



The Identification, Mapping, and Management of Seasonal Ponds in Forests of the Great Lakes Region

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Abstract

Seasonal ponds are small, isolated wetlands with variable hydrology, often occurring embedded in upland forests, which provide habitat for amphibians and invertebrates uniquely adapted to fishless waters. Seasonal ponds are challenging to identify due to their small size, ephemeral hydrology, diverse vegetation, and occurrence across a range of settings, yet in order to inform their conservation and management, it is essential to understand their distribution and how management impacts them. We conducted a systematic review to define and quantify attributes of seasonal ponds, summarize mapping and inventory methods, and synthesize forest harvesting impacts on ponds in the western Great Lakes and northeastern United States. Definitions of seasonal ponds differ regionally and for scientific vs. regulatory purposes; the necessity of documenting pond-dependent indicator species (*e.g.*, fairy shrimp) is one of the most vexing inconsistencies. Seasonal ponds are most effectively mapped in the spring, using a combination of aerial photographs or radar imagery and topographic information, especially in settings with small ponds or heavy canopies. Combining these mapping efforts with carefully stratified field validation is essential for developing a regional inventory of seasonal ponds. Most guidelines intended to reduce impacts of forest harvesting on pond ecosystems rely on buffers, which most effectively minimize physical or biological impacts when most lightly treated, although some impacts (particularly water levels) appear unavoidable when any harvesting occurs adjacent to seasonal ponds. Overall, distinct physical and biological impacts of harvesting differ in magnitude and direction, though most appear to subside over multi-decadal timescales.

Key Words Seasonal pond · Vernal pool · Ephemeral wetland · Remote sensing · Forest harvest · Indicator species

Introduction

Seasonal ponds are unique and important wetlands in many forested regions. They are also known as vernal or autumnal ponds or pools, ephemeral, temporary, intermittent, or

semi-permanent ponds. Seasonal ponds are characterized by the fundamental elements that define wetlands in general, including water at or near the surface for some portion of the year, hydric soils, and the presence of wetland vegetation (Cowardin et al. 1979), but are differentiated by: 1) having seasonally wet and dry periods; 2) being small, shallow, and hydrologically isolated with no continuous surface inflow or outflow; 3) providing habitat for organisms that require fishless conditions for successful reproduction (Colburn 2004; Calhoun and deMaynadier 2008). This dynamic hydrology is a foundational feature of these wetlands, allowing them to sustain organisms that require both wetland and terrestrial habitat or are adapted to periodic drought (Colburn et al. 2008; Semlitsch and Skelly 2008). Across the glaciated northeastern and north-central United States seasonal ponds occur in diverse settings, including embedded in upland forests, as part of large wetland complexes, or within forested swamps, marshes, or floodplains (Rheinhardt and Hollands

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2008; Cohen et al. 2016). The seasonal ponds embedded in forests are the focus of this review, as they are unique ecological features providing critical wetland habitat and functions within a primarily upland landscape.

In the ecological literature, seasonal ponds are best known for their role in the life cycles of amphibians and invertebrates, providing critical habitat for a range of invertebrates and amphibians, especially taxa that primarily reproduce in them, such as wood frogs (*Lithobates sylvaticus*), ambystomatid salamanders (*Ambystoma* spp.), and fairy shrimp (*Eubranchipus* spp.) (Batzer et al. 2004; Colburn 2004; Egan and Paton 2004; Colburn et al. 2008; Donner et al. 2015). Invertebrate and amphibian community composition depends upon pond characteristics including canopy cover, vegetation composition, water chemistry, and hydroperiod and as a result of interactions between these factors often have higher invertebrate species richness than surrounding upland forests (Brooks and Colburn 2012; Batzer 2013; Jeffries et al. 2016). Invertebrates represent the bulk of the species present in seasonal ponds and their food webs, and thus play a critical role in the trophic dynamics of seasonal ponds (Colburn et al. 2008). Beyond invertebrates, seasonal ponds provide foraging habitat for other organisms, including birds (McKinney and Paton 2009; Eakin et al. 2018), mammals (e.g., bats, shrews, foxes, hare; Brooks and Doyle 2001; Brooks and Ford 2005; Francl 2008; Eakin et al. 2018), reptiles (Refsnider and Linck 2012) and amphibians (Palik et al. 2001; Gahl et al. 2009; Schrank et al. 2015).

The small size (typically 0.02–0.1 ha) and seasonally variable hydrology of seasonal ponds makes them unusually dynamic ecosystems, even compared to other wetlands (Batzer et al. 2004; Brooks et al. 1998; Calhoun et al. 2003; Schrank et al. 2015; Timm et al. 2007). The hydrology of seasonal ponds, in terms of size, depth, and flooding duration, is driven by several factors. These include direct precipitation inputs, especially as spring snowmelt or early summer rain, and evapotranspiration during the growing season (Brooks and Hayashi 2002; Brooks 2004; Koning 2005; Boone et al. 2006; Leibowitz and Brooks 2008). Overland flow from uplands into ponds only occurs briefly (if at all) during snowmelt or large rain events, although groundwater inputs may be an important water source for some ponds (Brooks 2004; Boone et al. 2006). Seasonal ponds reach their maximum size and depth in the spring, although both can vary widely from year to year due to antecedent seasonal precipitation or individual storm events (Brooks and Hayashi 2002; Boone et al. 2006). In addition to this interannual variability, seasonal pond hydrology may be changing over longer timescales due to climate change, as shifts in temperature, precipitation intensity and frequency alter hydroperiods, especially in smaller or shallower ponds (Brooks 2004). Changing hydroperiods are important because flooding duration not only defines seasonal ponds as

such, but controls biogeochemical processes such as decomposition, denitrification, methane production, and mercury methylation, which feedback to climate change and environmental pollution (Brooks and Hayashi, 2002; Palik et al. 2006; Capps et al. 2014; Holgerson, 2015). Pond hydroperiod also influences organismal diversity and fecundity, with deviations from typical hydrology having stronger impacts on amphibian than invertebrate communities (Batzer et al. 2004; Egan and Paton 2004).

The ecology, hydrology, and biogeochemistry of seasonal ponds are tightly linked and strongly influenced by surrounding uplands, making them sensitive to forest management, land use change, and inputs of nutrients or contaminants (e.g., mercury, road salt; Karraker et al. 2008; Kolka et al. 2011; Benoit et al. 2013; Capps et al. 2014; Holgerson 2015; Powell and Babbitt 2017; Boche et al. 2019). This sensitivity is likely magnified compared to other wetlands because seasonal ponds have high perimeter-to-area (Palik et al. 2001; Palik et al. 2006; Cohen et al. 2016). Surrounding vegetation mediates solar insolation to ponds and provides them with leaf litter inputs that are a major contributor to detrital food webs (Holgerson et al. 2016; Batzer and Palik 2007). Trophic complexity interacts, in turn, with the life histories of organisms that use ponds. Most pond-dependent amphibians spend their larval stage in seasonal ponds, leave for uplands in their juvenile and adult stages, and return to ponds to reproduce; conversely, upland invertebrates may use ponds when they are dry (Batzer 2004). As “islands” embedded in an upland matrix, seasonal ponds depend upon proximity to each other (and continuity of upland habitat) for sustaining organismal populations and gene flow, such as through insect flight, amphibian migration, and the transport of invertebrate eggs via waterfowl (Berven and Grudzien 1990; Regosin et al. 2005; Colburn et al. 2008; Brooks and Colburn 2012; Gabrielsen et al. 2013; Smith et al. 2019; Winiarski et al. 2020).

The foundational ecology and hydrology of seasonal ponds have been described in a number of thorough books (Batzer et al. 1999; Colburn 2004; Calhoun and deMaynardier 2008; Batzer and Boix 2016). The present review is intended to supplement these works, sharing their scientific definition of seasonal ponds (*i.e.*, small, isolated wetlands with seasonally varying hydrology, which can provide valuable fishless habitat for organismal reproduction and foraging) while addressing management considerations and contemporary nuance related to equally important, yet not entirely scientific definitions. This definition affords latitude for seasonal ponds to occur across a variety of landscape positions, span a range of sizes, and hold water during the spring, autumn, or for most of the year, all while providing essentially similar wetland ecosystem functions and wildlife habitat. Wetland definitions used for regulatory purposes often differ from definitions

used by scientists, and as a case in point, the criteria used to classify seasonal ponds as jurisdictional wetlands differ between Federal and State governments (Mitsch and Gosselink, 1993). At the federal level, protections for wetlands under Section 404 of the Clean Water Act have been subject to changes in the definition of “waters of the U.S.” and wetlands considered to be “isolated, intra-state, non-navigable waters,” including seasonal ponds, have been excluded from protections under recent definitions (Zedler 2003; U.S. EPA 2015; Sullivan et al. 2020; U.S. EPA 2020).

Given these shifting federal protections, state definitions of jurisdictional wetlands are increasingly relevant seasonal pond conservation and management (Calhoun et al. 2017). In some states seasonal ponds are classified as jurisdictional wetlands based on hydrology, soils, and vegetation [*i.e.*, Connecticut, Minnesota, Rhode Island, Wisconsin; MN BWSR 2019; CT DEEP 2021; RIDEM 2021; WDNR 2021a,b] or proximity from other surface water bodies (*i.e.*, Michigan; MI EGLE 2021). In other states (*i.e.*, Massachusetts, Maine, New Hampshire, Vermont) regulatory protections for seasonal ponds are based on the wildlife habitat they provide and in order to be classified as jurisdictional wetlands, they must be used by “indicator” or “obligate” seasonal pond organisms (wood frogs, ambystomatid salamanders, fairy shrimp) or state rare or threatened organisms (*e.g.*, Blanding’s turtle in Maine; MEDEP 2019; MassWildlife 2020; 2021; NHDES 2021; VTDEC 2021). There are also some states (*i.e.*, New York) without statewide protections for seasonal ponds and only ponds considered to be of “unusual local importance” receive protections (NYDEC 2021). Ultimately, while seasonal pond definitions used by regulators and resource managers can differ from those used by scientists, there are examples of successful case-by-case seasonal pond conservation efforts involving a variety of stakeholders and their collective recognition that seasonal ponds are important landscape features even if they are not included in Federal or State jurisdictional definitions (Cohen et al. 2016; Calhoun et al. 2017; Golden et al. 2017; Levesque et al. 2019).

To inform the management and conservation of seasonal ponds, it is essential to define them, identify where they occur, and assess their sensitivity to landscape and global changes. The present review is intended to meet these objectives by addressing questions developed by a team of scientists, forest managers, and resource professionals from Federal, State, and Tribal governments, and nonprofit and private sectors focused on practical forest management concerns in landscapes with seasonal ponds in the western Great Lakes states and Northeastern United States.

Methods

We conducted this systematic review in order to address four specific questions arising from our conversations about seasonal ponds, including: 1) what are the fundamental physical and biological characteristics commonly observed in seasonal pond ecosystems, 2) what methods are used to map and inventory seasonal ponds, 3) where are seasonal ponds distributed across the landscape, and 4) how does forest harvesting in adjacent forests potentially impact seasonal ponds? With this literature review we aim to present the current state of knowledge about seasonal pond ecosystems to inform and support more effective research, conservation, and management efforts of seasonal ponds and their adjacent landscapes by scientists and resource managers.

We searched Web of Science and TreeSearch databases using combinations of broad terms, including synonyms for seasonal ponds (vernal, ephemeral, depressional, or woodland ponds or pools, temporary, autumnal, seasonal) and wetland water regime modifiers (temporarily flooded, saturated, seasonally flooded; Cowardin et al., 1979) to collect papers related to seasonal ponds that might be using a range of terms to describe them. This phase of literature searching resulted in 1040 papers. We judged the relevance of each record using the scientific definition for seasonal pond, rather than regulatory criteria, which differ between states, and therefore did not require study sites to be jurisdictional wetlands. We classified each accepted paper according to geographic location, type of study (*e.g.*, experiment, observation, model), and primary ecosystem factors (*e.g.*, flora, biogeochemistry, disturbance). The primary geographic focus of this review is the western Great Lakes states (*i.e.*, Minnesota, Wisconsin, Michigan), but we included studies conducted in the northeastern U.S. when Midwest-specific evidence was lacking. We also included papers that were identified by subject matter experts or appeared during manual searching that were not returned in our initial searches. To avoid reporting primary evidence multiple times, we did not include books, book chapters, or other review papers in our synthesis. The final bibliographic database included 180 papers meeting these criteria.

In our geographic region, we identified twelve papers that assessed the impacts of forest harvesting on seasonal ponds through either experimental or chronosequence studies. We summarized the details of these harvesting studies in Supplementary Table 2. We report the summary and synthesis of their findings to address our fourth question (Section 3.4) and calculated effect sizes for each treatment to estimate the magnitude and direction of harvesting impacts on different aspects of seasonal pond ecosystems.

Effect sizes (natural log of the treatment divided by the control) were calculated for key seasonal pond ecosystem components, including vegetation (basal area, canopy openness, sedge and grass abundance), hydrology (water depth, hydroperiod), biogeochemistry (leaf litter inputs, water temperature), invertebrates (abundance), amphibians (species richness, eggmass abundance, length), and birds (species richness, habitat guild).

Results and Discussion

What Do Seasonal Ponds In The Western Great Lakes Region Look Like?

The defining physical features of seasonal ponds embedded in upland forests (small size, lack of inlets or outlets, dynamic hydrology) interact in many ways to confer dramatic changes in configuration and structure over time. Fig. 1 illustrates how widely the appearance of a seasonal pond can change throughout the year; functional changes in the physical, vegetative, and organismal attributes of ponds occur in proportion to gross changes in their appearance. Wetland classification systems used in the western Great Lakes states describe seasonal ponds as seasonally flooded basins (Type 1 wetlands; Shaw and Fredine 1956; Eggers and Reed 2011) or palustrine wetlands with semi-permanent or seasonally flooded water regimes (Cowardin et al. 1979)

and are always jurisdictional wetlands in Minnesota and Wisconsin based on these classifications. There are a few classification systems for seasonal ponds based on vegetation, depression characteristics, and soil, but the applicability of these systems is limited in geographic scope given the wide range of biotic and abiotic characteristics of seasonal ponds across the region (Ciccotelli et al. 2011; Bried et al., 2009; Schrank et al. 2015, Previant and Nagel 2016). Seasonal ponds can be dominated by forest, shrub-scrub, or herbaceous vegetation, and often have mucky mineral or mineral soil substrates, but can have organic soils (Kolka et al., 2011; Bischof et al. 2013; Schrank et al. 2015). When dry and thus difficult to discern, persistent evidence of prior flooding such as matted leaves, inundation marks on tree trunks, or patches of isolated wetland vegetation in upland forests can be useful as characteristics for identifying potential ponds. However, seasonal ponds are most easily identifiable in spring, when they are at their maximum extent, which is typically 1000–1500 m², but can range from 4 m² to 5000 m² (Table 1). At this time of year, depths of seasonal ponds in the western Great Lakes states, range from 10–380 cm depending on the pond and antecedent precipitation (Table 1). Water typically remains above the surface in ponds for 2–6 months, although there are years when known ponds are dry or full year-round (Table 1; Hanson et al. 2009).

A wide array of invertebrate and amphibian taxa have been observed breeding in western Great Lakes states

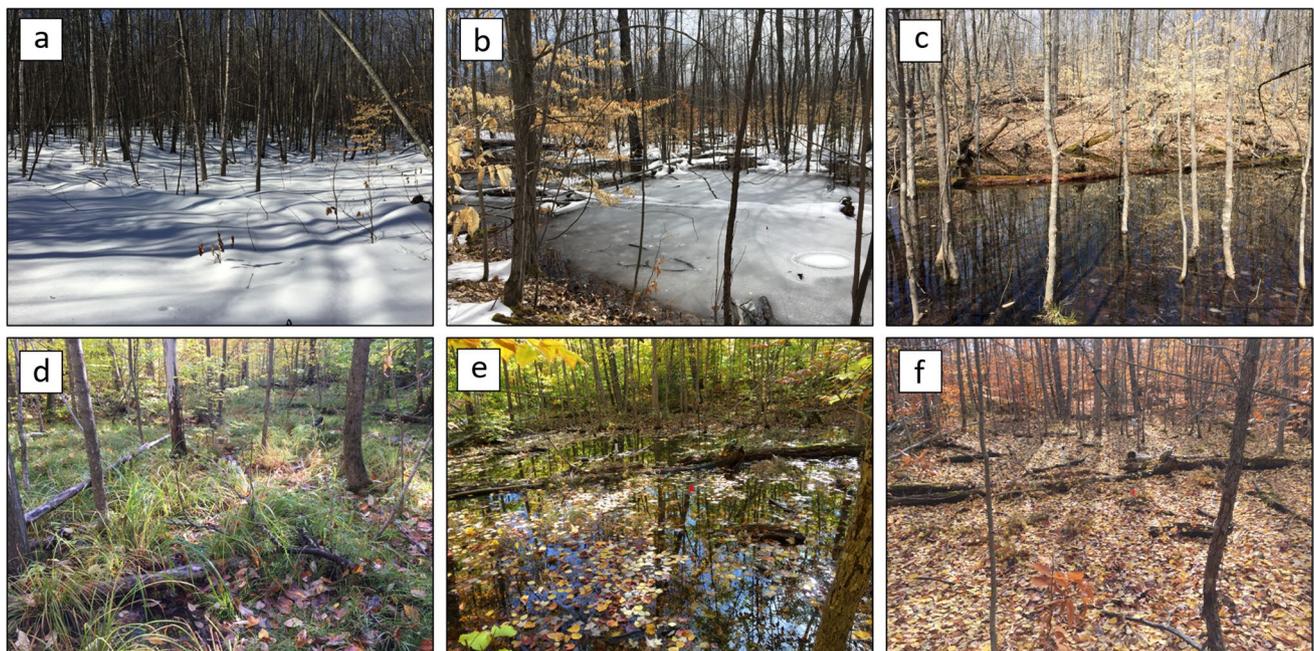


Fig. 1 A seasonal pond in northern Michigan under a range of hydrologic conditions throughout the year including winter (a), spring (b, c), summer (d), and autumn (e, f). This pond floods in spring, has a

dry period in summer, and can flood in autumn after large rain events, such as in panel e

Table 1 Seasonal pond physical characteristics for study sites in Minnesota, Wisconsin, and Michigan. Pond characteristics (area, volume, depth, hydroperiod, canopy cover) reported here as mean (range)

Study Region	Study	# ponds	Study Years	Max Pond Area (m ²)	Mean Pond Area (m ²)	Max Pond Volume (m ³)	Max Pond Depth (cm)	Mean Pond Depth (cm)	Hydroperiod	Canopy Cover (%)
Northern Minnesota Drift and Lake Plains Section, MN	Batzer et al. 2004	66**	1997–1999	200–2100					Ponds filled in late autumn or early spring, dry for variable periods in summer	79.5
	Bischof et al. 2013	16	2008	1250 (250, 3100)		59 (41, 93)		96 days (78, 125)	n/a (15, 92)	
			2009	1250 (250, 3100)		79 (47, 110)		100 days (70, 150)		
	Boche et al. 2019	10	2011	327 (24, 1200)						n/a (90, 97)
	Brooks et al. 2012	10	2010	1196 (277, 2851)		415 (63, 940)	55 (34, 79)		4 short, 4 intermediate, 2 long cycle	91 (87, 95)
	Kolka et al. 2011	4	2000–2005	n/a (200–1000)				n/a (7–24)		
	Palik and Kas-tendick 2010	4 (block 1)	2000	2000–5000		120 (90, 149)		70 (40, 120)	143 days (77, 205)	
		4 (block 2)				170 (140, 240)		100 (70, 140)	134 days (101, 189)	
		4 (block 3)				100 (80, 140)		50 (30, 110)	131 days (80, 204)	
		4 (block 4)				210 (130, 380)		80 (40, 110)	108 days (52, 189)	
Northern Superior Uplands, Western Superior Uplands, Northern Minnesota Drift and Lake Plains Sec-tions, MN	Palik et al. 2001	19*	1998–1999		200–2000		n/a (40, 179)		n/a (35–220 days)	
	Boone et al. 2006	4	2000–2002	243 (114, 324)		61 (27, 110)			75% of pools flooded until at least mid-July	
	Olker et al. 2013	38	2002		2077	51				66

Table 1 (continued)

Study Region	Study	# ponds	Study Years	Max Pond Area (m ²)	Mean Pond Area (m ²)	Max Pond Volume (m ³)	Max Pond Depth (cm)	Mean Pond Depth (cm)	Hydroperiod	Canopy Cover (%)
Kalamazoo County, MI	Caceres et al. 2008	3	2001			1050 (230, 2160)			ponds fill with snowmelt, rainwater in early spring (March-early April), typically dry in June	
Chequamegon-Nicolet National Forest, WI	Donner et al. 2015	1** (pond 18)	1992–1994, 2005–2007		402 (167, 827)			27 (10, 55)	ponds flooded 5–8 months beginning in spring (March/April)	
		1*** (pond 5)			678 (585, 746)			23 (21, 26)		
		1** (pond 23)			2681 (1347, 4153)			54 (27, 95)		
Ice Age National Scientific Reserve, WI	Little and Church 2018	33	2013–2014		796			49		86
Northern Highland Lake District, WI	Schneider and Frost 1996	5	1984–1990	163 (33, 302)		51 (4, 144)	60 (29, 107)		54 days (10, 101)	
University of Notre Dame Environmental Research Center, WI, MI	Francel 2008	17	2004–2006	0–2133					dry in July, August	89 (24–100)
Pictured Rocks National Lakeshore, MI	Previant and Nagel 2016	18	2009		1078					
	Schrank et al. 2015	21	2010	1240 (10, 5670)						

*Studies that only selected ponds with > 15 cm of water in spring

**Studies that only selected ponds with > 10 cm of water in spring

Table 2 Common amphibians, birds, mammals, and reptiles observed in Minnesota (MN), Wisconsin (WI), and Michigan (MI) seasonal ponds. State conservation status and seasonal pond breeding habitat preferences are noted

Organism	Common Name	Latin Name	Are seasonal ponds breeding habitat?	Conservation Status	Notes
Amphibians	Northern cricket frog	<i>Acris blanchardi</i>		Endangered (MN, WI)	
	Blue-spotted salamander	<i>Ambystoma laterale</i>	Yes, primary		
	Spotted salamander	<i>Ambystoma maculatum</i>	Yes, primary	Special concern (MN)	Only in Pine, Carlton counties (MN)
	Marbled salamander	<i>Ambystoma opacum</i>	Yes, primary	Endangered (MI)	
	Smallmouth salamander	<i>Ambystoma texanum</i>	Yes, primary	Endangered (MI)	
	Eastern tiger salamander	<i>Ambystoma tigrinum</i>			
	Fowler's toad	<i>Anaxyrus fowleri</i>			
	American toad	<i>Bufo americanus</i>			
	Four-toed salamander	<i>Hemidactylium scutatum</i>	Commonly used	Special concern (MN, WI)	High association with seasonal ponds (WI)
	Eastern gray treefrog	<i>Hyla versicolor</i>	Commonly used		
	Bullfrog	<i>Lithobates catesbeianus</i>			
	Green frog	<i>Lithobates clamitans</i>			
	Pickerel frog	<i>Lithobates palustris</i>		Special concern (WI, MI)	High association with seasonal ponds (WI)
	Northern leopard frog	<i>Lithobates pipiens</i>			
	Mink frog	<i>Lithobates septentrionalis</i>		Special concern (WI)	Moderate association with seasonal ponds (WI)
	Wood frog	<i>Lithobates sylvaticus</i>	Yes, primary		
	Eastern newt	<i>Notophthalmus viridescens</i>			
	Eastern red-backed salamander	<i>Plethodon cinereus</i>			
	Spring peeper	<i>Pseudacris crucifer</i>	Commonly used		
	Boreal chorus frog	<i>Pseudacris maculata</i>		Special concern (MI)	
Western chorus frog	<i>Pseudacris triseriata</i>				
Birds	Wood duck	<i>Aix sponsa</i>			
	Mallard	<i>Anas platyrhynchos</i>			
	Great blue heron	<i>Area herodias</i>			
	Red-shouldered hawk	<i>Buteo lineatus</i>		Special concern (MN), Threatened (WI, MI)	High association with seasonal ponds (WI)
	Least flycatcher	<i>Empidonax minimus</i>		Special concern (WI)	
	Rusty blackbird	<i>Euphagus carolinus</i>		Special concern (WI)	Moderate association with seasonal ponds (WI)
	Hooded merganser	<i>Lophodytes cucullatus</i>			
	Yellow-crowned night-heron	<i>Nyctanassa violacea</i>		Threatened (WI)	High association with seasonal ponds (WI)
	Black-crowned night-heron	<i>Nycticorax nycticorax</i>		Special concern (WI)	High association with seasonal ponds (WI)
	Prothonotary warbler	<i>Protonotaria citrea</i>		Special concern (WI, MI)	
	Ovenbird	<i>Seiurus aurocapillus</i>			
	Yellow-throated vireo	<i>Vireo flavifrons</i>			
Red-eyed vireo	<i>Vireo olivaceus</i>				

Table 2 (continued)

Organism	Common Name	Latin Name	Are seasonal ponds breeding habitat?	Conservation Status	Notes
Mammals	Big brown bat	<i>Eptesicus fuscus</i>		Special concern (MN), Threatened (WI)	Moderate association with seasonal ponds (WI)
	Silver-haired bat	<i>Lasionycteris noctivagans</i>		Special concern (WI)	High association with seasonal ponds (WI)
	Red bat	<i>Lasiurus borealis</i>			
	Hoary bat	<i>Lasiurus cinereus</i>			
	Little brown bat	<i>Myotis lucifugus</i>		Special concern (MI), Threatened (WI)	High association with seasonal ponds (WI)
	Northern long-eared bat	<i>Myotis septentrionalis</i>		Special concern (MI), Threatened (WI)	High association with seasonal ponds (WI)
	Indiana bat	<i>Myotis sodalis</i>		Endangered (MI, USA)	
	Woodland jumping mouse	<i>Napaeozapus insignis</i>		Special concern (WI)	Moderate association with seasonal ponds (WI)
	Tricolored bat	<i>Perimyotis subflavus</i>		Special concern (MN), Threatened (WI)	Moderate association with seasonal ponds (WI)
Reptiles	Spotted turtle	<i>Clemmys guttata</i>		Threatened (MI)	
	Blanding's turtle	<i>Emydoidea blandingii</i>		Special concern (WI, MI), Threatened (MN)	High association with seasonal ponds (WI)
	Wood turtle	<i>Glyptemys insculpta</i>		Special concern (MI), Threatened (MN, WI)	Moderate association with seasonal ponds (WI)
	Copperbelly water snake	<i>Nerodia erythrogaster neglecta</i>		Endangered (MI, federal)	
	Eastern massasauga	<i>Sistrurus catenatus catenatus</i>		Special concern (MI), Endangered (MN, WI, federal)	High association with seasonal ponds (WI)
	Eastern box turtle	<i>Terrapene carolina carolina</i>		Special concern (MI)	

Conservation status lists: MNDNR 2013; MNFI 2021; USFWS 2021; WDNR 2021

seasonal ponds, along with birds, bats, and other mammals that utilize ponds for foraging (Tables 2, 3). Invertebrates commonly identified in seasonal ponds include beetles, caddisflies, clams, crustaceans (fairy shrimp, clam shrimp, tadpole shrimp, seed shrimp, water fleas, copepods), damselflies, dragonflies, leeches, snails, true flies, true bugs, water mites, and worms (Supplementary Table 1; Kenk 1949; Hilsenhoff 1994; Schneider and Frost 1996; Palik et al. 2001; Batzer 2004; Batzer et al., 2004; Batzer et al. 2005; Caceres et al. 2008; Miller et al., 2008; Hanson et al. 2009; Hanson et al. 2010; Bischof et al. 2013; Resh et al. 2013). Crustaceans, especially fairy shrimp and clam shrimp are commonly associated with seasonal ponds and breeding in them for short periods of time during the spring. Fairy shrimp almost exclusively inhabit seasonal ponds and are often an indicator organism for regulatory purposes but may be absent in some years and easily missed due to their brief appearance (e.g., 2–4 weeks only; Dexter 1953; Egan and Paton 2004). Seasonal ponds also provide habitat for several beetle, dragonfly, and caddisfly species that are threatened,

endangered, or of special concern in the region (Table 3). Seasonal ponds are breeding habitat for many species of frogs and salamanders in the region, including wood frogs, spotted, blue-spotted, and marbled salamanders (Table 2). These taxa are commonly used as biological indicators of seasonal ponds, especially in New England state regulations (i.e., Maine, Massachusetts, Vermont) in addition to hydrologic, soil, and vegetative characteristics (MVPP 2018). In the context of this invertebrate and amphibian diversity, it is important to note that seasonal ponds can possess all requisite physical characteristics, particularly the hydrologic variability yet nonetheless lack indicator species due to prolonged drought followed by long dispersal distances or other barriers to recolonization (Hanson et al. 2009; Karraker and Gibbs 2009; Smith et al. 2019). This organismal requirement thus limits the number of seasonal ponds identified on the landscape if defining them according to some regulatory criteria.

The flora of seasonal ponds of the western Great Lakes region includes a diverse assemblage of woody plants

Table 3 Common invertebrates observed in Minnesota (MN), Wisconsin (WI), and Michigan (MI) seasonal pond ecosystems with state conservation status. Other common invertebrates observed in seasonal ponds are listed in Supplementary Table 1

Order	Family	Species	Common Name	Conservation Status
Coleoptera	Dytiscidae	<i>Agabetes acuductus</i>	Predaceous diving beetle	Special concern (WI)
		<i>Agabus aeruginosus</i>		
		<i>Agabus discolor</i>		
		<i>Agabus immaturus</i>		
		<i>Agabus leptapsis</i>		
		<i>Copelatus chevrolati</i>		
		<i>Dytiscus alaskanus</i>		
		<i>Hygrotus compar</i>		
		<i>Hygrotus farctus</i>		
		<i>Hygrotus marklini</i>		
		<i>Hygrotus sylvanus</i>		
		<i>Ilybius opacus</i>		
		<i>Laccornis deltoides</i>		
Odonata	Hydrophilidae	<i>Helophorus latipenis</i>		
	Aeshnidae	<i>Epiaeschna heros</i>	Swamp darner	Special concern (WI)
		<i>Aeschna subarctica</i>	Subarctic darner dragonfly	Special concern (MN)
		<i>Aeschna sitchensis</i>	Zigzag darner dragonfly	Special concern (MN)
	Corduliidae	<i>Somatochlora forcipata</i>	Forcinate emerald dragonfly	Special concern (MN)
		<i>Somatochlora hineana</i>	Hine's emerald dragonfly	Endangered (WI, MI, USA)
<i>Somatochlora incurvata</i>		Incurvate emerald dragonfly	Special concern (MI), Endangered (WI)	
Trichoptera	Leptoceridae	<i>Ylodes frontalis</i>	Long horned caddisflies	Threatened (MN)
		<i>Triaenodes flavescens</i>		Special concern (MN)
	Limnephilidae	<i>Limnephilus janus</i>	Northern caddisflies	Endangered (MN)
		<i>Limnephilus secludens</i>		Endangered (MN)
		<i>Limnephilus rossi</i>		Threatened (MN)
		<i>Anabolia ozburni</i>		Special concern (MN)
		<i>Limnephilus pallens</i>		Special concern (MI)
	Polycentropodidae	<i>Polycentropus milaca</i>	Tube casemaker caddisflies	Endangered (MN)
		<i>Polycentropus glacialis</i>		Threatened (MN)

Conservation status lists: MNDNR 2013; MNFI 2021; USFWS 2021; WDNR 2021

and herbaceous vegetation. Seasonal ponds support facultative to obligate wetland tree species [e.g., black and green ash (*Fraxinus nigra*, *F. pennsylvanica*), American elm (*Ulmus americana*)], and trees with wider wetland to upland ecological amplitudes, such as yellow birch (*Betula alleghaniensis*) and red maple (*Acer rubrum*)] (Previat and Nagel 2014; Palik et al. 2007; Diamond et al. 2019). No particular plant community can be consistently used to define and identify seasonal ponds across the region, although there are woody (red maple, black ash, American elm) and herbaceous taxa [duckweed (*Lemna* spp.), northern bugleweed (*Lycopus uniflorus*), dwarf raspberry (*Rubus pubescens*), blue skullcap (*Scutellaria lateriflora*), water parsnip (*Sium suave*), Tuckerman's sedge (*Carex tuckermanii*), fowl mannagrass (*Glyceria striata*)] that are found in seasonal ponds across all three states (Palik et al. 2007; Little and Church 2018, Schrank et al. 2015).

Seasonal pond plant communities often differ from nearby permanent wetlands in having more woody vegetation cover and higher proportions of woody species, annuals, and ferns (Little and Church 2018). Beyond these regional generalizations, individual pond characteristics such as hydroperiod or canopy cover influence plant community composition (Schrank et al. 2015; Palik et al. 2007). Ponds with longer hydroperiods possess more annual and perennial wetland forbs (facultative wetland, obligate wetland species), while those with shorter hydroperiods support a greater abundance of upland trees (obligate upland, facultative upland, facultative species; Palik et al. 2007). Ponds with more open canopies typically have higher abundances of obligate wetland grass, sedge, and shrub taxa while denser canopies are associated with greater abundances of upland forb, sedge, and shrub taxa and facultative wetland species (Palik et al. 2007; Schrank et al. 2015).

How Are Seasonal Ponds Mapped And Inventoried?

Mapping and inventorying seasonal ponds are critical for minimizing the impacts of management activities on these unique ecosystems. Seasonal ponds, and other wetlands, are mapped and inventoried several ways. Photointerpretation of aerial black and white or color infrared photographs taken during the leaf-off period is the most commonly used method. Aerial photos in scales ranging from 1:4000–1:40,000 have been used to map ponds across the Great Lakes and northeastern U.S. (Burne 2001; Palik et al. 2003; Faccio et al. 2013; Previat and Nagel 2016). In Maine, Massachusetts, Minnesota seasonal pond inventories, 80–96% of photo delineated potential seasonal ponds met the physical criteria of seasonal ponds (*i.e.*, forested context, ephemeral hydrology, hydrologically isolated) as well as fundamental wetland conditions (Brooks et al. 1998; Burne 2001; Calhoun et al. 2003; Palik et al. 2003; Faccio et al. 2013). In Minnesota 100% of the correctly identified ponds also met the criteria to be considered jurisdictional wetlands. In Maine and Massachusetts, the presence of pond-breeding amphibian adults or eggs or fairy shrimp are required for regulatory status; these organisms were present in the majority of validated ponds in Massachusetts (85%), Maine (46–73%), and Vermont (54%). However, many ponds had only one indicator species, and in Maine less than 5% of ponds had three or more key species (Brooks et al. 1998; Calhoun et al. 2003; Faccio et al. 2013).

The scale of the aerial photographs used for seasonal pond delineation does influence the number of potential (and validated) ponds identified. The USFWS National Wetland Inventory (NWI) maps (1:24,000 scale), accurately map other wetland types and can be used as an initial seasonal pond inventory tool at the state or regional levels across the area covered by this review (Kudray and Gale 2000; Calhoun et al. 2003; USFWS 2020). Even with a minimum mapping unit of 5000 m², NWI maps included 45–79% of the ponds identified with finer resolution aerial photos (*i.e.*, 1:12,000 scale) in Maine. However, these tools have their limits – finer resolution photos (1:4800 scale) identified threefold more seasonal ponds than the 1:12,000 scale inventory (Calhoun et al. 2003; Baldwin and deMaynadier 2009). While the scale of the aerial photos impacts the number of seasonal ponds identified, it does not necessarily influence the size of the ponds being identified. In north central Minnesota, similar seasonal pond sizes (100–2500 m²) were detected using 1:15,840 and 1:24,000 photos, and in Maine the median sizes of seasonal ponds did not differ for 1:4800 (295 m²) vs. 1:12,000 (157 m²) scale photos (Calhoun et al. 2003; Palik et al. 2003; Batzer et al. 2004). Despite the widespread use and overall good performance of wetland mapping with aerial photos, the method has some drawbacks when applied to seasonal ponds. Photo quality, artifacts, and

timing, interpreter experience and topographic shading can all influence the number of seasonal ponds identified (Burne 2001; Faccio et al. 2013). Consistence and reliability when attempting to map small ponds with aerial photos. This is a problem given that majority of ponds mapped in Vermont, Maine, and Massachusetts are <500 m² in area (Brooks et al. 1998; Calhoun et al. 2003; Baldwin and deMaynadier 2009; Faccio et al. 2013). In Massachusetts, seasonal ponds larger than 1100 m² in area were consistently identified using 1:12,000 scale photos, but ponds smaller than 250 m² were considered to be below a reliable mapping size (Brooks et al. 1998; Burne 2001). Landscape setting also poses challenges for photointerpretation; seasonal ponds in wooded wetland complexes are often missed using photos of any scale, and often found in field surveys (Calhoun et al. 2003).

Moderate to heavy canopy cover, especially coniferous or mixed forests, pose the greatest challenge to seasonal pond identification (Calhoun et al. 2003; Faccio et al. 2013; Resh et al. 2013). In conifer-dominated regions of Maine and Vermont, fewer seasonal ponds were identified from aerial imagery, and up to 35% of ponds were missed by photogrammetric inventory efforts (Calhoun et al. 2003; Faccio et al. 2013). In the same regions of Maine, transect surveys identified 15 times more ponds compared to the photo interpretation, despite the large-scale photos being used (DiMauro and Hunter 2002; Calhoun et al. 2003; Baldwin and deMaynadier 2009). The ponds missed in these Maine and Vermont inventories were wetlands that also had indicator species per state regulations and if the scientific definition of seasonal ponds was used there would likely have been even more seasonal ponds missing from the inventories. Seasonal pond inventory in Minnesota, which does not require indicator species presence, missed only an estimated 10% of ponds, despite coniferous cover and utilizing 1:12,000 scale photos (Palik et al. 2003). This is possibly due to the slightly larger ponds commonly reported in Minnesota compared to in Maine (Calhoun et al. 2003; Palik et al. 2003).

Many seasonal pond inventories do not assess errors of omission or discuss the uncertainties associated with delineating ponds, so it can be difficult to determine whether the greatest hinderances to seasonal pond mapping efforts are methodological or natural factors. In general, natural factors such as conifer cover appear to influence ponds delineation and accuracy more than methodological factors such as photo scale. Photo scale does influence the number of seasonal ponds identified, but even the finest resolution photos still fail to capture very small seasonal ponds (<100 m²), especially under closed canopies (Calhoun et al. 2003; Van Meter et al. 2008; Baldwin and deMaynadier 2009). Inventories that do not capture small seasonal ponds underestimate the overall value of ecosystem services provided by seasonal ponds, as small ponds provide as much biological function per unit area as large ponds (Calhoun et al. 2003; Batzer

et al. 2004; Egan and Paton 2004). Given these limitations of scale, aerial photography is most appropriate for high-level pond identification, which subsequently can be improved by other methods (Van Meter et al. 2008; Carpenter et al. 2011).

Additional methods, including remote sensing or geostatistical approaches, can improve seasonal pond mapping accuracy in all settings, which may be especially important in areas with heavy canopy cover or small pond size. Low frequency radar (*e.g.*, synthetic aperture radar; SAR) is able to detect the presence of standing water in both leaf-on and leaf-off conditions and light detection and ranging (LiDAR) can be used to derive digital elevation models (DEM), topographic indices, and isolated depression maps, regardless of canopy cover (Schmitt and Brisco 2013; Bourgeau-Chavez et al. 2016). SAR images have been used to identify points switching from flooded (in spring) to non-flooded (summer) condition, likely indicating a seasonal pond (Bourgeau-Chavez et al. 2016). In Michigan, these images alone were able to identify 23–49% of the potential seasonal ponds but missed 14–22% of ponds. This method's errors of omission were somewhat lower than those in regions with heavy canopy cover although its accuracy was no better than the Minnesota photo-based inventory (Calhoun et al. 2003; Palik et al. 2003).

Used in combination, aerial photographs, radar imagery, and topographic information result in the most effective pond identification and mapping. Combining SAR with DEM-derived isolated depression and topographic position index maps significantly improved the accuracy of seasonal pond identification in Michigan; 91% of the seasonal ponds were verified in the field and only 5% were missed (Bourgeau-Chavez et al. 2016). In Massachusetts a combination of aerial photos and geospatial layers (DEMs, land use/land cover, and hydrographic layers) were used to identify topographic depressions located with non-permanent water that were potential seasonal ponds (Wu et al. 2014). This geospatial analysis method identified almost threefold more potential seasonal ponds than aerial imagery alone, and successfully mapped 94–98% of them and missed about 8% (Burne 2001; Wu et al. 2014). Almost half of the potential ponds were 50–250 m² in size, which was below the minimum mapping size reliably used with aerial photography in the region (Burne 2001).

Geospatial products such as topographic or compound wetness indices (TWI, CTI) that identify drainage positions and topographic depressions have been used to delineate many types of wetlands, including seasonal ponds (Creed et al. 2008, Rampi et al. 2014; Wu et al. 2015). CTI maps were used to identify wetlands >0.2 ha in size with 65–98% accuracy (depending on ecoregion and flow direction algorithm) and identified significantly more wetlands in northern Minnesota than the NWI map (Rampi

et al. 2014). In Massachusetts, two efforts have used topographic indices in conjunction with other landscape variables (*e.g.*, elevation, slope, aspect, soil type, land use/land cover) to model seasonal ponds (Grant 2005; Cormier et al. 2013). In western Massachusetts, one geostatistical analysis predicted 65% of the potential seasonal ponds in the statewide map and 63% of those which had been confirmed on based on organism presence (Grant 2005). That effort revealed seasonal ponds were more frequently found in sand, gravel, or alluvial sediments, and less frequently on steep slopes or near developed land (Grant 2005). Similar statistical methods predicted 74–97% of confirmed seasonal ponds in eastern Massachusetts, showing that ponds were negatively associated with slope, green light reflectance, and developed land cover, and positively associated with forested and open herbaceous land cover (Cormier et al. 2013).

Topographically based tools used in conjunction with aerial imagery are better at identifying seasonal ponds than aerial photos alone, due in varying degrees to canopy cover and the size and dynamic hydroperiods of seasonal ponds (Brooks et al. 1998; Wu et al. 2014). There are several other benefits to using geospatial approaches in seasonal pond inventories. First, geospatial tools can be implemented consistently and repeatably, rather than being dependent on photointerpreter skill, subjectivity, or spring moisture conditions (Carpenter et al. 2011; Wu et al. 2014). Second, the influence of geostatistical tools (*e.g.*, processing algorithms) and model inputs (*e.g.*, topographic thresholds) upon predictive performance can be quantitatively assessed and systematically adjusted to improve accuracy. Third, high-resolution geospatial layers (*e.g.*, DEMs, land cover) can be obtained or derived for large areas and used for statewide seasonal pond assessments that complement or expand existing aerial photo-based ones. However, the strength of these methods does not make them sufficient on their own for a comprehensive inventory. Assessing the accuracy of any remotely based method requires field surveys, which are frequently of small extent knowing to their intensive nature (*e.g.*, 4 km², Bourgeau-Chavez et al. 2016). Developing large-scale assessments from tools that appear to perform well in small, specific settings may thus result in problems of precision or accuracy in different landscapes. Ultimately, carefully stratified field validation is essential to developing a widespread successful seasonal pond inventory, especially in regions where remote sensing methods likely underestimate pond abundances or management is common (Calhoun et al. 2003; Van Meter et al. 2008).

How Are Seasonal Ponds Distributed Across Landscapes In The Region?

Across the western Great Lakes and northeastern U.S. the legacy of glaciation and resulting glacial landforms influence the distribution of seasonal ponds (Palik et al. 2003; Colburn 2004; Rheinhardt and Hollands 2008). Seasonal ponds are associated with several major landforms across the region, most notably moraines, outwash plains, and lacustrine plains (Schneider and Frost, 1996; Batzer et al. 2004; Palik et al. 2007; Bried and Edinger 2009; Resh et al. 2013). More specific landform – pond associations differ across the landscapes of the study region. In north central Minnesota, seasonal ponds are most common on ground and end moraines (76% of ponds used by Batzer et al. 2004; one pond per 10 ha) and outwash plains (18% of ponds, one pond per 20 ha), with few ponds occurring on lacustrine plains (6% of ponds, one pond per 33 ha). In this region, pond distributions are strongly controlled by glacial landform differences, which alone explain 88% of the variation in pond distribution (Palik et al., 2003). In eastern Upper Michigan, outwash and lacustrine plains and dunes are most extensive, and seasonal pond densities are much lower, averaging one pond per 400–588 ha (Resh et al. 2013; Previant and Nagel 2016; VanderMeer et al. 2020). Seasonal pond densities in New England are more similar to Minnesota, ranging from one pond every 20 ha in the Adirondack region of New York to one pond per 42 ha and one per 91 ha in the Connecticut River Valley and Quabbin Reservoir watershed of Massachusetts, (Stone 1992; Brooks et al. 1998; Karaker et al. 2008). Although none of these studies explicitly compared pond distributions among glacial landforms, most of the studied landscapes were comprised of shallow till, with smaller components of outwash and lacustrine or marine plain landforms (Loiselle 2003; Stone et al. 2018). In sum, it appears that across the northern glaciated region that is the subject of this review, pond densities are highest in the till parent materials (especially moraines), likely due to a combination of ice-mediated depressional topography and drainage-impeding impervious layers (e.g., dense till or fragipans), and lower in outwash plains (mostly level with coarse, freely draining substrates) or lacustrine landforms, which are often poorly drained and connected to the regional water table but lack topographic depressions.

How Does Forest Harvesting Impact Seasonal Ponds?

Seasonal pond forest harvesting studies tend to be small scale experiments designed to assess how modern forest management standards and best management practices (BMPs) affect seasonal ponds in the Midwest and Northeast. Their controlled experimental designs provide keen insights

into structural and functional changes in pond ecosystems, but the number of studies is not sufficient to test the breadth of existing seasonal pond BMPs in all forest types. Forest management guidelines are similar for wetlands in general and seasonal ponds in particular. They include limiting or restricting removals within ponds, routing roads or skidder trails around ponds, minimizing rutting, soil disturbance, and compaction within pond basins, keeping slash out of ponds, and leaving a filter strip or buffer of trees around ponds (Calhoun and deMaynadier 2004; USFS 2012; Catanzaro et al. 2013; MFRC 2013; MI DNR 2018). Guidelines for buffer width and harvesting activity within the buffer vary across states and are the primary focus of the limited available literature.

In the western Great Lakes states and Northeast, five experiments have addressed modern forest harvesting impacts on various aspects of seasonal pond ecosystems. These studies were conducted in typical managed forest landscapes, in 60–100 years old stands, with treatments spanning a gradient of disturbance around the seasonal ponds. The control condition in each study was an uncut upland surrounding each seasonal ponds, with treatments ranging from typical management (e.g., upland harvesting with some type of buffer around pond) to severe and experimental (e.g., upland clearcut right down to the pond edge). Two of these studies were conducted in trembling aspen (*Populus tremuloides*) forests in north central Minnesota. The first experiment used the Minnesota Forest Resources Council guideline (15 m buffer around seasonal ponds) to develop the harvesting treatments (upland clearcut with an uncut buffer, partially cut buffer, or no buffer; MFRC 2013). At this study site, the impacts of harvesting around 16 seasonal ponds on hydrology (Kolka et al. 2011), invertebrates (Hanson et al. 2010), birds (Hanowski et al. 2006), and vegetation communities (Palik and Kastendick 2010) were assessed. Another study of similar forests in the region assessed the impacts of harvesting right to the edge of six seasonal ponds on invertebrate communities (Hanson et al. 2009). Two of the other harvesting experiments were conducted in the mixed hemlock-hardwood and mixed conifer-deciduous forests of east central Maine. These studies focused on the impact of harvesting on amphibian movement, reproduction, growth, and community composition (Patrick et al. 2006; Veysey et al. 2009; Freidenfelds et al. 2011; Powell and Babbitt 2017). One of these experiments used 30 m and 100 m buffers around seasonal ponds based on state guidelines (Calhoun and deMaynadier 2004) and recommendations (Semlitsch 1998) to study the impact of upland clearcutting on seasonal ponds, along with an uncut upland control (Veysey et al. 2009; Freidenfelds et al. 2011; Powell and Babbitt 2017). The experimental design for Patrick et al. (2006) used four different treatments (uncut control, partial cut, clearcut to pond boundary with and without

CWD remaining), each along a 90° arc of the pond margin around each pond. The fifth experiment, based in Connecticut, harvested all trees in a 25 m wedge along a 90° arc of the margins of six ponds in mixed deciduous-coniferous forest (Skelly et al. 2014). These five studies are summarized in detail in Supplementary Table 2.

Vegetation Responses

Harvesting upland forests surrounding ponds immediately increases canopy openness (Patrick et al. 2006; Palik and Kastendick 2010; Skelly et al. 2014). In Minnesota, the magnitude of changes in pond vegetation communities scaled with the intensity of harvest removals around the ponds, being least for full buffers (buffers with no removals), intermediate for partial buffers (*i.e.*, some harvest removals within the buffer zone), and largest for clearcuts extending right to the margin of the pond (Palik and Kastendick 2010). Plant communities did not change significantly in the control treatments over the six years of the study, reflecting the relative consistency of this component of the pond ecosystem and suggesting that the effects observed were due to experimental treatments rather than temporal dynamics. Vegetation changes were most significant in the ground layer and shrub/large regeneration layers and included increased cover of sedges and grasses and increased abundance of willow (*Salix* sp.), alder (*Alnus incana*), and trembling aspen (*P. tremuloides*). Importantly, some of the vegetation changes may have occurred subsequent to the treatments due to conditions that they created, rather than directly with the treatments themselves. Namely, windthrow of mature trees in full and partially cut buffers removed up to 50% of the retained basal area, suggesting the potential for positive feedbacks or unanticipated impacts even in the case of full buffering according to BMPs (Hanson et al. 2010; Palik and Kastendick 2010). Overall, forested buffers around seasonal ponds were able to mitigate some of the changes in plant community composition resulting from upland harvesting, although the partial buffer treatments were less effective at mitigating changes in the plant communities than the full buffer treatments.

Hydrologic Responses

The loss of vegetation due to harvesting or other disturbances can alter the stand water balance, with decreased evapotranspiration leading to increased runoff, baseflow, shallow subsurface water storage, and groundwater recharge (Buttle et al. 2018). Forest harvesting around seasonal ponds in Minnesota significantly increased their water levels compared to control ponds, regardless of buffer types (Kolka et al. 2011). In the first year, mean water levels were deepest in the clearcut-to-edge ponds and in subsequent years

differences between clearcut-to-edge and buffer treatment ponds varied. Notably, rapid aspen regrowth and an associated increase in transpiration in the clearcut-to-edge treatment may have driven the lower water levels and shorter hydroperiods measured in these ponds compared to the partial or full buffer treatments after the second year post-harvest (Palik and Pregitzer 1993; Buttle et al. 2018). In the treatments where full or partial buffers were retained, wet periods persisted longer than either the control or clearcut-to-edge ponds, likely due to slower leaf area recover and lower transpiration demand (Kolka et al. 2011). Water levels at the treatment ponds remained higher than the control ponds until the 5th year post-harvest, by which time there were no significant differences in water levels among treatments. In summary, experimental results suggest that any level of adjacent upland harvesting (regardless of buffer) can change stand-level water balance enough to increase water levels and hydroperiods in seasonal ponds, for at least several years after management. Compared to this study in forests dominated by fast-growing aspen, hydrologic recovery times for seasonal ponds may be slower where vegetation regrowth is delayed, or in stands dominated by species with lower growth or transpiration rates (Palik and Pregitzer 1993; Ford et al. 2011; Matheny et al. 2014; Buttle et al. 2018). Furthermore, water levels are not the only component of seasonal pond hydrology impacted by management on adjacent uplands. In addition to altering water levels, cutting to the edge of ponds resulted in warmer water temperatures in the Connecticut study (+1.1 °C), which may alter pond energy budgets, evaporation rates, and biological functions (Brooks 2004; Capps et al. 2014; Skelly et al. 2014).

Invertebrate Response

Seasonal pond characteristics including hydroperiod, canopy cover, water chemistry, soil type, leaf litter inputs influence invertebrate assemblages, but the relationships between these environmental variables and invertebrate communities are often difficult to discern (Batzer 2013). Invertebrate communities are resilient to variation in many environmental variables, but among them appear to be most sensitive to changes in hydroperiod (Schneider and Frost 1996; Brooks 2000; Batzer et al. 2004; Bischof et al. 2013). Management has the potential to act additively or synergistically with natural variation in hydroperiod. Harvest-induced hydrologic changes in seasonal ponds, such as those described in section 3.4.2, along with changes in canopy openness (3.4.1) have impacted the invertebrate community composition of ponds in all harvested treatments (Hanson et al. 2009, 2010). Changes in these invertebrate communities, which required 3–4 years to emerge, were largest in ponds in the clearcut-to-edge ponds (Hanson et al. 2010). Most notably, fairy shrimp (found almost exclusively in seasonal ponds) were

significantly more abundant in the control ponds than the clearcut-to-edge ponds (Hanson et al. 2010). In the Hanson et al. (2009, 2010) studies, invertebrate community composition and hydroperiod were distinctly related, though environmental variables including canopy openness, water depth, and total phosphorus also influenced invertebrate community composition and abundance. Year of observation also explained some of the variation in invertebrate communities, suggesting that compared to vegetation, temporal dynamics are likely more significant for invertebrates, which may also make them more responsive to management impacts. However, compared to hydrologic changes (which occurred regardless of buffer size), invertebrate community changes appear to be mitigated to some extent by buffers around the seasonal ponds, with taxa in ponds with uncut buffers changing less than the communities in ponds with partially cut buffers.

Amphibian Responses

Pond-breeding amphibians use seasonal ponds and adjacent uplands to complete their life cycles. As a result, seasonal pond forest harvesting experiments have more frequently studied amphibian movement, productivity, and community composition than other aspects of these ecosystems. These studies have often assessed amphibian movement between wetland and upland habitats by quantifying mobility indices such as travel distances or home range. In Maine, amphibian movement depended on species and sex; female wood frogs moved the shortest distance from uncut control ponds and furthest from ponds with 30 m buffers; spotted salamanders generally traveled further than the frogs, with some individuals traveling over 400 m from the pond (Vesey et al. 2009; Freidenfelds et al. 2011). Salamander movement early in the growing season was strongly influenced by weather. Salamanders in the 100 m buffer treatment were more likely to move than those in the control when cumulative precipitation was low and salamanders in all treatments were less likely to move as minimum temperatures increased. About 48% of salamanders from ponds with 100 m buffers remained in the buffer area, while only 22% of salamanders crossed adjacent clearcuts to reach uncut upland forest (Vesey et al. 2009). Freidenfelds et al. (2011) observed that 50% of wood frogs remained within the 100 m buffers compared to only 18% of frogs at the 30 m buffer sites. With 30 m of buffer, 64% of frogs migrated through the clearcut to surrounding forest and even with 100 m of uncut forest buffer 25% of frogs migrated to adjacent forest. Overall, larger uncut forested buffers around seasonal ponds provided more protected terrestrial upland habitat and reduced the number of amphibians traveling through clearcut areas to reach undisturbed upland forest.

The influence of management on amphibian reproductive success is less consistent than its impacts on amphibian movements due to the different water depth, hydroperiod, and water temperature requirements frogs and salamanders have for breeding ponds (Skelly et al. 2002; Egan and Paton 2004). Amphibian productivity, including metamorph abundance and size in the Maine study ponds was strongly mediated by pond hydroperiod, but the relationships differed between control and buffered ponds (Powell and Babbitt 2017). In control ponds spotted salamander and wood frog eggmass abundance was not related to mean hydroperiod; in buffer treatments salamander eggmass abundance increased with hydroperiods and there was no influence on wood frog eggmass abundance. For both species, increased variability in hydroperiod decreased eggmass abundance. Longer hydroperiods increased salamander metamorph abundance for all ponds and salamander length increased with longer hydroperiods in buffered ponds. For frogs, longer hydroperiods resulted in longer wood frogs in buffered ponds, but shorter frogs in control ponds. While inter-pool and inter-annual variability was observed, generally, amphibian reproduction and growth were most sensitive to the 30 m buffer treatments and salamanders were impacted more than frogs (Powell and Babbitt 2017).

In addition to impacting amphibian movement and reproduction, forest harvesting alters amphibian community composition. In Connecticut, clearcut-to-edge ponds averaged 1.2 more amphibian species per year than uncut control ponds (Skelly et al. 2014). The presence of canopy tolerant species including spotted salamander, wood frog, and marbled salamander was not affected by adjacent upland cutting, but canopy intolerant species including gray treefrog (*Hyla versicolor*), green frog (*Rana clamitans*), and spring peeper (*Pseudacris crucifer*), were more prevalent in the cut edge ponds (Skelly et al. 2014). Management also affected species distributions in uplands (Patrick et al. 2006). Overall lower abundances of all amphibians were recorded in clearcut treatments than uncut or partially cut treatments, and all amphibian species showed significantly higher juvenile capture rates in uncut and partial cut than clearcut treatments. Adult habitat use differed from the juveniles for some species; juvenile and adult wood frogs, spotted and red-backed (*Plethodon cinereus*) salamanders preferred the uncut and partially cut habitat, while adult green frogs and bullfrogs (*Lithobates catesbeianus*) were more tolerant of the cut habitat. In both studies, amphibians that primarily breed in seasonal ponds (*i.e.*, wood frog, ambystomatid salamanders) were more common in the uncut or partially buffered habitats and amphibian communities differed distinctly between uncut and cut forest habitats. Overall, invertebrate communities tend to withstand fluctuations in the environment

surrounding seasonal ponds, while amphibians are more sensitive to upland or within pond changes.

Avian Responses

While invertebrates and amphibians require seasonal ponds to complete their life cycles, seasonal ponds are visited by other fauna, including breeding or migrating birds. In Minnesota, seasonal ponds with uncut or partially cut buffers had more individual birds across all migration and nesting guilds and a greater number of species compared to ponds in uncut forests (Hanowski et al. 2006). Bird communities around the buffered ponds had more taxa associated with early successional habitat, including alder flycatcher (*Empidonax alnorum*), common yellowthroat (*Geothlypis trichas*), American yellow warbler (*Dendroica petechia*), and American robin (*Turdus migratorius*), and fewer interior forest associated birds [e.g., eastern wood pewee (*Contopus virens*), white-breasted nuthatch (*Sitta carolinensis*), ovenbird (*Seiurus aurocapilla*), red-eyed vireo (*Vireo olivaceus*)]. Differences in community composition between control and treatment ponds became more pronounced over four years of study, and dissimilarity increased in the order of control, uncut buffer, partial buffer, and clearcut-to-edge ponds. Residual forest patches, whether around seasonal ponds or on adjacent uplands provided habitat for forest-associated bird species (Hanowski et al. 2006). Collectively, these results suggest that compared to the shorter dispersal distances and smaller home ranges of invertebrates (section 3.4.3) and amphibians (3.4.4), the highly mobile avifauna may be more resilient to management in landscapes with seasonal ponds.

Long-term Studies

If seasonal pond management experiments are few and far between, studies that address long-term pond responses to management are vanishingly rare. Nonetheless, the few empirical studies that do assess longer (decadal) timescales offer much-needed context for the ecosystem responses described in previous sections, which mostly have been generated by studies running for 5 or fewer years after management. Chronosequences reporting seasonal pond characteristics across a range of stand ages after harvest reveal how changes in forest ecosystems, such as altered canopy cover or composition, impact seasonal ponds. Across a 100-year chronosequence of sugar maple-basswood forests in northern Minnesota, stand age explained little of the variation in most seasonal pond characteristics, including hydroperiod, water depth and chemistry, large deadwood, vegetation cover, amphibian calling or taxa abundance, and invertebrate abundance or species richness (Palik et al. 2001). In that study, canopy openness, rather than stand age itself, was a stronger predictor of variation in these aspects of seasonal

pond ecosystems, especially invertebrate abundance or species richness. In nearby young, middle-age, and mature aspen stands, regional drought influenced seasonal pond invertebrate communities (decreased abundance) more than stand age or canopy openness, although there was a decrease in mean taxonomic richness with increasing stand age (Hanson et al. 2009). In a longitudinal study of four seasonal ponds in Wisconsin, the timing of peak spotted and blue-spotted salamander abundances changed between the 1990s and the 2000s, regardless of upland forest management activities (Donner et al. 2015). In the years 2005–2007 vs. 1992–1994, peak salamander numbers occurred 10–12 days earlier, and air (+4.8 °C) and water temperatures (+3.7 °C) increased over the same interval. These results suggest that climate warming may have more influence on amphibian emergence than upland forest management. It is worth noting that 1992–1994 were some unusually cold years in the Midwest, even compared to the long term, and 2005–2007 were normal to warm, so temperature differences between these time periods may be due to both natural variation and climate change. Over these longer timescales, climate change-related shifts in precipitation also pose a threat to seasonal ponds, as they are likely to alter one of the most important controls on pond functioning – hydrology (Brooks 2009).

Synthesis And Potential Future Trajectories

Collectively, seasonal pond harvesting experiments indicate that buffers around seasonal ponds effectively mitigate some impacts of adjacent upland forest harvesting on seasonal pond ecosystems (Patrick et al. 2006; Semlitsch et al. 2009; Hanson et al. 2010; Palik and Kastendick 2010). The width and canopy cover of the buffer influences the magnitude of management impacts and in general, wider and more intact buffers (vs. those with partial harvesting) are more effective at mitigating management impacts on seasonal pond vegetation (Section 3.4.1), invertebrate (3.4.3) and amphibian (3.4.4) community composition and structure. However, seasonal pond hydrology changes regardless of buffer characteristics (3.4.2), due to decreased transpiration and increased runoff when adjacent upland forests are cut (Kolka et al. 2011). Because seasonal pond hydrology is driven by the water balance at scales larger than the pond itself (i.e., stand to landscape level), no amount of buffer will prevent changes to pond hydrology.

Retention of buffers can preserve some upland habitat for amphibians (Section 3.4.4), but even the largest reported buffers (100 m) are too small to capture all the upland habitat used by amphibians, whose dispersal distances often exceed 100 m and can be over 1000 m (Regosin et al. 2005; Gamble et al. 2006; Gamble et al. 2007; Vesey et al. 2009; Freidenfelds et al. 2011). If buffers are intended to sustain

high quality terrestrial habitat for amphibians, 15 m is far too narrow, and even 100 m falls short of some buffer width recommendations (*e.g.*, 165 m; Semlitsch 1998), acknowledging that experimental buffers of this size may be operationally impractical in some settings (Semlitsch and Bodie 2003; Calhoun and deMaynadier 2004). In addition to buffer width, the size of the harvested area beyond the buffer also influences amphibian survival. Overall, smaller open (harvested) areas likely have fewer negative impacts on amphibians than larger clearcut openings (*e.g.*, 2–4 ha; Knapp et al. 2003; Semlitsch et al. 2009); conversely, smaller openings may dampen the generally positive effects of harvesting on avifauna (3.4.5; especially early-successional taxa). Clearly, it will often be difficult to rectify buffer widths, harvest opening sizes, and biological impacts, especially in settings with high seasonal pond densities. In this regard one way forward may be to re-envision buffer design as part of the larger harvest prescription, and to test new approaches with operational-scale experiments. For example, the potential for windthrow of buffer trees (section 3.4.1; Hanson et al. 2010; Palik and Kastendick 2010) suggests that a wider buffer with a more “feathered” (*i.e.*, patchy) distribution of residual trees on the windward side of a pond, with a closer buffer on the leeward side may be able to optimize harvesting and ecological concerns.

Making forest management decisions at a landscape level rather than at the stand level could allow for the identification and management of clusters of seasonal ponds, rather than on a pond-by-pond basis. In landscapes with high densities of seasonal ponds, such as ground moraines in Minnesota or the portions of the Quabbin Reservoir in Massachusetts where ponds are within 300 m of each other, identifying clusters of seasonal ponds for preservation can be one way to preserve high quality upland and wetland habitat for amphibians while also maintaining the linkages between these habitats that maintains wetland ecosystem functions in seasonal ponds (Brooks et al. 1998; Palik et al. 2003). In practice, Calhoun and deMaynadier (2004) recommend treating a cluster of pools within 400 m of each other as a unit with the recommended buffer around the entire cluster. This approach preserves the linkages between upland and wetland ecosystems and allows for undisturbed terrestrial habitat between ponds and might make planning and implementing forest management easier, at least in some locations (Preisser et al. 2000; Semlitsch and Bodie 2003; Petranka et al. 2004; Baldwin et al. 2006; Gamble et al. 2006).

Forest harvesting experiments (and this synthesis of them) seek to provide the much-needed assessment of seasonal pond BMPs, but these efforts carry several caveats. First, it is challenging to draw consistent and widely applicable conclusions from so few studies, especially because some metrics of seasonal pond ecosystems (*e.g.*, vegetation or hydrology) have only been reported in one experiment

and others such as water chemistry, have not been directly reported at all. Second, study duration is a limiting factor; the studies reviewed herein monitored ponds for 2–6 years following harvest, despite revealing that some impacts (*e.g.*, canopy cover, fairy shrimp abundance) had not returned to pre-harvest conditions during the monitoring period. Chronosequences provide longer-term context on the connections between forest stand age and seasonal pond characteristics, but since seasonal ponds are so spatially diverse and temporally dynamic, even well-designed space for time substitutions do not necessarily capture the response to disturbance or recovery of all types of ponds. Third, while the available harvesting experiments provide a robust assessment of current forest management guidelines, their small size makes them unable to explicitly address connections between multiple ponds and upland forest patches, or larger scale management such as landscape-level vegetation management projects that combine harvest, fire, and other actions. We hope that documenting these gaps and limitations in the existing primary literature will facilitate further research to close them, especially in settings with both high and low densities of seasonal ponds.

From the existing harvesting studies, we can begin to assess the recovery timescale and trajectory of many aspects of seasonal pond ecosystems. Most of the experimental data is focused in the first five years following harvest and indicates that during that period seasonal pond vegetation, hydrology, biogeochemical cycling, and organismal communities (invertebrates, amphibians, and birds) are shifted from their pre-harvesting condition, although the magnitude and direction depends on the response variable of interest (Fig. 2a). These changes occur immediately or shortly (2–4 years) after adjacent forest harvesting, even with buffers, and did not diminish enough for ponds to return to pre-disturbance conditions by the end of the study monitoring periods. The chronosequence study provides a longer-term picture into seasonal pond recovery and some ecosystem characteristics, such as canopy openness and leaf litter inputs, remained altered even many decades following harvest. The tight linkages between canopy cover and hydroperiod and many other aspects of seasonal pond characteristics and functions means that long-term recovery of these ecosystems is likely dependent on the return of the vegetation immediately around the pond as well as in the upland forest. The loss of trees adjacent to seasonal ponds can have cascading impacts, altering leaf litter inputs to pond basins, increasing sunlight and water temperature, altering water levels, and impacting water chemistry and carbon dynamics (Palik et al. 2001; Kolka et al. 2011; Capps et al. 2014; Skelly et al. 2014; Holgerson et al. 2016). While total invertebrate species richness may not change much following upland harvest, the loss of riparian vegetation could disrupt the food web for a long time (10–15 years), favoring the

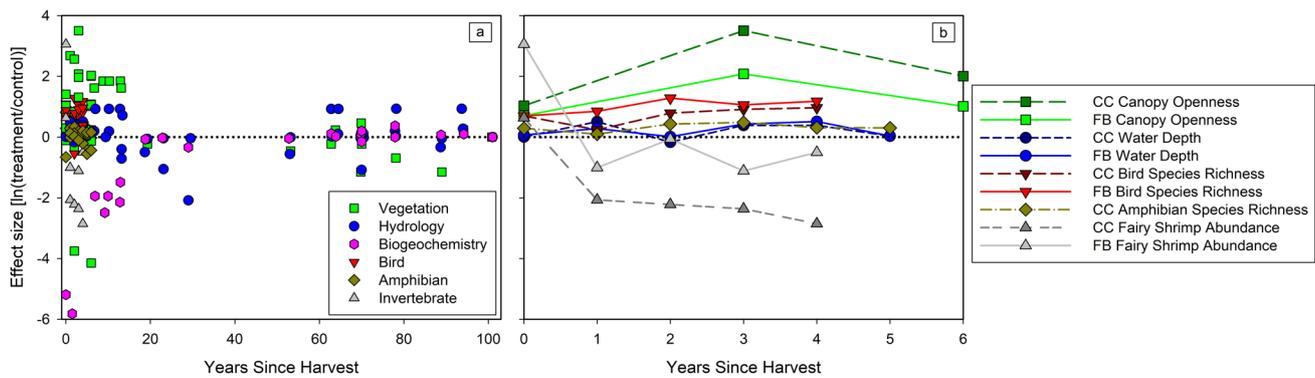


Fig. 2 Seasonal pond ecosystem responses (effect sizes) to clearcut-to-edge and full buffer harvesting treatments based on forest harvesting and chronosequence studies over the long-term (a) and in the immediate period following harvest (b). Year 0 represents pre-harvest conditions

diet generalists and scrapers over the shredder, filterer, and gatherer taxa (Batzer and Palik 2007; Hanson et al. 2009; Smyers et al. 2011; Holgerson et al. 2016). The abundance of invertebrate taxa that are sensitive to water temperatures, including fairy shrimp, responds dramatically to warmer temperatures and will likely remain low until canopy cover and water temperatures recover. In the sugar maple-basswood stands of the chronosequence study, the canopy cover had recovered to around 90% by 20 years post-harvest and it is likely other ecosystem metrics influenced by canopy openness would also recover 10–20 years post-harvest (Fig. 2a; Palik et al. 2001).

Within the short-term, the magnitude of distinct physical and biological changes resulting from harvesting can be estimated with effect sizes (Fig. 2b). The loss of upland (full buffer) or riparian (clearcut-to-edge treatment) trees and the resulting increase in canopy openness is the largest change to seasonal pond ecosystems, and this effect persists for at least 10 years (Palik et al. 2001; Palik and Kastendick 2010). The magnitude of the impacts of harvesting on unique seasonal pond invertebrate (*i.e.*, fairy shrimp) are similar to the change in canopy cover, although the invertebrate response is negative and does not show signs of a recovery trajectory in the short-term in the clearcut-to-edge ponds (Hanson et al. 2010). Both bird and amphibian communities respond less than either canopy cover or fairy shrimp to harvesting and their positive effect sizes represent slight increases in species richness in the short-term (Hanowski et al. 2006; Skelly et al. 2014). While altered water depths and hydroperiods can impact amphibian reproduction and growth, within pond alterations likely do not have as much of a negative impact on amphibians as the loss of suitable upland habitat that they require for their adult life stage (Semlitsch and Bodie 2003). The hydrologic response to harvesting is the smallest, perhaps reflecting natural water depth and hydroperiod variability, although the impacts of harvesting overlaid on the natural variability in pond hydrology could become

compounded and the hydrologic disturbance might have an additive or synergistic effect with higher water years and could result in a more significant disturbance effect especially as climate continues to change (Brooks 2004). While a relatively rapid recovery of water levels and hydroperiod was observed following clearcut in an aspen dominated forest, this is likely not a pattern that will be evident in all forest types, particularly those with slower growing species (Kolka et al. 2011). Watershed-wide hydrologic recovery typically does not occur before 10 years following forest harvesting activities and can take longer, suggesting that seasonal pond hydrologic recovery might follow a similar timescale (Buttle et al. 2018). Buffers around ponds appear to keep these dynamic ecosystems closer to the range of their natural variability, suggesting that management guidelines that include full forested buffers around ponds help minimize the effects of harvesting on seasonal pond ecosystems. Although most differences between treatment and control ponds appear to subside over multi-decadal timescales, long-term monitoring or revisits to previously harvested sites are necessary to fully understand the impacts of forest harvesting on seasonal pond ecosystems and the trajectory of their recovery.

Conservation And Management: Challenges And Opportunities

While most seasonal ponds are individually quite small, they are common features across much of the western Great Lakes states and Northeast and conserving them contributes to maintaining forest ecosystem services more broadly (Calhoun et al. 2017). The principal factors that challenge seasonal pond conservation include inconsistent definitions, lack of thorough inventories, limited regulatory protections, and landowner attitudes towards pond conservation (Semlitsch and Bodie 2003; Zedler 2003; Jansujwicz et al. 2013; Calhoun et al. 2017; Levesque et al. 2019). Identifying and inventorying seasonal ponds is the principal scientific task

needed to conserve these unique ecosystems. Mapping seasonal ponds using multiple remote sensing approaches (Section 3.2), especially in settings with small ponds or dense canopy cover, is the first step in developing larger, more reliable seasonal pond maps (Faccio et al. 2016). Admittedly, improvements to current mapping methods are needed, but these translate to research opportunities. Such opportunities include using pre/post-harvest aerial imagery assessment of seasonal ponds under coniferous cover to more accurately estimate pond densities in these forest types or using multiple months or years of imagery to identify seasonal pond size or hydroperiodicity. Field surveys of seasonal ponds are also critical for developing accurate inventories and conservation strategies, which creates opportunities at the intersection of science and society. The ephemeral nature of seasonal ponds makes them challenging to verify during the short periods of time when they are most easily identified, and in response, many states have developed community science projects to address this challenge (e.g., Michigan Vernal Pools Partnership, Vermont Vernal Pool Monitoring Project).

Community science efforts to verify potential seasonal ponds have been successfully used to expand maps of seasonal ponds and collect additional data about pond hydrology, vegetation community, and organism presence (Faccio et al. 2016). Community scientists play an essential role in identifying and monitoring seasonal ponds that would otherwise be missed by researchers and managers and contributing to the development of policies and management guidelines (Oscarson and Calhoun 2007; Jansujwicz et al. 2013; McGreavy et al. 2016). Community science programs can educate the public and landowners about the value, characteristics, and presence of seasonal ponds in their communities and volunteers can be important advocates for the conservation of ponds. The data generated by these efforts can be used to develop proactive planning and management plans at local levels that complement and even strengthen federal and statewide regulations (McGreavy et al. 2016). Successful conservation efforts are those that foster awareness of these unique ecosystems, include community participation in monitoring and decision making, and take landscape and population-scale impacts into account (Preisser et al. 2000; Oscarson and Calhoun 2007; Calhoun et al. 2014; McGreavy et al. 2016). Collective conservation efforts provide important opportunities for organizations and partners to build relationships, discuss different perspectives and challenges, and find commonalities (Levesque et al. 2017). These efforts have been particularly successful in Maine. Here, strong relationships and collaboration between diverse stakeholder groups has allowed for integrated top-down regulatory and bottom-up voluntary programs, resulting in conservation and management strategies that protect ponds and fit the needs of local communities (Calhoun et al.

2014; Floress et al., 2017). This collaboration linked scientists and resource managers and resulted in widely used forest management guidelines that lay out strategies, such as buffers, for seasonal pond conservation within an actively managed forest (Calhoun and deMaynadier 2004; Calhoun et al. 2014). Fostering similar working groups in other states is essential for developing and maintaining seasonal pond conservation efforts. As part of that, long-term research on seasonal ponds, especially related to harvesting and BMPs is sorely needed to increase our collective knowledge of seasonal ponds, and our ability to conserve them.

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Data availability All data produced from this study are provided in this manuscript or supplementary material.

Code Availability Not applicable.

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Declarations

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