations because they composed a relatively small percentage of interpolated points (<0.17%) and were likely exposed during WD events.

APPENDIX K

MACROPHYTE SPECIES SAMPLED

Macrophyte species sampled across 21 lakes in Massachusetts according to macrophyte functional traits. Traits and assignment of traits are based on Grime et al. (1990), Willby et al. (2000), Capers et al. (2010), Arthaud et al. (2012), and Wilcox and Meeker (1991).

Macrophyte Taxa	Abbreviation	Status	Morphotype	Longevity	Amphibious	Fecundity
Bryophyte	Bry	Native	LC		No	
Brasenia schreberi	Bsch	Native	EC	Pr	No	Mv
Cabomba caroliniana	Ccar	Nonnative	EC	Pr	No	Hv
Ceratophyllum demersum	Cdem	Native	EC	Pr	No	Mv
Chara species	Cha		LC	A	No	Hv
Elodea canadensis	Ecan	Native	EC	Pr	No	Lv
Elatine minima	Ela	Native	MF	A	Yes	Hv
Eleocharis species	Ele	Native	MF	P	Yes	Mv
Ericaulon aquaticum	Eaqu	Native	LR	P	Yes	Mv
Gratiola aurea	Gaur	Native	MF	P	Yes	M
Isoetes species	Iso	Native	LR	P	No	H
Juncus species	Jun		MF		Yes	
Myriophyllum heterophyllum	Mhet	Nonnative	EC	Pr	Yes	Mv
Myriophyllum humile	Mhum	Native	LC	Pr	Yes	Mv
Myriophllum spicatum	Mspi	Nonnative	EC	Pr	Yes	Mv
Myriophyllum tenellum	Mten	Native	LC	Pr	No	Mv
Najas flexilis	Nfle	Native	LC	A	No	Mv
Najas guadalupensis	Ngua	Native	LC	A	No	Mv
Najas minor	Nmin	Nonnative	LC	A	No	M
Nitella species	Nit		LC	A	No	Hv
Nymphaea odorata	Nodo	Native	EC	Pr	No	Mv
Nuphar variegata	Nvar	Native	EC	Pr	Yes	Hv
Persicaria amphibia	Poly	Native	EC	Pr	Yes	Mv
Pontederia cordata	Pcor	Native	LR	Pr	Yes	Mv
Potamogeton amplifolius	Pamp	Native	EC	Pr	No	Lv
Potamogeton bicupulatus	Pbic	Native	LC	Pr	No	Mv
Potamgeton crispus	Pcri	Nonnative	EC	Pr	No	Hv
Potamogeton epihydrus	Pepi	Native	LC	Pr	No	Lv
Potamogeton foliosus	Pfol	Native	EC	Pr	No	Mv
Potamogeton gramineus	Pgra	Native	LC	Pr	Yes	Mv
Potamogeton illinoensis	Pill	Native	EC	Pr	No	Mv
Potamogeton perfoliatus	Pper	Native	EC	Pr	No	Mv
Potamogeton pusillus	Ppus	Native	LC	Ar	No	Hv
Potamogeton robbinsii	Prob	Native	LC	Pr	No	Mv
Potamogeton spirillus	Pspi	Native	LC	Pr	No	Mv
Potamogeton zosteriformis	Pzos	Native	LC	Pr	No	Mv
Sagitarria species	Sag	Native	LR	Pr	Yes	Hv

Macrophyte Taxa	Abbreviation	Status	Morphotype	Longevity	Amphibious	Fecundity
Sparganium erectum	Sere	Native	EC	Pr	Yes	Hv
Stuckenia pectinata	Spec	Native	LC	Pr	No	
Utricularia species	Utr		EC	Ar	No	Mv
Vallisneria americana	Vame	Native	EC	Pr	No	Mv

Trait Codes: Morphotype: *MF* = mat-former, *LR* = low rosette, *LC* = low caulescent, *EC* = erect caulescent. Longevity: *P* = perennial without storage organ, *Pr* = perennial with storage organ, *A* = annual without storage organ, *Ar* = annual with storage organ. Fecundity: *Lv* = low number of reproductive organs, seeds and vegetative propagules, *M* = moderate number of reproductive organs, seeds only, *Mv* = moderate number of reproductive organs, seeds and vegetative propagules, *H* = high number of reproductive organs, seeds only, *Hv* = high number of reproductive organs, seeds and vegetative propagules.

APPENDIX L.

MODEL COMPONENTS FOR HABITAT RESPONSES

Model structure for physical habitat components. A random intercept of lake was included in each model in addition to the fixed effect predictors.

Habitat Response Variable	Full Fixed Predictor Set	Error Distribution	Link Function	Observational Unit
Macrophyte Biomass (g)	DMag, Depth, ShoreType, Herb, ResDens, Alka, Secchi, TP, Csub, Silt, Fetch, Slope, OM*	Gamma	Log	Contour
Macrophyte Biovolume (%)	DMag, Depth, ShoreType, Herb, ResDens, Alka, Secchi, TP, Csub, Silt, Fetch, Slope, OM*	Gamma	Log	Contour
Silt Sediment (%)	Mag, Depth, ShoreType, Fetch, Slope, MBiomass	Beta	Logit	Contour
Coarse Sediment (%)	Mag, Depth, ShoreType, Fetch, Slope, MBiomass	Beta	Logit	Contour
Sediment OM* (%)	Mag, Depth, ShoreType, Fetch, Slope, MBiomass	Beta	Logit	Contour
Coarse Wood Abundance	Mag, ResDens, ShoreType, Fetch, Slope	Negative Binomial	Log	Site
Coarse Wood Complexity	Mag, ResDens, ShoreType, Fetch, Slope, CWD	Negative Binomial	Log	Site

*Modeled using a subset of 15 lakes and not included as a predictor in full dataset models.

APPENDIX M

ESTIMATES FOR TOP MODELS OF FUNCTIONAL TRAIT STATES

Top models for macrophyte functional trait states that include a drawdown magnitude-depth interaction. Model terms include estimates (β) for drawdown magnitude at 0.5m and 1m (subscripted), depth contrast (e.g., 1m – 0.5m), drawdown magnitude-depth interactions, and for other environmental covariates (subscripted). See Table # for environmental variable subscript codes. Absence of a random lake intercept indicates a negligible variance term (e.g., <0.001). Associated standard errors for estimates are in parentheses. Bolded values indicate a significant correlation at $p = 0.05$ alpha level.

Macrophyte Trait	Drawdown Magnitude		Depth		Drawdown Magnitude*Depth		Other Covariates	
Longevity	β	*p*	β	*p*	β	*p*	β	*p*
Perennials (with & without storage organs)	$\beta_{0.5m} = -0.26(0.24)$ $\beta_{1m} = -0.57(0.30)$	0.275 0.055	**$\beta_{1-0.5m} = -0.82(0.29)$**	**0.005**	$\beta_{1-0.5m} = -0.31(0.32)$	0.328	$\beta_{Alka} = -0.40(0.22)$ $\beta_{Herb} = -0.94(0.53)$ $RandI_{Lake} = 0.28$	0.068 0.075
Annuals without storage organs	**$\beta_{0.5m} = 0.43(0.20)$** **$\beta_{1m} = 0.68(0.26)$**	**0.028** **0.008**	**$\beta_{1-0.5m} = 0.99(0.29)$**	**<0.001**	$\beta_{1-0.5m} = 0.25(0.30)$	0.403	**$\beta_{Alka} = 0.46(0.18)$** **$\beta_{Herb} = 1.11(0.44)$** $\beta_{Secchi} = 0.31(0.18)$	**0.009** **0.011** 0.085
Fecundity								
Moderate no. of reprod. organs, seeds + veg.	$\beta_{0.5m} = -0.24(0.21)$ $\beta_{1m} = -0.25(0.27)$	0.248 0.348	$\beta_{1-0.5m} = -0.45(0.30)$	0.132	$\beta_{1-0.5m} = -0.013(0.32)$	0.966	$RandI_{Lake} = 0.16$	
High no. of reprod. organs, seeds + veg.	$\beta_{0.5m} = 0.27(0.26)$ $\beta_{1m} = 0.34(0.27)$	0.287 0.219	$\beta_{1-0.5m} = 0.26(0.31)$	0.399	$\beta_{1-0.5m} = 0.071(0.31)$	0.818	$\beta_{Csub} = -0.37(0.20)$ $\beta_{Slope} = -0.25(0.18)$ $RandI_{Lake} = 0.36$	0.065 0.160
Morphotype								
Erect caulescent	$\beta_{0.5m} = -0.24(0.19)$ $\beta_{1m} = -0.23(0.25)$	0.203 0.351	**$\beta_{1-0.5m} = -0.62(0.30)$**	**0.037**	$\beta_{1-0.5m} = 0.0074(0.31)$	0.981	$\beta_{Alka} = 0.27(0.17)$ **$\beta_{Secchi} = -0.38(0.19)$**	0.108 **0.041**
Low caulescent	$\beta_{0.5m} = 0.11(0.23)$ $\beta_{1m} = 0.29(0.29)$	0.647 0.312	**$\beta_{1-0.5m} = 0.94(0.29)$**	**0.001**	$\beta_{1-0.5m} = 0.19(0.31)$	0.541	$\beta_{Herb} = 0.83(0.52)$ **$\beta_{Secchi} = 0.67(0.24)$**	0.113 **0.005**

Macrophyte Trait	Drawdown Magnitude		Depth		Drawdown Magnitude*Depth		Other Covariates	
							$\text{RandI}_{\text{Lake}}$ = 0.30	
Amphibious	**$\beta_{0.5m}$ = 0.41(0.20)**	**0.045**	**$\beta_{1\text{-}0.5m}$ = -0.75(0.27)**	**0.006**	$\beta_{1\text{-}0.5m}$ = -0.46(0.28)	0.100	**β_{Herb} = -1.23(0.34)**	**< 0.001**
	β_{1m} = -0.051(0.24)	0.830					**β_{Alks} = 0.58(0.19)**	**0.002**
							β_{Csub} = -0.34(0.16)	**0.038**
							β_{Fe} = 0.42(0.18)	**0.020**

APPENDIX N

MUSSEL SAMPLING DATES

Lake sample dates for pre-drawdown (living densities) and post-drawdown surveys (mortality) relative to drawdown initiation (2015, 2017) and water level decline cessation (i.e., stable winter drawdown water levels) dates (2017 only). Drawdown rates were calculated only for 2017 drawdown events when mortality surveys were conducted. '-'= not applicable in our study. Drawdown end dates refer to when water levels reach normal pool levels in spring/summer of the subsequent year.

Lake	Year Sampled	Dates Sampled, Pre-drawdown	Water Level Decline Start Date	Water Level Decline End Date	Date Sampled, Post-drawdown	Mean Drawdown Rate (cm/day)	Max Drawdown Rate (cm/day)	Drawdown End Date
Buel	2015	9/26-9/27	10/30	-	-	-	-	5/13
	2017	9/18-9/21	10/31	-	-	-	-	
Congamond	2015	9/30-10/3	-	-	-	-	-	-
	2017	10/4-10/6	-	-	-	-	-	-
Quacumquasit	2015	10/7-10/13	-	-	-	-	-	-
	2017	9/27-9/29	-	-	-	-	-	-
Ashmere	2015	9/28-9/29	10/21	-	-	-	-	4/12
	2017	-	10/23	12/5	11/18	2.63	24.0	
Greenwater	2017	9/13-9/15	10/30	12/28	-	-	-	
Hamilton	2017	9/23-9/26	10/16	11/15	11/11	1.42	28.8	
Richmond	2015	9/19-9/20	11/1	-	-	-	-	3/18
	2017	-	10/31	11/27	11/30	2.64	15.6	
Stockbridge	2015	10/4-10/5	10/15	-	-	-	-	4/4
	2017	-	10/25	11/29	12/4	2.95	25.2	
Wickaboag	2017	10/1-10/3	10/17	11/12	11/11	1.66	73.2	
Garfield	2017	-	10/17	12/13	12/2	3.91	27.6	
Goose	2017	-	10/15	11/23	11/21	3.52	28.8	
Onota	2017	-	10/16	12/3	12/6	5.01	86.4	
Otis	2017	-	10/14	12/9	12/8	3.67	12.2	

APPENDIX O

PHYSICAL HABITAT CHARACTERISTICS

Lake physical habitat characteristics at quadrat (n = 54 per lake), transect (n = 6 per lake), and site (n = 3 per lake) levels. Values represent means and standard deviations are indicated in brackets. Dominant substrates are listed as the first and second most frequently observed size-classes. Results (*W*, *p*) of comparison between control and drawdown lakes using a Mann-Whitney test.

	Quadrat				*Transect*		*Site*
Lake	Depth to Refusal (cm)	Macrophyte Cover (%)	Relative Depth (cm)	Dominant Substrate	Macrophyte Cover (%)	Slope (%)	Effective Fetch (m)
Control							
Buel	20.3[8.0]	35.2[17]	-1.5 [4.6]	sand, pebble	37.9[35]	11.6[4.9]	270.7[38.7]
Congamond	16.9[9.8]	1.3[3.0]	-0.3 [10.1]	sand, pebble	28.7[32.9]	10.1[5.4]	207[59.4]
Quacumquasit	14.3[8.6]	26.1[26]	-0.6 [3.9]	sand, gravel	37[34.1]	7.2[3.2]	296.5[47.7]
Mean	**17.2[9.1]**	**21.0[23]**	**-0.8 [6.8]**	**sand, pebble**	**34.5[33.3]**	**9.6[4.8]**	**258.1[61.2]**
Drawdown							
Greenwater	13.1[9.4]	2.5[6.0]	6.8 [7.8]	cobble, pebble	10.3[17.1]	11.4[5.7]	180.2[41.1]
Hamilton	43.2[23.8]	14.6[15]	2.4 [8.9]	sand, pebble	8.6[9.2]	17.7[18.9]	226.2[50]
Wickaboag	14.1[9.4]	2.7[5.0]	2.0 [7.8]	pebble, sand	29.8[26.4]	6.7[2.3]	340.2[27.1]
Ashmere	-	-	-	-	26[29.2]	12.8[8.4]	167.8[18]
Richmond	-	-	-	-	11.7[19.4]	8.6[2.1]	371.5[19.7]
Stockbridge	-	-	-	-	11[20]	9.2[3.7]	403.4[33.3]
Mean	**25.2[21.9]**	**6.6[11]**	**3.7 [8.5]**	**pebble, sand**	**16.2[21.4]**	**11.1[9.0]**	**281.5[100]**
W	*12278*	*17156*	*8552*	-	*212.5(253.5)*	*156.5(170.5)*	*536*
p	*0.317*	*<0.001*	*<0.001*	-	*0.099(0.004)*	*0.874(0.800)*	*0.209*

Transect *W* and *p*-values represent results from comparisons at the 0.5-m, with results from the 1-m depths in parentheses. Quadrat-level measurements were not measured in Ashmere, Richmond, and Stockbridge lakes.

APPENDIX P

MACROINVERTEBRATE FUNCTIONAL TRAIT ASSIGNMENT.

Macroinvertebrate functional traits for collected taxa. Macroinvertebrates are listed by levels of taxonomy with Taxa ID as the lowest taxonomic level feasible for identification. Functional traits (highlighted in gray) and their associated trait states are: FFG (functional feeding group): PR = predator, CG = collector-gatherer, CF = collector-filterer, HB = herbivore, SH = shredder; Voltinism: multi = multivoltine, uni = univoltine, semi = semivoltine; Habit: SW = swimmer, SP = sprawler, CB = climber, CN = clinger, BU = burrower, SK = skater; Swim refers to swimming capability: yes or no. Taxa are listed alphabetically.

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	FFG	Voltinism	Habit	Swim
Acariformes	Arthropoda	Arachnida	Acariformes					PR		SW	Yes
Aeshna	Arthropoda	Insecta	Odonata	Aeshnidae		Aeshna		PR	semi	CB	Yes
Aeshnidae	Arthropoda	Insecta	Odonata	Aeshnidae				PR	semi		
Agraylea	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Agraylea		HB	uni	CB	No
Amnicola	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae		Amnicola		HB	uni	CB	No
Amphipoda	Crustacea	Malacostraca	Amphipoda					CG		SP	Yes
Ancylidae	Mollusca	Gastropoda	Basommatophora	Ancylidae				HB	multi	CN	No
Baetidae	Arthropoda	Insecta	Ephemeroptera	Baetidae				CG	multi	SW	Yes
Baetis	Arthropoda	Insecta	Ephemeroptera	Baetidae		Baetis		CG	multi	SW	Yes
BezziaPalpomyia	Arthropoda	Insecta	Diptera	Ceratopogonidae		BezziaPalpomyia		PR	uni	SP	No
Bithyia tentaculata	Mollusca	Gastropoda	Littorinimorpha	Bithyniidae		Bithyia	tentaculata	HB	multi	CB	No
Caecidotea	Crustacea	Malacostraca	Isopoda	Asellidae		Caecidotea		CG	uni	CN	
Caenidae	Arthropoda	Insecta	Ephemeroptera	Caenidae				CG	multi	SP	Yes
Caenis	Arthropoda	Insecta	Ephemeroptera	Caenidae		Caenis		CG	multi	SP	Yes
Calanoida	Crustacea	Copepoda	Calanoida					CF	multi	SW	Yes
Cambaridae	Crustacea	Malacostraca	Decapoda	Cambaridae				CG			Yes
Campeloma decisum	Mollusca	Gastropoda	Architaenioglossa	Viviparidae		Campeloma	decisum	HB	semi	CB	No

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	FFG	Voltinism	Habit	Swim
Carabidae	Arthropoda	Insecta	Coleoptera	Carabidae				PR		CN	Yes
Ceraclea	Arthropoda	Insecta	Trichoptera	Leptoceridae		Ceraclea		CG	uni	SP	Yes
Ceratopogonidae	Arthropoda	Insecta	Diptera	Ceratopogonidae				PR	uni	SP	No
Choroterpes	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae		Choroterpes		CG	uni	CN	Yes
Chrysomelidae	Arthropoda	Insecta	Coleoptera	Chrysomelidae				SH		CN	
Chrysops	Arthropoda	Insecta	Diptera	Tabanidae		Chrysops		PR	uni	SP	
Cladocera	Crustacea	Branchiopoda	Cladocera					CF	multi	SW	Yes
Climacia	Arthropoda	Insecta	Neuroptera	Sisyridae		Climacia		PR	uni	CB	No
Coenagrionidae	Arthropoda	Insecta	Odonata	Coenagrionidae				PR	uni	CB	Yes
Coleoptera	Arthropoda	Insecta	Coleoptera								
Collembola	Arthropoda	Entognatha	Collembola					CG			
Copepoda	Crustacea	Copepoda						CF	multi	SW	Yes
Corbicula fluminea	Mollusca	Bivalvia	Veneroida	Cyrenidae		Corbicula	fluminea	CF	multi	BU	No
Corduliidae	Arthropoda	Insecta	Odonata	Corduliidae				PR	semi	SP	Yes
Corixidae	Arthropoda	Insecta	Hemiptera	Corixidae				HB	multi	SW	Yes
Crambidae	Arthropoda	Insecta	Lepidoptera	Crambidae				HB	uni		No
Crangonyx	Crustacea	Malacostraca	Amphipoda	Crangonyctidae		Crangonyx		CG	uni	SP	Yes
Cyclopoida	Crustacea	Copepoda	Cyclopoida					CF	multi	SW	Yes
Cyrnellus	Arthropoda	Insecta	Trichoptera	Polycentropodidae		Cyrnellus		CF	uni	CN	No
Diploperla	Arthropoda	Insecta	Plecoptera	Perlodidae		Diploperla		PR	uni	CN	Yes
Ectopria	Arthropoda	Insecta	Coleoptera	Psephenidae		Ectopria		HB	semi	CN	No
Elliptio complanata	Mollusca	Bivalvia	Unionida	Unionidae		Elliptio	complanata	CF	semi	BU	No
Elmidae	Arthropoda	Insecta	Coleoptera	Elmidae				CG	semi	CN	No
Entomobbyidae	Arthropoda	Entognatha	Collembola	Entomobbyidae				CG			
Ephemera	Arthropoda	Insecta	Ephemeroptera	Ephemeridae		Ephemera		CG	semi	BU	Yes

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	FFG	Voltinism	Habit	Swim
Ephemerellidae	Arthropoda	Insecta	Ephemeroptera	Ephemerellidae				CG	uni	CN	Yes
Eurylophella	Arthropoda	Insecta	Ephemeroptera	Ephemerellidae		Eurylophella		CG	uni	CN	Yes
Faxonius	Crustacea	Malacostraca	Decapoda	Cambaridae		Faxonius		CG			Yes
Ferrisia californica	Mollusca	Gastropoda	Basommatophora	Ancylidae		Ferrisia	californica	HB	multi	CB	No
Gammarus	Crustacea	Malacostraca	Amphipoda	Gammaridae		Gammarus		CG	uni	SP	Yes
Gastropoda	Mollusca	Gastropoda									
Gerridae	Arthropoda	Insecta	Hemiptera	Gerridae				PR		SW	Yes
Gomphus	Arthropoda	Insecta	Odonata	Gomphidae		Gomphus		PR	semi	BU	Yes
Gyraulus circumstriatus	Mollusca	Gastropoda	Basommatophora	Planorbidae		Gyraulus	circumstriatus	HB	multi	CB	No
Gyraulus parvus	Mollusca	Gastropoda	Basommatophora	Planorbidae		Gyraulus	parvus	HB	multi	CB	No
Gyrinus	Arthropoda	Insecta	Coleoptera	Gyrinidae		Gyrinus		PR		SW	Yes
Haliplus	Arthropoda	Insecta	Coleoptera	Haliplidae		Haliplus		HB	multi	SW	Yes
Hebridae	Arthropoda	Insecta	Hemiptera	Hebridae				PR	multi	SK	Yes
Helisoma	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma		HB		CB	No
Helisoma anceps	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma	anceps	HB	uni	CB	No
Helisoma campanulatum	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma	campanulatum	HB	uni	CB	No
Helisoma trivolvis	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma	trivolvis	CG	uni	CB	No
Hemerodromia	Arthropoda	Insecta	Diptera	Empididae		Hemerodromia		PR	uni	SP	No
Hemiptera	Arthropoda	Insecta	Hemiptera					PR			
Heptageniidae	Arthropoda	Insecta	Ephemeroptera	Heptageniidae				HB	uni	CN	Yes
Hirudinea	Annelida	Hirudinea									
Hyalella	Crustacea	Malacostraca	Amphipoda	Hyalellidae		Hyalella		CG	multi	SP	Yes
Hydrobiidae	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae				HB		CB	No
Hydrometridae	Arthropoda	Insecta	Hemiptera	Hydrometridae				PR	multi	SK	Yes
Hydroptila	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Hydroptila		HB	uni	CN	No

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	FFG	Voltinism	Habit	Swim
Hydroptilidae	Arthropoda	Insecta	Trichoptera	Hydroptilidae					uni		No
Ishnura	Arthropoda	Insecta	Odonata	Coenagrionidae		Ischnura		PR	uni	CB	Yes
Isotomidae	Arthropoda	Entognatha	Collembola	Isotomidae				CG			
Laevapex fuscus	Mollusca	Gastropoda	Basommatophora	Ancylidae		Laevapex	fuscus	HB	uni	CB	No
Lampsilis radiata	Mollusca	Bivalvia	Unionida	Unionidae		Lampsilis	radiata	CF	semi	BU	No
Lepidoptera	Arthropoda	Insecta	Lepidoptera								
Leptoceridae	Arthropoda	Insecta	Trichoptera	Leptoceridae				CG			
Leptocerus	Arthropoda	Insecta	Trichoptera	Leptoceridae		Leptocerus		SH	multi	SW	Yes
Leptophlebiidae	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae				CG	uni	CN	Yes
Lestes	Arthropoda	Insecta	Odonata	Lestidae		Lestes		PR	uni	CB	Yes
Libellulidae	Arthropoda	Insecta	Odonata	Libellulidae				PR		SP	Yes
Limonia	Arthropoda	Insecta	Diptera	Tipulidae		Limonia		SH	uni	BU	No
Lymnaeidae	Mollusca	Gastropoda	Basommatophora	Lymnaeidae				HB	multi	CB	No
Mesoveliidae	Arthropoda	Insecta	Hemiptera	Mesoveliidae				PR	multi	SK	Yes
Mystacides	Arthropoda	Insecta	Trichoptera	Leptoceridae		Mystacides		CG	uni	SP	Yes
Nectopsyche	Arthropoda	Insecta	Trichoptera	Leptoceridae		Nectopsyche		HB	uni	CB	Yes
Nehalennia	Arthropoda	Insecta	Odonata	Coenagrionidae		Nehalennia		PR		CB	
Nematoda	Nematoda										
Noctuidae	Arthropoda	Insecta	Lepidoptera	Noctuidae				HB		BU	
NonTanypodinae	Arthropoda	Insecta	Diptera	Chironomidae	NonTanypodinae						
Notonectidae	Arthropoda	Insecta	Hemiptera	Notonectidae				PR		SW	Yes
Nyctiophylax	Arthropoda	Insecta	Trichoptera	Polycentropodidae		Nyctiophylax		PR	uni	CN	No
Odonata	Arthropoda	Insecta	Odonata					PR			
Oecetis	Arthropoda	Insecta	Trichoptera	Leptoceridae		Oecetis		PR	uni	CN	Yes
Oligochaeta	Annelida	Oligochaeta						CG			

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	FFG	Voltinism	Habit	Swim
Optioservus	Arthropoda	Insecta	Coleoptera	Elmidae		Optioservus		HB	semi	CN	No
Orthotricia	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Orthotricia		CG	uni	CN	No
Ostracoda	Crustacea	Ostracoda						CG			Yes
Oulimnus	Arthropoda	Insecta	Coleoptera	Elmidae		Oulimnus		HB	semi	CN	No
Oxyethira	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Oxyethira		HB	uni	CB	No
Paracloeodes	Arthropoda	Insecta	Ephemeroptera	Baetidae		Paracloeodes		HB	multi	SW	Yes
Peltodytes	Arthropoda	Insecta	Coleoptera	Haliplidae		Peltodytes		HB		CB	
Peltoperlidae	Arthropoda	Insecta	Plecoptera	Peltoperlidae				SH	semi	CN	
Perithemis	Arthropoda	Insecta	Odonata	Libellulidae		Perithemis		PR		SP	Yes
Phoridae	Arthropoda	Insecta	Diptera	Phoridae				CG		BU	
Phylocentropus	Arthropoda	Insecta	Trichoptera	Dipseudopsidae		Phylocentropus		CF	uni	BU	
Physidae	Mollusca	Gastropoda	Basommatophora	Physidae				HB	multi	CB	No
Planorbidae	Mollusca	Gastropoda	Basommatophora	Planorbidae				HB	multi	CB	No
Pleidae	Arthropoda	Insecta	Hemiptera	Pleidae				PR	multi	CB	Yes
Poduridae	Arthropoda	Entognatha	Collembola	Poduridae				CG			
Polycentropus	Arthropoda	Insecta	Trichoptera	Polycentropodidae		Polycentropus		PR	uni	CN	No
Procloeon	Arthropoda	Insecta	Ephemeroptera	Baetidae		Procloeon		CG	multi	SW	Yes
Promenetus exacuous	Mollusca	Gastropoda	Basommatophora	Planorbidae		Promenetus	exacuous	HB	multi	CB	No
Pyganodon cataracta	Mollusca	Bivalvia	Unionida	Unionidae		Pyganodon	cataracta	CF	semi	BU	No
Scirtidae	Arthropoda	Insecta	Coleoptera	Scirtidae				HB		CB	
Sialis	Arthropoda	Insecta	Megaloptera	Sialidae		Sialis		PR	uni	BU	No
Sminthuridae	Arthropoda	Entognatha	Collembola	Sminthuridae				CG			
Somatochlora	Arthropoda	Insecta	Odonata	Corduliidae		Somatochlora		PR	semi	SP	Yes
Sphaeriidae	Mollusca	Bivalvia	Veneroida	Sphaeriidae				CF	multi	BU	No
Stenacron	Arthropoda	Insecta	Ephemeroptera	Heptageniidae		Stenacron		CG	uni	CN	Yes

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	FFG	Voltinism	Habit	Swim
Stenelmis	Arthropoda	Insecta	Coleoptera	Elmidae		Stenelmis		HB	uni	CN	No
Stenonema	Arthropoda	Insecta	Ephemeroptera	Heptageniidae		Stenonema		HB	uni	CN	Yes
Sympetrum	Arthropoda	Insecta	Odonata	Libellulidae		Sympetrum		PR	uni	SP	Yes
Tanypodinae	Arthropoda	Insecta	Diptera	Chironomidae	Tanypodinae			PR	uni	SP	No
Tipulidae	Arthropoda	Insecta		Tipulidae				SH	uni	BU	No
Triaenodes	Arthropoda	Insecta	Trichoptera	Leptoceridae		Triaenodes		SH		SW	Yes
Trichoptera	Arthropoda	Insecta	Trichoptera								
Tropisternus	Arthropoda	Insecta	Coleoptera	Hydrophilidae		Tropisternus		PR	multi	CB	
Turbellaria	Platyhelminthes	Turbellaria									
Valvata tricarinata	Mollusca	Gastropoda	Heterostropha	Valvatidae		Valvata	tricarinata	HB	uni	CB	No
Veliidae	Arthropoda	Insecta	Hemiptera	Veliidae				PR	multi	SK	Yes
Veneroida	Mollusca	Bivalvia	Veneroida					CF	multi	BU	No
Viviparus georgianus	Mollusca	Gastropoda	Architaenioglossa	Viviparidae		Viviparus	georgianus	HB	semi	CB	No

APPENDIX Q

TOTAL ABUNDANCES OF COLLECTED MACROINVERTEBRATE TAXA BY HABITAT

Total abundance of macroinvertebrate taxa in cobble (n = 66) and macrophyte (n = 70) littoral mesohabitat across all sites (in gray). Empty abundance cells indicate zero individuals. Macroinvertebrates are divided into taxonomic levels and were identified to the lowest feasible level (Taxa ID). Taxa are listed alphabetically.

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	Cobble	Macrophyte
Acariformes	Arthropoda	Arachnida	Acariformes					1866	1576
Aeshna	Arthropoda	Insecta	Odonata	Aeshnidae		Aeshna			2
Aeshnidae	Arthropoda	Insecta	Odonata	Aeshnidae					2
Agraylea	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Agraylea		13	151
Amnicola	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae		Amnicola		3156	8408
Amphipoda	Crustacea	Malacostraca	Amphipoda					1	
Ancylidae	Mollusca	Gastropoda	Basommatophora	Ancylidae				43	81
Baetidae	Arthropoda	Insecta	Ephemeroptera	Baetidae				36	50
Baetis	Arthropoda	Insecta	Ephemeroptera	Baetidae		Baetis		1	
BezziaPalpomyia	Arthropoda	Insecta	Diptera	Ceratopogonidae		BezziaPalpomyia		24	256
Bithyia tentaculata	Mollusca	Gastropoda	Littorinimorpha	Bithyniidae		Bithyia	tentaculata		6
Caecidotea	Crustacea	Malacostraca	Isopoda	Asellidae		Caecidotea		529	2350
Caenidae	Arthropoda	Insecta	Ephemeroptera	Caenidae				1	
Caenis	Arthropoda	Insecta	Ephemeroptera	Caenidae		Caenis		133	7169
Calanoida	Crustacea	Copepoda	Calanoida					74	780
Cambaridae	Crustacea	Malacostraca	Decapoda	Cambaridae				1	
Campeloma decisum	Mollusca	Gastropoda	Architaenioglossa	Viviparidae		Campeloma	decisum		2
Carabidae	Arthropoda	Insecta	Coleoptera	Carabidae					1

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	Cobble	Macrophyte
Ceraclea	Arthropoda	Insecta	Trichoptera	Leptoceridae		Ceraclea		14	195
Ceratopogonidae	Arthropoda	Insecta	Diptera	Ceratopogonidae				2	7
Choroterpes	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae		Choroterpes		1105	16
Chrysomelidae	Arthropoda	Insecta	Coleoptera	Chrysomelidae					5
Chrysops	Arthropoda	Insecta	Diptera	Tabanidae		Chrysops			6
Cladocera	Crustacea	Branchiopoda	Cladocera					522	9107
Climacia	Arthropoda	Insecta	Neuroptera	Sisyridae		Climacia			1
Coenagrionidae	Arthropoda	Insecta	Odonata	Coenagrionidae				2	29
Coleoptera	Arthropoda	Insecta	Coleoptera					1	3
Collembola	Arthropoda	Entognatha	Collembola					3	
Copepoda	Crustacea	Copepoda						1	
Corbicula fluminea	Mollusca	Bivalvia	Veneroida	Cyrenidae		Corbicula	fluminea	8	
Corduliidae	Arthropoda	Insecta	Odonata	Corduliidae				1	10
Corixidae	Arthropoda	Insecta	Hemiptera	Corixidae					6
Crambidae	Arthropoda	Insecta	Lepidoptera	Crambidae				2	80
Crangonyx	Crustacea	Malacostraca	Amphipoda	Crangonyctidae		Crangonyx		1373	4647
Cyclopoida	Crustacea	Copepoda	Cyclopoida					48	1203
Cyrnellus	Arthropoda	Insecta	Trichoptera	Polycentropodidae		Cyrnellus			1
Diploperla	Arthropoda	Insecta	Plecoptera	Perlodidae		Diploperla		18	
Ectopria	Arthropoda	Insecta	Coleoptera	Psephenidae		Ectopria		202	2
Elliptio complanata	Mollusca	Bivalvia	Unionida	Unionidae		Elliptio	complanata	40	9
Elmidae	Arthropoda	Insecta	Coleoptera	Elmidae					5
Entomobbyidae	Arthropoda	Entognatha	Collembola	Entomobbyidae				1	2
Ephemera	Arthropoda	Insecta	Ephemeroptera	Ephemeridae		Ephemera		8	
Ephemerellidae	Arthropoda	Insecta	Ephemeroptera	Ephemerellidae				4	6

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	Cobble	Macrophyte
Eurylophella	Arthropoda	Insecta	Ephemeroptera	Ephemerellidae		Eurylophella			88
Faxonius	Crustacea	Malacostraca	Decapoda	Cambaridae		Faxonius		1	
Ferrisia californica	Mollusca	Gastropoda	Basommatophora	Ancylidae		Ferrisia	californica	4	
Gammarus	Crustacea	Malacostraca	Amphipoda	Gammaridae		Gammarus		37	12
Gastropoda	Mollusca	Gastropoda						265	162
Gerridae	Arthropoda	Insecta	Hemiptera	Gerridae					1
Gomphus	Arthropoda	Insecta	Odonata	Gomphidae		Gomphus		2	9
Gyraulus circumstriatus	Mollusca	Gastropoda	Basommatophora	Planorbidae		Gyraulus	circumstriatus	1	
Gyraulus parvus	Mollusca	Gastropoda	Basommatophora	Planorbidae		Gyraulus	parvus	386	1889
Gyrinus	Arthropoda	Insecta	Coleoptera	Gyrinidae		Gyrinus			11
Haliplus	Arthropoda	Insecta	Coleoptera	Haliplidae		Haliplus			118
Hebridae	Arthropoda	Insecta	Hemiptera	Hebridae					11
Helisoma	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma		1	3
Helisoma anceps	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma	anceps		6
Helisoma campanulatum	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma	campanulatum	1	1
Helisoma trivolvis	Mollusca	Gastropoda	Basommatophora	Planorbidae		Helisoma	trivolvis	6	6
Hemerodromia	Arthropoda	Insecta	Diptera	Empididae		Hemerodromia		16	36
Hemiptera	Arthropoda	Insecta	Hemiptera					11	16
Heptageniidae	Arthropoda	Insecta	Ephemeroptera	Heptageniidae				375	
Hirudinea	Annelida	Hirudinea						380	860
Hyalella	Crustacea	Malacostraca	Amphipoda	Hyalellidae		Hyalella		582	3324
Hydrobiidae	Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae				4	1
Hydrometridae	Arthropoda	Insecta	Hemiptera	Hydrometridae					1
Hydroptila	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Hydroptila		38	388

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	Cobble	Macrophyte
Hydroptilidae	Arthropoda	Insecta	Trichoptera	Hydroptilidae				90	868
Ishnura	Arthropoda	Insecta	Odonata	Coenagrionidae		Ischnura		15	643
Isotomidae	Arthropoda	Entognatha	Collembola	Isotomidae				24	31
Laevapex fuscus	Mollusca	Gastropoda	Basommatophora	Ancylidae		Laevapex	fuscus		11
Lampsilis radiata	Mollusca	Bivalvia	Unionida	Unionidae		Lampsilis	radiata		1
Lepidoptera	Arthropoda	Insecta	Lepidoptera					3	16
Leptoceridae	Arthropoda	Insecta	Trichoptera	Leptoceridae				22	115
Leptocerus	Arthropoda	Insecta	Trichoptera	Leptoceridae		Leptocerus			7
Leptophlebiidae	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae				140	14
Lestes	Arthropoda	Insecta	Odonata	Lestidae		Lestes			4
Libellulidae	Arthropoda	Insecta	Odonata	Libellulidae				3	10
Limonia	Arthropoda	Insecta	Diptera	Tipulidae		Limonia			4
Lymnaeidae	Mollusca	Gastropoda	Basommatophora	Lymnaeidae				1	
Mesoveliidae	Arthropoda	Insecta	Hemiptera	Mesoveliidae				10	56
Mystacides	Arthropoda	Insecta	Trichoptera	Leptoceridae		Mystacides		17	5
Nectopsyche	Arthropoda	Insecta	Trichoptera	Leptoceridae		Nectopsyche		23	1548
Nehalennia	Arthropoda	Insecta	Odonata	Coenagrionidae		Nehalennia			17
Nematoda	Nematoda							27	334
Noctuidae	Arthropoda	Insecta	Lepidoptera	Noctuidae					34
NonTanypodinae	Arthropoda	Insecta	Diptera	Chironomidae	NonTanypodinae			7329	10206
Notonectidae	Arthropoda	Insecta	Hemiptera	Notonectidae					1
Nyctiophylax	Arthropoda	Insecta	Trichoptera	Polycentropodidae		Nyctiophylax		3	
Odonata	Arthropoda	Insecta	Odonata						2
Oecetis	Arthropoda	Insecta	Trichoptera	Leptoceridae		Oecetis		12	477
Oligochaeta	Annelida	Oligochaeta						839	7570

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	Cobble	Macrophyte
Optioservus	Arthropoda	Insecta	Coleoptera	Elmidae		Optioservus		30	64
Orthotricia	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Orthotricia		112	496
Ostracoda	Crustacea	Ostracoda						10	211
Oulimnus	Arthropoda	Insecta	Coleoptera	Elmidae		Oulimnus		137	1
Oxyethira	Arthropoda	Insecta	Trichoptera	Hydroptilidae		Oxyethira		10	709
Paracloeodes	Arthropoda	Insecta	Ephemeroptera	Baetidae		Paracloeodes			1
Peltodytes	Arthropoda	Insecta	Coleoptera	Haliplidae		Peltodytes		2	18
Peltoperlidae	Arthropoda	Insecta	Plecoptera	Peltoperlidae				12	
Perithemis	Arthropoda	Insecta	Odonata	Libellulidae		Perithemis		1	
Phoridae	Arthropoda	Insecta	Diptera	Phoridae					1
Phylocentropus	Arthropoda	Insecta	Trichoptera	Dipseudopsidae		Phylocentropus		7	2
Physidae	Mollusca	Gastropoda	Basommatophora	Physidae				12	778
Planorbidae	Mollusca	Gastropoda	Basommatophora	Planorbidae					679
Pleidae	Arthropoda	Insecta	Hemiptera	Pleidae					12
Poduridae	Arthropoda	Entognatha	Collembola	Poduridae				1	
Polycentropus	Arthropoda	Insecta	Trichoptera	Polycentropodidae		Polycentropus		1091	346
Procloeon	Arthropoda	Insecta	Ephemeroptera	Baetidae		Procloeon		185	301
Promenetus exacuous	Mollusca	Gastropoda	Basommatophora	Planorbidae		Promenetus	exacuous	48	87
Pyganodon cataracta	Mollusca	Bivalvia	Unionida	Unionidae		Pyganodon	cataracta	2	
Scirtidae	Arthropoda	Insecta	Coleoptera	Scirtidae					2
Sialis	Arthropoda	Insecta	Megaloptera	Sialidae		Sialis		23	15
Sminthuridae	Arthropoda	Entognatha	Collembola	Sminthuridae				2	
Somatochlora	Arthropoda	Insecta	Odonata	Corduliidae		Somatochlora			10
Sphaeriidae	Mollusca	Bivalvia	Veneroida	Sphaeriidae				121	389

Taxa ID	Phylum	Class	Order	Family	Subfamily	Genus	Species	Cobble	Macrophyte
Stenacron	Arthropoda	Insecta	Ephemeroptera	Heptageniidae		Stenacron		687	15
Stenelmis	Arthropoda	Insecta	Coleoptera	Elmidae		Stenelmis		2	16
Stenonema	Arthropoda	Insecta	Ephemeroptera	Heptageniidae		Stenonema		3157	23
Sympetrum	Arthropoda	Insecta	Odonata	Libellulidae		Sympetrum		19	250
Tanypodinae	Arthropoda	Insecta	Diptera	Chironomidae	Tanypodinae			754	2158
Tipulidae	Arthropoda	Insecta		Tipulidae					4
Triaenodes	Arthropoda	Insecta	Trichoptera	Leptoceridae		Triaenodes		8	119
Trichoptera	Arthropoda	Insecta	Trichoptera					4	27
Tropisternus	Arthropoda	Insecta	Coleoptera	Hydrophilidae		Tropisternus			11
Turbellaria	Platyhelminthes	Turbellaria						232	430
Valvata tricarinata	Mollusca	Gastropoda	Heterostropha	Valvatidae		Valvata	tricarinata		175
Veliidae	Arthropoda	Insecta	Hemiptera	Veliidae				4	227
Veneroida	Mollusca	Bivalvia	Veneroida					58	211
Viviparus georgianus	Mollusca	Gastropoda	Architaenioglossa	Viviparidae		Viviparus	georgianus	24	39

APPENDIX R

ABUNDANCE OF DOMINANT COBBLE MACROINVERTEBRATE TAXA

Mean relative abundance and standard deviation for cobble associated macroinvertebrate taxa with >1% relative abundance averaged across all sites. Refer to Appendix B for higher taxonomic levels.

Order	Family	Genus/Species	Mean	SD
Diptera	Chironomidae	NonTanypodinae (informal subfamily)	23.37	16.78
Ephemertoptera	Heptageniidae	*Stenonema*	18.73	17.27
Ephemeroptera	Leptophlebiidae	*Choroterpes*	7.77	8.91
Littorinimorpha	Hydrobiidae	*Amnicola*	6.49	12.16
Trichoptera	Polycentropodidae	*Polycentropus*	5.08	5.75
Cladocera			4.49	8.70
Diptera	Chironomidae	Tanypodinae (subfamily)	4.17	3.34
Ephemertoptera	Heptageniidae	*Stenacron*	4.06	5.46
Oligochaeta (class)			3.03	3.46
Amphipoda	Crangonyctidae	*Crangonyx*	3.00	5.52
Acariformes			2.93	4.97
Amphipoda	Hyalellidae	*Hyalella*	2.21	4.72
Isopoda	Asellidae	*Caecidotea*	2.05	4.67
Basommatophora	Planorbidae	*Gyraulus parvus*	1.42	2.99
Ephemertoptera	Heptageniidae		1.16	6.69
Ephemertoptera	Baetidae	*Procloeon*	1.16	1.51

APPENDIX S

ABUNDANCE OF DOMINANT MACROPHYTE MACROINVERTEBRATE TAXA

Mean relative abundance and standard deviation for macrophyte associated macroinvertebrate taxa with >1% relative abundance averaged across all sites. Refer to Appendix B for higher taxonomic levels.

Order	Family	Genus/Species	Mean	SD
Diptera	Chironomidae	NonTanypodinae (informal subfamily)	16.86	12.96
Cladocera			13.22	18.03
Littorinimorpha	Hydrobiidae	*Amnicola*	11.42	16.06
Oligochaeta (class)			11.05	10.94
Ephemeroptera	Caenidae	*Caenis*	8.28	11.97
Amphipoda	Hyalellidae	*Hyalella*	3.69	4.63
Diptera	Chironomidae	Tanypodinae (subfamily)	3.38	2.44
Amphipoda	Crangonyctidae	*Crangonyx*	3.27	6.34
Acariformes			2.51	4.35
Isopoda	Asellidae	*Caecidotea*	2.42	6.00
Basommatophora	Planorbidae	*Gyraulus parvus*	2.26	5.99
Calanoida			2.03	9.30
Trichoptera	Leptoceridae	*Nectopsyche*	1.84	4.42
Cyclopoida			1.47	2.13
Basommatophora	Physidae		1.19	2.15
Trichoptera	Hydroptilidae	*Oxyethira*	1.16	2.03

APPENDIX T

SUMMARY OF ENVIRONMENTAL COVARIATE MEASURES

Mean ± standard deviation of shoreline site-level environmental covariates specific to mesohabitat types (cobble, macrophyte) or common across mesohabitats (canopy cover, slope, fetch).

Lake	Cobble			Macrophyte					
	Cholorphyll-*a* (mg L^{-1})	B-length (mm)	Embeddedness (%)	Cover (%)	Biomass (g)	Richness	Canopy Cover	Slope (%)	Fetch
Ashmere	16.3 ± 7.1	45.4 ± 7.2	0.26 ± 0.2	0.9 ± 0.1	110.8 ± 64.1	3.0 ± 1.6	11.2 ± 5.4	9.4 ± 2.7	139.1 ± 57.9
Buel	119.0 ± 38.5	48.8 ± 13.2	0.17 ± 0.1	1 ± 0	419.2 ± 304.8	2.6 ± 1.1	10.8 ± 5.8	14.2 ± 6.3	240.9 ± 39.9
Congamond	31.4 ± 19.9	36.0 ± 4.5	0.03 ± 0.1	0.9 ± 0.1	238. ± 131.4	3.0 ± 1.0	11.1 ± 5.5	9.3 ± 2.3	229.6 ± 63.4
Garfield	34.3 ± 24.5	43.7 ± 6.6	0.12 ± 0.2	0.9 ± 0.1	182.8 ± 86.0	3.6 ± 0.9	12.4 ± 6.2	10.6 ± 3.3	208.0 ± 85.2
Goose	18.9 ± 18.6	40.4 ± 3.8	0.08 ± 0.1	0.6 ± 0.4	91.0 ± 70.1	3.0 ± 1.6	10.2 ± 7.2	8.0 ± 5.2	144.9 ± 74.4
Greenwater	2.8 ± 1.1	56.0 ± 3.0	0.08 ± 0.1	0.8 ± 0.1	146.4 ± 171.8	2.2 ± 1.1	11.1 ± 6.1	15.0 ± 6.4	149.1 ± 57.2
Hamilton	5.7 ± 9.2	43.5 ± 3.2	0.13 ± 0.2	0.6 ± 0.2	95.3 ± 83.0	1.6 ± 0.9	11.5 ± 5.6	12.5 ± 6.3	147.9 ± 91.2
Onota	38.0 ± 30.1	49.4 ± 8.0	0.08 ± 0.1	0.6 ± 0.3	428.8 ± 380.9	1.2 ± 0.5	8.3 ± 7.4	12.0 ± 6.1	364.1 ± 183.8
Otis	18.3 ± 15.3	45.8 ± 4.4	0.12 ± 0.1	0.7 ± 0.2	92.0 ± 63.6	2.2 ± 0.8	11. ± 6.3	10.6 ± 5.2	231.9 ± 147.3
Quacumquasit	69.9 ± 20.1	40.6 ± 7.3	0.36 ± 0.2	0.9 ± 0.1	204.0 ± 126.1	4.8 ± 1.9	12.1 ± 4.3	7.4 ± 2.2	278.5 ± 81.8
Richmond	42.0 ± 35.6	46.9 ± 11.9	0.25 ± 0.2	0.9 ± 0.1	161.8 ± 98.1	2.8 ± 1.5	13.9 ± 4.5	7.7 ± 5.0	301.2 ± 83.2
Stockbridge	66.0 ± 33.0	46.7 ± 6.0	0.16 ± 0.2	0.7 ± 0.4	135.4 ± 125.9	3.0 ± 0	8.7 ± 5.3	10.8 ± 4.8	308.6 ± 154.3
Wickaboag	4.7 ± 4.4	37.6 ± 3.0	0.04 ± 0.1	0.4 ± 0.3	175.8 ± 223.0	1.6 ± 0.9	11.5 ± 5.6	12.8 ± 7.1	309.6 ± 72.1
Wyola	7.6	31.9	0.10	0.7 ± 0.3	56.7 ± 30.4	2.6 ± 0.9	9.8 ± 6.2	11.7 ± 4.6	169.3 ± 106.3

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