Reproduction and abundance of the wood frog (*Lithobates sylvaticus*) in post-harvest variable retention forests

by

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Abstract

Many aquatic-breeding amphibians require freshwater habitat for reproduction and terrestrial habitat for refuge, foraging, and overwintering. Variable retention harvesting is a technique where live trees and other forest features are retained during timber harvesting in patterns that emulate natural disturbance. Wood frogs (*Lithobates sylvaticus*) are often associated with closed-canopy deciduous forests and utilize ephemeral (temporary) wetlands for reproduction. The objectives of this thesis were to (1) investigate the factors influencing upland abundance of wood frogs in post-harvest variable retention forests and (2) investigate the effects of wetland size and forest canopy on hydroperiod and tadpole performance in ephemeral wetlands of Alberta's boreal mixedwood. To address these objectives, I used pitfall traps to live capture wood frogs across 4 levels of retention harvest (clearcut [0%], 20%, 50%, and unharvested control [100%]), and 2 forest types (deciduous and conifer), in 17-year post harvest forests at the EMEND experiment in northwest Alberta. I mapped breeding sites to account for breeding site proximity and used a LiDAR-based terrain moisture index (Depth-to-Water) to account for soil moisture. I also monitored 15 small ephemeral breeding wetlands from May to August 2015, at which I documented drying dates to assess relationships between wetland size (surface area, maximum depth), forest canopy cover, and hydroperiod. In 12 of the 15 wetlands, I measured tadpole performance by sampling tadpoles over repeated sampling sessions until tadpoles completed metamorphosis or until wetlands dried. I also measured physiochemical parameters (pH, conductivity, and temperature) and primary productivity (periphyton growth) to compare conditions between open- and closed-canopy wetlands.

Abundance of adult wood frogs varied by season, with most captures occurring during early spring and summer months (May and June). Harvest retention level alone had no effect on abundance, but in late season (July and August), there was a significant interaction between retention and forest type where abundance decreased with retention level in deciduous sites, and increased with retention level in conifer sites. The interaction effect, however, was weak, and differences in capture rates between retention levels were small. During late season, capture rates were higher in conifer forests relative to deciduous forests, with soil moisture (lower Depth-to-Water) significantly and positively related to capture rates. These results suggest early regeneration of aspen and availability of moist microhabitats create suitable upland habitat for wood frogs in early seral stage mixedwood forests. Among breeding wetlands, hydroperiod was related to wetland size, but not forest canopy cover. Depth was most related to hydroperiod and may therefore serve as a useful criterion for prioritizing protection of ephemeral breeding wetlands during forest harvesting. Growth and development of wood frog tadpoles were faster in wetlands with less surrounding canopy cover. Water temperature was higher in open-canopy wetlands relative to closed-canopy wetlands, which may help explain observed differences in performance. There was, however, were no significant difference in primary productivity between open- and closed-canopy wetlands.

I conclude that timber retention level has a weak effect on abundance of adult wood frogs in 17-year post harvest stands, and is dependent on forest type and season. Natural regeneration of deciduous species post-harvest may help provide suitable upland habitat for wood frogs in both deciduous and conifer forests. Protection of ephemeral wetlands with adequate depth and hydroperiod will help maintain local populations of wood frogs and other amphibians in managed forests in the boreal mixedwood.

Preface

Animal research ethics approval was required for the research activities conducted in this study. Approval was obtained from the University of Alberta Animal Care and Use Committee under a single animal-use protocol: AUP 00001162 - Effects of variable retention timber harvesting on amphibian populations in the boreal mixedwood forest - on June 9, 2014.

Dedication

For my Dad. For every frog hunting excursion to Ferguson Lake and Forests for the World, and for letting me convert the garden into a toad farm.

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Chapter 1: General Introduction

1.1 - Amphibian life history and habitat requirements

Amphibians are one of the most threatened vertebrate groups, with habitat loss and alteration often considered the primary driver behind many population declines (Collins and Storfer, 2003; Houlahan et al., 2000; Stuart et al., 2004). Many aquatic-breeding amphibian species have multi-stage life histories, requiring both aquatic and terrestrial habitat, and connectivity between these habitat types, to complete their life cycles (Semlitsch, 2000). For these species, successful reproduction is dependent on the availability and quality of aquatic habitat. Adults lay eggs in freshwater, where they hatch into aquatic larvae, that grow and metamorphose into semi-terrestrial juveniles, or in some cases, remain in the aquatic environment for the rest of their lives. Outside the breeding season, adults and post-metamorphic juveniles utilize terrestrial habitats for foraging, refuge, and overwintering activities (Baldwin et al., 2006; Regosin et al., 2005). The terrestrial environment is also important for annual breeding migrations and dispersal of post-metamorphic amphibians from natal breeding sites (Semlitsch, 2008). Due to these complex life histories and habitat requirements, loss or alteration of aquatic or terrestrial habitats may be detrimental to the persistence of populations (Gibbs, 1998). It is therefore necessary to consider both habitats when assessing impacts of land use changes to amphibian populations that use both habitats (Baldwin et al., 2006).

1.2 - Forest disturbance and amphibian habitat

Understanding the response of amphibians to human-mediated disturbance - such as that resulting from timber harvesting - is challenging, due to the complex life-histories, multiple habitat requirements, and natural fluctuations in population size exhibited by this group (Marsh and Trenham, 2001; Patrick et al., 2006; Popescu et al., 2012). Effects of different management practices may vary depending on the life stage considered. Eggs and larvae are primarily affected by conditions in the aquatic breeding environment, whereas alteration of both terrestrial and aquatic habitats can affect terrestrial life stages (Popescu et al., 2012; Semlitsch et al., 2009).

Timber harvesting and subsequent forest regeneration can affect terrestrial environments by altering conditions important for amphibians such as forest canopy cover, tree species composition, understory vegetation, and forest microhabitat (DeMaynadier and Hunter, 1999, 1995; Patrick et al., 2006; Semlitsch, 2000). Amphibians are vulnerable to water loss and require cool, moist conditions, and adequate refuge sites (DeMaynadier and Hunter, 1995; Semlitsch et al., 2009), thus potentially limiting activity and survival in terrestrial environments disturbed by forest harvesting (DeMaynadier and Hunter, 1999; Rittenhouse et al., 2009, 2008). Retention-based harvesting techniques, where some percentage of live trees are left unharvested on the cutblock, have been proposed as an alternative to clearcutting to reduce the negative effects on forest-associated species (DeMaynadier and Hunter, 1995), although the effects of these techniques on amphibian populations are poorly understood (Blomquist and Hunter, 2010; Karraker and Welsh, 2006; Patrick et al., 2006).

Aquatic habitat is also potentially altered following forest management. Removal of trees and vegetation adjacent to breeding wetlands can affect the reproductive success of amphibians by altering pool conditions, as well as reducing the retention time of surface water. In some cases, disturbance resulting from timber harvesting operations can inadvertently create new breeding pools (DiMauro and Hunter, 2002). Breeding wetlands must retain water long enough for larvae to complete development and reach metamorphosis. Hydroperiod – the amount of time a wetland contains surface water – is therefore a key determinant of amphibian reproductive success (Babbitt et al., 2003; Herrmann et al., 2005; Skelly et al., 1999; Snodgrass et al., 2000) and may be influenced by wetland size and vegetation cover (Brooks and Hayashi, 2002; Tsai et al., 2007). In addition, changes in vegetation and forest canopy surrounding breeding wetlands can influence physical and biological conditions (e.g. temperature, primary production) important for larval growth and development (Halverson et al., 2003; Skelly et al., 2002; Werner and Glennemeier, 1999). As such, understanding the factors related to wetland permanence, as well as the effect of the forest canopy on the larval life stage, can assist forest managers in prioritizing the protection of breeding wetlands and tailoring management plans to support reproductive success of amphibian populations.

1.3 - Boreal mixedwood forest

Alberta's boreal mixedwood forest (Figure 1-1) covers approximately 40% of the province (Rowe, 1972) and includes 3 natural subregions: the Dry Mixedwood, Central Mixedwood, and Northern Mixedwood (Natural Regions Committee, 2006). The boreal mixedwood is characterized by a mosaic of both uniform and mixed forest stands. Dominant tree species include trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*) in drier upland sites, and black spruce (*Picea mariana*), tamarack (*Larix laricina*), and paper birch (*Betula papyfera*) in wetter lowland sites (Natural Regions Committee, 2006; Prepas et al., 2001). Jack pine (*Pinus banksiana*) is also found in areas with well-drained sandy soils. Understory vegetation includes woody shrubs, mosses, sedges, and graminoids. Dominant soil types are grey luvisols in uplands and mesisols in wetlands (Natural Regions Committee, 2006). The hydrological landscape of the region is highly varied. Stretches of forest are interspersed with lakes, rivers and other wetlands. Wetlands include mostly treed and shrubby fens on organic deposits with about 5% marshes and other mineral wetlands. Elevations range from 150 to 1225 m, and although relief is not extreme, small changes in local elevation create moisture gradients sufficient to separate upland and lowland areas, and support the development of wetlands (Natural Regions Committee, 2006).

1.4 - Variable retention timber harvesting

In the western boreal forest, the forest industry historically focused on harvesting conifer species for saw wood, leaving large areas relatively undeveloped (Foote and Krogman, 2006). In the early 1990s, improved timber extraction and processing allowed harvesting of trembling aspen for pulp and paper, resulting in expansion of forest harvest operations (Foote and Krogman, 2006; Hannon et al., 2002). Over the last several decades, timber harvesting has increased in Alberta, with over 75% of the mixedwood forest leased to forest companies (Prepas et al., 2001). In response to increasing public concern over threats to boreal biodiversity, as well as a shift toward more sustainable resource development, new forest management techniques evolved that sought to maintain forest ecosystems and biodiversity while still allowing for economically viable timber harvesting (Venier et al., 2014).

Natural disturbance events, primarily forest fire and insect outbreaks, are important in shaping boreal landscapes and influencing forest ecosystems (Bergeron et al., 2004). Variable retention harvesting is a technique where live trees and other forest features are retained during harvest operations in patterns meant to emulate those found following natural disturbance (Gradowski et al., 2010; Lindenmayer et al., 2012). Based on the premise that boreal species have adapted to periodic disturbance, variable retention forestry aims to maintain heterogeneity in forest structure, species diversity, and ecosystem function (Gradowski et al., 2010; Lindenmayer et al., 2012). In its most basic context, retention harvesting involves retaining important structural elements and habitat features to maintain spatial continuity of key habitat features across managed forest landscapes (Gustafsson et al., 2012).

EMEND (Ecosystem-based Management Emulating Natural Disturbance) is a large-scale variable retention timber harvest experiment located in Northwest Alberta (Figure 1-1). As a collaborative initiative among academic, government, and industry stakeholders, EMEND was conceived to test hypotheses related to disturbance-based timber harvesting. More specifically, the goal of EMEND was to determine the amount of retention required to maintain ecosystem function in the boreal forest (Volney et al., 1999). The concept was to apply different levels of green tree retention as harvest treatments and compare them to forest stands that had arisen by natural disturbance. Forest harvest treatments were applied in 1998 with the experiment expected to continue for 80-100 years, thus simulating a typical stand rotation. Previous research at EMEND has examined the effect of retention harvesting on a number of different taxa including invertebrates (Abele et al., 2014; Jacobs et al., 2007; Lee et al., 2017; Pinzon et al., 2012; Work et al., 2010), songbirds (Harrison et al., 2005; Odsen, 2015) and understory vegetation (Craig and Macdonald, 2009; Macdonald and Fenniak, 2007). No studies, however, have examined amphibians within the EMEND context.

1.5 Study Species – Wood Frog (*Lithobates sylvaticus*)

The wood frog (*Lithobates sylvaticus*) is the most widespread amphibian species in North America (Martof, 1970) and is widely distributed in Alberta, including the boreal mixedwood (Russell and Bauer, 2000). Adults range between 30 - 60 mm in length and reach ages up to 4 to 6 years depending on sex and geographic region (Bastien and Leclair, 1992; Gustafson et al., 2015; Leclair et al., 2000). Wood frogs are freeze-tolerant (Storey and Storey, 1984), allowing them to overwinter above the frost line, usually beneath leaf litter or other forest debris (Baldwin et al., 2006; Regosin et al., 2003). They are explosive breeders, with adults gathering at breeding sites in early spring and mating females depositing egg clutches over the course of several days to several weeks, depending on the region (Berven, 1990; Petranka and Thomas, 1995; Stevens et al., 2004). In Alberta, breeding occurs in late April to June (depending on latitude and altitude) usually lasting 2-3 weeks (Russell and Bauer, 2000; Stevens et al., 2004). Females lay large globular egg masses, which are often attached to aquatic vegetation in shallow water (Russell and Bauer, 2000). After eggs hatch, tadpoles take 6-12 weeks to complete development and reach metamorphosis (Russell and Bauer, 2000).

Although often described as a forest-specialist species in eastern North America (Demaynadier and Hunter, 1998), wood frogs are considered more of a habitat generalist in many parts in their range, including Alberta (Hannon et al., 2002) and can be found in a variety of habitat types (Rittenhouse and Semlitsch, 2007). In Alberta, wood frogs tend to be associated with deciduous forest cover rather than conifer forest (Browne et al., 2009; Constible et al., 2001; Roberts and Lewin, 1979). Outside of the breeding season, they can be highly terrestrial (Russell and Bauer, 2000), with adults sometimes found several hundred meters from breeding sites (Baldwin et al., 2006; Rittenhouse and Semlitsch, 2009). Wood frogs are highly philopatric to breeding sites (Green and Bailey, 2015; Vasconcelos and Calhoun, 2004) with distance to breeding sites and other water bodies influencing their distributions in terrestrial environments. Many studies have also shown that wood frogs seek out moist microhabitats in upland environments (Baldwin et al., 2006; Rittenhouse and Semlitsch, 2009, 2007) and may stay relatively close to water in post-breeding months (Taylor, 2013).

Wood frogs may utilize a variety of standing water bodies for breeding. Ephemeral wetlands, also known as vernal pools, are wetlands that dry annually most years (Colburn, 2004). In some parts of their range, including eastern North America, wood frogs, are considered an “obligate” vernal pool species, as they are dependent on fish-free ephemeral wetlands for reproduction (DiMauro and Hunter, 2002). However, in Alberta, wood frogs breed in a variety of permanent and temporary standing water (Hannon et al., 2002) including beaver ponds (Anderson et al., 2015; Stevens et al., 2006), shallow lakes (Eaton, 2004; Eaton et al., 2005), and ephemeral wetlands (Eaton, 2004; Okonkwo, 2011).

Ephemeral wetlands are a common feature in the boreal mixedwood (Okonkwo, 2011) and are known to be breeding habitat for wood frogs and other amphibians (Eaton, 2004; Okonkwo, 2011). Despite their importance as habitat for wood frogs and other amphibians, ephemeral wetlands have no official protection during timber harvesting or other land-use activities. Removal of trees and vegetation around an ephemeral wetland has the potential to alter conditions that are important for reproductive success of wood frogs and other amphibians, such as wetland hydroperiod, and thermal and biological conditions influential on growth and development of amphibian larvae.

1.6 Summary of Thesis

Alberta's boreal region is expected to experience increases in timber harvesting over the next several decades (Foote and Krogman, 2006) as well as corresponding changes in forest type, stand ages, and successional trajectories across post-harvest landscapes. It is therefore imperative to understand the influence of current forest management practices on boreal species. Despite some research on amphibians in Alberta's boreal region (Browne et al., 2009; Constible et al., 2001; Hannon et al., 2002; Macdonald et al., 2006; Okonkwo, 2011; Roberts and Lewin, 1979), the influence of variable retention harvesting and forest regeneration on amphibian habitat and populations remains largely unstudied. Therefore, the objectives of this thesis are to (1) investigate the factors influencing upland abundance of wood frogs in post-harvest variable retention forests and (2) investigate the effects of wetland size and forest canopy on hydroperiod and tadpole performance. The sections addressing each objective are presented as stand-alone chapters, and therefore some material is repeated.

In Chapter 2, I investigate the influence of stand-scale forest habitat (percent tree retention and forest cover type), soil moisture, and breeding site proximity, on terrestrial abundance of wood frogs in variable retention mixedwood forest stands, 17-years post-harvest. No attempt was made to assess immediate post-harvest responses since the EMEND experiment was already established prior to the start of this work. Thus, results reflect responses of wood frogs after initial recovery from harvest and not immediate impact from post-harvest conditions. My primary questions are: (1) How does wood frog abundance vary among different retention levels and forest types in post-harvest forest stands and (2) Which habitat features (retention level, forest type, soil moisture, breeding site proximity) best explain variation in relative abundance patterns? I addressed these questions by using pitfall trapping arrays to live capture wood frogs across 4 levels of retention harvest (clearcut [0%], 20%, 50%, and unharvested control [100%]) and 2 forest types (deciduous and conifer), in 17-year post harvest forest stands at EMEND. I mapped all breeding sites within each study area to account for breeding site proximity and used a LiDAR-based terrain moisture index (Depth-to-Water) to account for soil moisture at sampling locations.

In Chapter 3, I investigate the influence of wetland size and forest canopy cover on the breeding suitability of small ephemeral wetlands. My primary questions are: (1) How do wetland size and forest canopy influence hydroperiod? (2) How do wetland size and forest canopy influence tadpole performance (growth and development)? and (3) How do physiochemical and biological parameters that may affect tadpole growth and development vary between open- and closed-canopy ephemeral wetlands? I addressed these questions by monitoring 15 small ephemeral breeding wetlands from May to August 2015 within EMEND and the surrounding area. I documented drying dates of wetlands to assess relationships between wetland size (surface area, maximum depth), forest canopy cover, and hydroperiod. In 12 of 15 wetlands, I measured tadpole performance by sampling larval populations until tadpoles had completed metamorphosis or until individual wetlands dried. I also measured physiochemical parameters (pH, conductivity, and temperature) and primary productivity to compare open- and closed-canopy wetlands.

The intent of this study is to provide information on wood frogs and their use of upland post-harvest habitats, and ephemeral breeding wetlands. This information can be applied by forest managers and other land-use practitioners for management efforts focused on conserving habitat and populations of wood frogs and other amphibian species in Alberta’s boreal mixedwood.

1.7 Figures

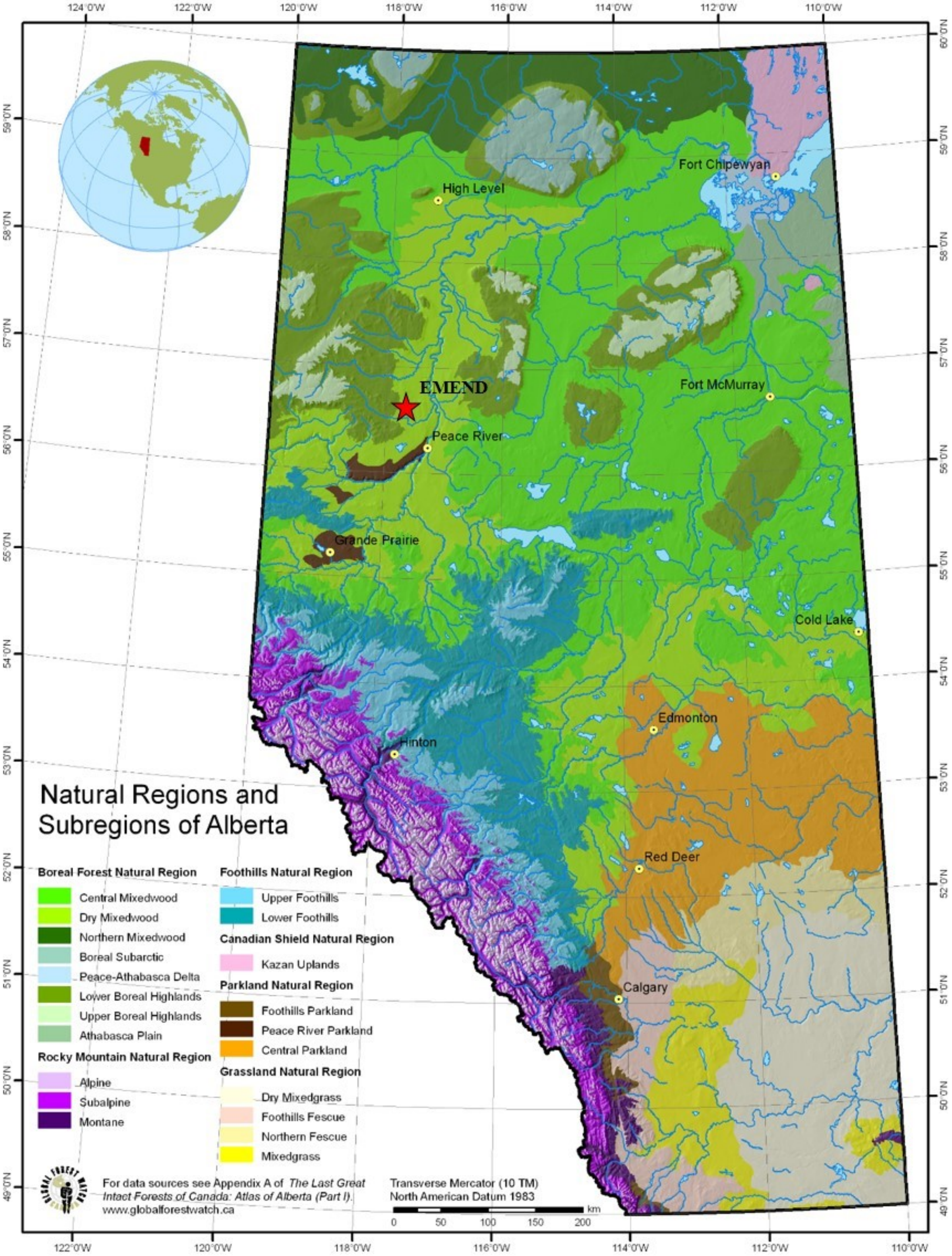

Figure 1-1. Map of natural subregions of Alberta, including the 3 subregions making up the boreal mixedwood (Central Mixedwood, Dry Mixedwood, Northern Mixedwood). Location of EMEND shown northwest of Peace River (red star). Map modified from: globalforestwatch.ca

Chapter 2 – Factors influencing relative abundance of wood frogs in post-harvest variable retention forests

2.1 - Introduction

Amphibians are the most threatened vertebrate group worldwide (Stuart et al., 2004), and their complex life histories and habitat requirements makes predicting of their responses to disturbance challenging (Cushman, 2006; Popescu et al., 2012; Semlitsch, 2000). Most amphibian research in North America has focused on aquatic breeding habitat, with less effort allocated to the terrestrial environment (Regosin et al., 2003; Trenham and Shaffer, 2005). However, despite the necessity of aquatic habitat for reproduction, many aquatic-breeding amphibians spend most of their lives in the terrestrial environment (Semlitsch and Bodie, 2003; Semlitsch, 1998). It is therefore imperative that the terrestrial environment be considered during land management activities in order to conserve amphibian species.

For many aquatic-breeding amphibian species, the terrestrial environment provides habitat outside the breeding season for foraging, refuge, and overwintering (Baldwin et al., 2006; Regosin et al., 2005). Suitable terrestrial habitats are also needed for post-breeding migrations, where adult amphibians move between breeding sites and summer foraging grounds (Semlitsch, 2008), and for dispersal of juvenile amphibians from natal breeding sites to new breeding sites, following metamorphosis (Semlitsch, 2008). Juvenile dispersal is crucial as it represents the primary means by which nearby populations interact (Berven and Grudzien, 1990; Semlitsch, 2008) and connectivity among local populations ultimately affects local and regional dynamics of populations (Marsh and Trenham, 2001). Alteration or disturbance of terrestrial environments may therefore have detrimental effects on amphibian populations at local and regional scales.

Forest harvesting can affect terrestrial environments by altering microhabitats important for amphibians (DeMaynadier and Hunter, 1995; Semlitsch, 2000). Amphibians are ectothermic, with most species having moist, permeable skin, making them prone to desiccation and thus potentially limiting their activity in disturbed habitats where microhabitat conditions have been unfavorably altered (DeMaynadier and Hunter, 1999). The physiological vulnerability of wood frogs and other amphibians to water loss means they require cool, moist conditions, and adequate refuge sites on the forest floor (Semlitsch et al., 2009). Changes in structural elements of forest microhabitats from forest harvesting, such as distribution and abundance of coarse woody debris (DeMaynadier and Hunter, 1995; Patrick et al., 2006; Semlitsch et al., 2009), understory vegetation cover (Chen et al., 1999; Dodd, 2010) , and leaf litter (Constible et al., 2001; DeMaynadier and Hunter, 1995; Rittenhouse and Semlitsch, 2007) may affect amphibian populations, as these elements provide refuge and foraging habitat in post-harvest forests.

The effects of timber harvesting and forest management on amphibians have been well-studied in North America, and the response of amphibians is variable across studies. Generally, the effects of forest management depend largely on the species considered, life history stage, geographic region, and the temporal and spatial scale of study (DeMaynadier and Hunter, 1995; Popescu et al., 2012; Semlitsch et al., 2009). For amphibian species considered to be forest-specialists (those that prefer closed forest canopy), clearcut timber harvesting usually results in reductions in abundance relative to intact forest comparisons (Popescu et al., 2012). Retention-based harvesting techniques, where some percentage of live trees are left unharvested within a cutblock, have been proposed as an alternative to clearcutting; this approach is expected to reduce the negative effects on forest-associated species (DeMaynadier and Hunter, 1995). However, the effects of these newer harvest techniques on amphibians are currently poorly understood (Blomquist and Hunter, 2010; Karraker and Welsh, 2006; Patrick et al., 2006).

The Boreal Forest is one of the largest forest biomes in the world (Brandt, 2009). In Canada, the boreal forest represents approximately 75% of the productive forest (Prepas et al., 2001). Alberta's boreal mixedwood forest (Figure 2-1) covers approximately 40% of the province (Rowe, 1972) and includes 3 natural subregions: the Dry Mixedwood, Central Mixedwood, and Northern Mixedwood (Natural Regions Committee, 2006). The western boreal, which includes Alberta's boreal mixedwood, is unique in that it was largely undeveloped by humans until recently (Brandt et al., 2013). However, in the early 1990s, improved timber extraction and processing technology allowed harvesting of trembling aspen for pulp and paper production, resulting in expansion of harvesting operations (Foote and Krogman, 2006; Hannon et al., 2002). Over the last two decades, timber harvesting has increased in Alberta, with over 75% of the mixedwood forest leased to forest companies (Prepas et al., 2001) potentially threatening native wildlife and boreal biodiversity (Norton et al., 2000).

Increasing public concern over threats to boreal biodiversity, as well as a general shift toward sustainable resource development, have led to new forest management techniques that attempt to mimic natural disturbance patterns to maintain forest ecosystems and biodiversity while still permitting economically viable resource extraction (Venier et al., 2014). Natural disturbance events, primarily forest fire and insect outbreaks, have been important in shaping boreal landscapes and influencing forest ecosystems (Bergeron et al., 2004). Variable retention harvesting is a technique where live trees and other forest features are retained during harvest operations in patterns meant to emulate those found following natural disturbance (Gradowski et al., 2010; Lindenmayer et al., 2012), with the assumption that forest structure heterogeneity, species diversity, and ecosystem function will be maintained within these harvested areas at close to natural levels (Gradowski et al., 2010; Lindenmayer et al., 2012).

The wood frog (*Lithobates sylvaticus*) is the most widespread amphibian species in North America (Martof, 1970) and is widely distributed in Alberta, including across the boreal mixedwood (Russell and Bauer, 2000). Although often described as a forest-specialist species (Demaynadier and Hunter, 1998), the wood frog is considered a habitat generalist in many parts of its range, including Alberta (Hannon et al., 2002), where it is found in a variety of habitats (Rittenhouse and Semlitsch, 2007). In Alberta, wood frogs tend to be associated with deciduous rather than conifer forests (Constible et al., 2001; Roberts and Lewin, 1979). In Northeastern Alberta, Roberts and Lewin (1979) found higher densities of wood frogs in aspen forest compared to sites dominated by conifer species (white spruce, black spruce, jack pine), and mixedwood stands. Similarly, working in mixedwood stands of different disturbance history (unharvested, recent harvest, and recent burn), Constible et al. (2001) found that wood frog abundance was positively associated with deciduous leaf litter, but negatively associated with moss and lichen cover, which are more typical of conifer forests in the boreal (Macdonald and Fenniak, 2006).

The presence and abundance of many amphibian species is often related to breeding site proximity or density (Guerry and Hunter, 2002; Mazerolle, 2003). Outside of the breeding season, wood frogs can be highly terrestrial (Russell et al., 2000), with adults sometimes found several hundred meters from breeding sites (Baldwin et al., 2006; Rittenhouse and Semlitsch, 2009). However, adults of this species are also highly philopatric to breeding sites (Green and Bailey, 2015; Vasconcelos and Calhoun, 2004) and distance to breeding sites and other water bodies may be an important predictor of local abundance in uplands. In Alberta's boreal mixedwood, MacDonald et al. (2006) found that wood frogs were more abundant in forest sites closer to large lakes (up to 100 m) relative to those farther upland (400-1200 m). Many studies have also shown that wood frogs seek out moist microhabitats in upland environments (Baldwin et al., 2006; Rittenhouse and Semlitsch, 2009, 2007) and may stay relatively close to water in post-breeding months (Taylor, 2013). In Alberta, Roberts and Lewin (1979) found the highest density of wood frogs were within 50 m of water bodies and in moist habitats characterized by wetland and water-associated plant species including willows (*Salix* spp)., sedges, horsetails and grasses (Roberts and Lewin, 1979). Consideration of breeding site proximity and soil moisture is therefore essential to understanding patterns in terrestrial abundance in post-harvest forest stands.

Previous studies of wood frog responses to forest management have found that wood frogs prefer closed-canopy habitat (Blomquist and Hunter, 2010; DeMaynadier and Hunter, 1999; Demaynadier and Hunter, 1998; Patrick et al., 2006; Rothermel and Semlitsch, 2002; Vasconcelos and Calhoun, 2004) and will alter their behaviors to avoid clearcut, open, or forest edges (DeMaynadier and Hunter, 1999; Patrick et al., 2006; Popescu and Hunter, 2011). Studies from the eastern part of its range have found that clearcut forest harvesting results in reduced wood frog abundance (Popescu et al., 2012; Semlitsch et al., 2009) and survival (Rittenhouse et al., 2008). However, other studies, including those from Alberta, have found that habitat use is not limited by recent clearcuts and early seral stage forest stands (Constible et al., 2001; Hannon et al., 2002; Macdonald et al., 2006). One Alberta study examining abundance of amphibians in uplands in relation to differing forest buffer widths around large boreal lakes found that although wood frog abundance often varied considerably between individual pitfall traps, there were no consistent differences in abundance among lakes with different buffer sizes, and even reported abundances in clearcuts comparable to those in unharvested forest (Hannon et al., 2002). Similarly, using visual encounter surveys, Constible et al. (2001) actually observed higher wood frog encounters in clearcuts relative to unharvested and naturally burned forest sites.

Although previous research has been conducted in Alberta on wood frogs and other amphibians in relation to forest management, studies were typically performed on populations centered on large wetlands and lakes (Browne et al., 2009; Hannon et al., 2002; Macdonald et al., 2006). No studies in Alberta have examined responses to variable retention forest management. In this study, I investigated the patterns of abundance of wood frogs in uplands under 2 levels of green tree retention (20% and 50%), clearcut harvest (0% retention), and unharvested stands (100% retention) of 2 forest cover types (deciduous and coniferous) in 17-year post harvest forests. The objectives were to (1) determine if terrestrial use by wood frogs was limited in different retention levels or forest types in early seral forest stands; and (2) determine which factors (i.e. forest habitat, breeding site proximity, and predicted soil moisture) best explained seasonal variation in upland abundance of wood frogs.

I hypothesized that wood frog abundance would be limited primarily by abundance of mature deciduous canopy cover, as this would be expected to provide greater inputs of preferred forest microhabitat (leaf litter, woody debris) for refuge, foraging, and overwintering. In deciduous forest, I predicted greater relative abundance (more captures per unit effort) in unharvested controls (100% retention) and 50% retention, relative to 20% retention and clearcut (0% retention) treatment stands. In conifer forest, I expected the opposite trend – with higher abundance in lower retention (20%) and clearcuts relative to controls and 50% retention, since 17-year aspen regeneration and understory development would provide more suitable refuge and foraging habitat compared to mature conifer (controls) and 50% retention stands. I also predicted that relative abundance of wood frogs in uplands would be related to breeding site proximity, since adults of this species are highly philopatric and have maximum migration distances between 300-350 m (Baldwin et al., 2006; Freidenfelds et al., 2011). Finally, I predicted relative abundance would be related to local measures of soil moisture, since wood frogs seek out moist microhabitats during post-breeding movements (Baldwin et al., 2006; Rittenhouse and Semlitsch, 2007). As such, I expected abundance to be higher at sites characterized by higher predicted soil moisture, irrespective of retention treatment or forest type. I also predicted a stronger effect of retention and soil moisture later in the active season (e.g. late summer), when moisture is more limiting, compared to early spring and summer. Early spring movements of wood frogs should correspond with post-breeding migrations from breeding sites to upland foraging habitat, whereas the late season period corresponds to movements related to foraging activity and movement to overwintering sites. Previous research has shown that wood frogs readily traverse clearcuts when moving between habitats in early spring, but that use of these open habitats may be limited later in the active season (Freidenfelds et al., 2011).

2.2 - Methods

Study sites – EMEND research area

Study sites were located at the EMEND research forest in the boreal mixedwood forest located in the Clear Hills Uplands, Lower Foothills Ecoregion of Alberta, approximately 90 km northwest of Peace River, Alberta. The research forest is ~1000 ha divided into 10 timber harvest units (hereafter, Blocks), located in the DMI (Daishowa-Marubeni International) P2 forest management area, in the townships 89 and 90 Range 03 W6M (Figure 2-2). Each Block is categorized as 1 of 4 forest cover types: conifer-dominated (CDOM), deciduous-dominated (DDOM), mixedwood (MIX), and deciduous-dominated with conifer understory (DDOMU). Blocks may contain one or several forest cover types and are partitioned into several smaller harvest treatments (hereafter, compartments), ranging from 3 to 13.5 hectares. Each compartment is subject to 1 of 8 different harvest treatments, including 6 levels of green tree retention and 2 prescribed burn treatments. Green tree retention treatments include 10%, 20%, 50% and 75% retention, as well as unharvested controls and clear-cuts (100% and 0% retention, respectively). Prescribed burn treatments include 100% prescribed burns on unharvested stands and 10% retention with slash burn. Most harvesting treatments were applied in 1998 with wood frog sampling occurring in treatments representing 16-17 years of post-harvest regeneration over a 2-year period (2014 and 2015).

Study site selection

For this study, 4 study sites (EMEND Blocks) were selected based on the following criteria: (1) they had the conifer or deciduous forest cover types for harvest treatments (20% and 50% retention, clearcut, and unharvested control) (2) treatment compartments were adjacent to one another, and (3) they contained active wood frog breeding sites (seasonal or permanent wetlands) either within the block or just outside block boundaries (see *Locating Breeding Sites and Egg*

Mass Surveys). The presence of breeding sites was deemed necessary to ensure the presence of local wood frog populations. Study sites chosen included EMEND blocks A and I (deciduous-dominated) and blocks G and H (conifer-dominated). For clarity, deciduous (A and I) and conifer (G and H) study sites will henceforth be referred to as D1/D2 and C1/C2, respectively. One study site in the deciduous category (D2) was originally classified as DDOMU (deciduous-dominated with conifer understory) but was mostly deciduous (>70%); other candidate deciduous sites lacked active breeding sites.

Wood frog sampling

Seasonal abundance and terrestrial distribution of wood frogs was assessed using capture-mark-recapture (CMR) methods. To estimate relative abundance of wood frogs, 4 pitfall trap and drift fence arrays (hereafter, pitfall arrays) were installed in each treatment compartment resulting in a total of 64 pitfall arrays across all study sites (4 arrays x 4 treatment compartments x 4 study sites = 64 arrays). Pitfall arrays are commonly used to sample amphibians where fencing acts to guide amphibians into pitfall traps (Bury and Corn, 1987; Fisher et al., 2008). Arrays were placed randomly within compartments, but were buffered to be at least 50 m from other arrays, adjacent treatment boundaries, roads, and obvious water features to control for edge effects and confounding variables (Figure 2-3).

Each pitfall array consisted of 4 pitfall traps (7.5 L buckets, Pro Western Plastics©, St. Albert, Alberta) connected by woven silt fencing (Everbilt© - Model# 883132EB). Buckets were approximately 25 cm in diameter and 30 cm deep. Arrays had one trap located centrally and connected to 3 terminal traps by 5 m sections of silt fencing radiating from the center trap and separated by ~120° (Figure 2-4). Fencing was dug into a 10-cm trench and buried to prevent frogs from burrowing underneath. Once buried, fencing was approximately 50 cm high. Buckets were buried so tops were flush with the soil. Bucket lids were suspended 20 cm above traps by 3 small sticks to provide shade and prevent flooding and entry of excess debris. A moist sponge and 1-2 cm of water were placed in each trap to maintain a cool, moist environment for captured frogs. To prevent captured frogs from escaping, a piece of black polyethylene sheeting (4 mm thick, HDX© - model # CF0404 - 50B) was secured over the top of each trap, and 2 bisecting openings were cut that extended just short of the bucket edge (forming a cross-pattern). This allowed frogs to fall freely into buckets, but created a small barrier at the edge that discouraged escape. A small stick was placed in each trap to allow small mammals to escape.

Trapping sessions

Sampling was conducted at 2 study sites in 2014 (D1 and C1) between July 14 – August 25 over 2 trapping sessions: (1) July 14 – August 1 and (2) August 7 – 25. In May 2015, arrays were installed at 2 additional study sites (D2 and C2) and trapping was conducted in all 4 study sites over 4 trapping sessions (with one exception; see below): (1) May 10 - June 3, (2) June 8 – July 2, (3) July 7 –31, and (4) August 5 –24, effectively encompassing the main active season of the study species. In C2, installation of pitfall arrays was not complete until the start of June. As such, trapping was conducted over 3 trapping sessions (2 – 4) at C2 in 2015. Captures for trapping sessions were separated into (1) Early (session 1+2) and Late (sessions 3+4) season categories, to assess seasonal differences in wood frog abundance (see *Statistical analysis*).

During trapping sessions, traps were open and arrays were checked every 2-4 days. Captured frogs were weighed to the nearest 0.1 g, measured Snout-to-Urostyle length (SUL; cm), marked using toe-clipping, and released 10-15 m away from the site of capture. Frogs were given a mark specific to each pitfall array, but not specific to individuals. Marking of frogs in this manner allowed identification of individuals at other pitfall arrays and prevented re-counting individuals in abundance estimates. Between trapping sessions, lids were secured on top of traps to prevent unintentional capture and mortality of amphibians or small mammals. All capture, marking, and handling procedures were approved by the University of Alberta Animal Care and Use Committee (Protocol 00001162) and Alberta Fish and Wildlife (Research Permit and Collection Licenses: 56484 and 56485).

Frog age classes

Wood frogs were classified into 2 age classes based on body size and date of capture. Individuals were classed as adults if they were > 27 mm SUL or if they were ≤ 27 mm SUL and caught in May or June (sessions 1 and 2). Individuals ≤ 27 mm SUL and caught in May or June were assumed to be frogs that had metamorphosed the previous year (2014) and survived the previous winter. Individuals ≤ 27 mm SUL and captured in July and August (sessions 3 and 4) were assumed to be recently emerged froglets based on known dates of metamorphosis from nearby breeding sites and classed as Young-of-the-Year (YOY). Adults do not necessarily represent mature breeding individuals, but rather individuals that have survived at least one winter.

Locating breeding sites and egg mass surveys

In 2014 and 2015, all breeding sites were identified within a 1.5 km radius around the center of each study site (approximate center of all pitfall arrays; Figure 2-5). This area encompassed the estimated maximum migration distances (home ranges) for adult wood frogs between breeding pools and upland habitat (Baldwin et al., 2006; Regosin et al., 2003) as well as the average dispersal distances for YOY wood frogs (Berven and Grudzien, 1990), thus ensuring that all breeding sites surrounding pitfall arrays were accounted for. Egg mass count surveys were used at all breeding sites to estimate reproductive effort (breeding population size). Egg mass counts are a commonly used proxy for the size of breeding wood frog populations since number of breeding females at a site is approximately correlated with the number of egg masses deposited (Crouch and Paton, 2000). Details of egg mass count surveys are provided in Chapter 3. Based on the information above, a ‘population’ in this study was defined by the all breeding sites (and captured wood frogs) within the 1.5 km search radius of each study site. A ‘breeding population’ refers specifically to the number of breeding females (inferred from the number of egg masses) at individual breeding sites. Therefore, each study site consisted of a single population, composed of 1 to several breeding populations, depending on the number of breeding sites

Proximity to breeding sites

Euclidean distance of each pitfall array to the nearest breeding site was measured and used as an index of breeding site proximity using the “Generate Near Table” tool in ArcMap 10.3 (ESRI, 2016). Wood frogs show high breeding site fidelity (Berven and Grudzien, 1990; Vasconcelos and Calhoun, 2004) with the location of breeding sites influencing upland distributions outside of the breeding season. Breeding sites were only included in proximity analysis if (1) they supported relatively large breeding populations (egg mass counts > 3) or (2) they retained water past May 31. In study sites D1 and C1, several small ephemeral breeding sites were identified that supported very small breeding populations (1-3 egg masses) but dried rapidly following egg deposition (before May 31). These sites were all small ATV ruts on access trails where prolonged use had compacted clay and created water-filled depressions that wood frogs used for breeding. Given the highly ephemeral nature of such sites, they were considered less likely to influence nearby upland captures compared to larger, more permanent breeding wetlands that supported larger breeding populations (> 3 egg masses).

Estimating soil wetness

As an estimate of wetness at pitfall arrays, the mean predicted Depth-to-Water (DTW) was used from the Wet Areas Mapping (WAM) model. WAM is a LiDAR-based terrain moisture model that predicts expected flow channels and associated water accumulation (depth to water) patterns at 1 m resolution digital elevation (Murphy et al., 2008; White et al., 2012). It can be used to delineate hydrological features, particularly those that are small or temporary in nature (Murphy et al., 2008; White et al., 2012). DTW is defined as the depth to the expected water table; fully saturated soil or surface water is predicted when DTW equals zero, whereas higher values indicate increasing levels of dryness (Murphy et al., 2008). The main adjustable parameter in the WAM model is the Flow Initiation Threshold (FIT) which represents the catchment area over which water is expected to accumulate (White et al., 2012). Lower FIT values (0.5 and 1 ha) provide a more optimistic prediction of wet areas that might be typical of wetter, early spring conditions, whereas higher FIT values (8 and 16 ha) mimic drier, late-summer conditions (White et al., 2012).

Mean DTW was calculated using the focal statistics tool in ArcMap 10.3 (Environmental Systems Research Institute, 2016) from 20 m circular buffers around each pitfall array. A buffer size of 20 m was chosen to be consistent with my sampling design and to prevent overlapping buffers between adjacent pitfall arrays. This buffer size also corresponds approximately to maximum horizontal movement distances estimated for wood frogs from telemetry data (Coster et al., 2014). There are 7 FIT threshold values available within the WAM model (0.5, 1, 2, 4, 8, 12, and 16 ha); preliminary univariate general linear mixed models (GLMMs) were used to determine the best FIT to use in final analyses. A set of univariate models were run separately for early and late season captures, and the most supported model (ie. FIT value) for each season was assessed using AICc (Table A2-7). Preliminary analysis on both early and late season captures showed little difference between models using untransformed and Ln-transformed DTW, and so untransformed values were used in all analyses. For early season, almost all FIT models ranked lower than a null model (no DTW effect included) except FIT 0.5. The difference in support between 0.5 ha model and the null model, however, was marginal (Δ AICc < 2). For late season, the 8 ha FIT was the best supported model so this value was chosen for all final analyses to keep the moisture index consistent between early and late season models.

Statistical analysis

Descriptive statistics are presented among study sites and compartments (green tree retention levels) for both sampling years (2014 and 2015) for the number of adult, YOY, and total wood frog captures. Captures were converted to "Catch per Unit Effort" (CPUE) [(total frog captures at array/ # of trap nights) * 100]. This gave a standardized measure of captures that accounted for differences in sampling effort among pitfall arrays. Trap nights refer to the number of nights pitfall arrays were actively trapping.

Generalized linear mixed models (GLMMs) with a Gaussian response were used to test which habitat variables had the greatest influence on adult wood frog captures among different study sites (see below for treatment of YOY captures). Standardized wood frog captures (CPUE) were pooled across all trapping sessions for only adult frogs and used as the final response variable. Pitfall arrays therefore acted as independent units of observation. Standardized captures were used since there were small differences in sampling effort among pitfall arrays. CPUE values were natural log transformed to meet regression assumptions; normality and homoscedasticity were assessed visually using boxplots and Shapiro-Wilks tests. Transformed data met all assumptions aside from 3 outliers with high capture numbers. These outliers were retained in all models to avoid loss of data. Gaussian GLMMs were used instead of count models like Poisson regression since I used standardized wood frog capture rates (CPUE – captures/100 trap nights) which contained continuous values.

All models included forest treatment variables of retention level and forest cover since these variables are central to the EMEND experimental design and my research questions. Inclusion of other predictors, including breeding site proximity, and predicted soil (terrain) moisture (mean DTW), as well as their interaction terms, were first examined as univariate GLMMs to assess their individual importance. Significance of individual predictors was determined using log-likelihood ratio tests where nested candidate models were compared to a null model with only random effects (study area). Models were evaluated as having good fit if they explained significantly more variation in adult wood frog captures compared to a null model with no fixed effects. Fixed effects included retention level, forest type, soil moisture, breeding proximity, and interaction terms. Study site was included as a random effect in all models to account for any unmeasured variation among study sites.

YOY frogs represent a distinct and highly vagile life history stage; differences in the number and type of breeding sites (permanent vs. ephemeral wetlands) among study sites meant some study sites had few to no YOY, while others had many. Given this high variation, YOY frogs were removed from all analyses to prevent inflation of abundance estimates. Capture rates are summarized for 2014, but because fewer study sites were sampled (n = 2) and the sampling season was truncated (mid-July to August), GLMMs were not constructed for 2014. All analyses were conducted in R version 3.2.5 (R Development Core Team, 2016).

2.3 Results

Capture summary

In 2014, 114 wood frogs were captured over 1152 trap nights between July 14 and August 25 (86 adults, 28 YOY), with 56 captures in D1 (49 adults; 7 YOY) and 58 captures in C1 (37 adults; 21 YOY). In 2015, 847 wood frogs were captured over 4238 trap nights between May 10 and August 24 across 4 study sites (Figure 2-6). Of these captures, 482 were adults and 365 were YOY. Capture rates were not comparable between years due to large differences in sampling effort.

In 2015, both adult and YOY capture rates varied among study sites and seasons. For all study sites, adult capture rates were higher during the early season compared to the late season (Figure 2-7). The opposite trend was apartment for YOY, with capture rates much higher during late season compared to early season. Almost all YOY captures occurred during late season sampling (July and August), which coincided with metamorph emergence at nearby breeding sites.

In 2015, YOY captures were higher in the 2 conifer study sites (C1 and C2) compared to the 2 deciduous sites (D1 and D2). YOY captures at 3 study sites (D2, C1, and C2) reflected the fact that some or all breeding habitats at these sites retained water long enough for tadpole to metamorphose (Table A2-4). There was only a single YOY capture at one deciduous study site (D1) as a result of premature drying of all breeding habitats.

GLMMs and seasonal capture rates

In 2015, the final model for early season captures included only the study design variables of retention level ($p = 0.550$) and forest cover type ($p = 0.794$) with neither significantly explaining variation in capture rates (Table 2-1). No consistent trends were apparent in adult capture rates across retention levels in either forest type during early season sampling in 2015. For late season captures, the final model included 3 variables: retention level that alone was not significant ($p = 0.523$), and significant variables of forest type ($p = 0.031$), and the interaction between forest type and retention ($p = 0.025$; Table 2-1). With respect to forest type, abundance was significantly higher in the 2 conifer study sites compared to deciduous sites during the late season (Figure 2-7). The significant interaction between forest type and retention in late season indicates that there was a significant effect of retention that depended on forest type. During late season, relative abundance generally decreased with retention level in deciduous sites, with slightly higher capture rates observed in clearcuts and 20% retention relative to 50% retention and controls (Figure 2-7). In contrast, conifer sites saw relative abundance increase with retention level during late season, with capture rates slightly higher in 50% retention and controls relative to 20% and clearcuts. The interaction effect, however, was weak, and differences in capture rates between retention levels were relatively small.

Breeding site proximity had no significant effect on adult wood frog capture rates in either season, and was not included in either of the final models. Soil moisture was significant in initial models for the late season only ($ß = -0.084 \pm 0.035$; $p = 0.032$), with higher capture rates observed at pitfall arrays with higher predicted moisture (lower DTW; Table A2-9). Soil moisture was correlated with forest type, with conifer sites having higher predicted moisture than deciduous sites (Figure A2-2). Moisture and associated interaction terms were therefore excluded from the final model.

Breeding sites and reproductive effort

The number of breeding sites varied considerably among the 4 study sites, as did their permanency (hydroperiod) and associated reproductive effort (number of egg masses) (Figure 2-5; Table A2-4).

Site D1 had 8 ephemeral breeding sites that dried prior to successful metamorph emergence. Egg mass counts at these sites ranged from 2 to 27 ($\mu = 11.1 \pm 8.8$). Site D2 had a single ephemeral breeding site containing 2 egg masses. Although this represents a relatively small breeding population, the site was included in proximity analysis since it never completely dried and allowed for successful metamorphosis and YOY emergence. Site C1 was characterized by 2 large beaver ponds within a large valley that ran north to south and bisected terrestrial sampling sites. Both beaver ponds were permanent, lasting the entire summer, and represented the majority of wood frog breeding, with the northern site (GBN) and southern site (GBS) both supporting high numbers of egg masses (269 and 285, respectively). Six smaller ephemeral breeding sites were located closer to upland pitfall arrays, all of which dried prior to metamorphosis and supported comparatively low reproductive effort (range: 1-10 masses). Site C2 contained a single seasonal breeding site located approximately central to upland trapping sites. Reproductive effort (based on 2016 egg mass surveys) was 37 masses.

2.4 - Discussion

Retention level and forest type

During early season, there was no consistent trends in abundance across retention levels in either forest type. In the late season, however, there was significant interaction between retention level and forest type. In deciduous sites, late season capture rates generally decreased with retention level, whereas in conifer sites, capture rates increased with retention level. The interaction effect, however, was weak, and differences in capture rates between retention levels were relatively small and marked by high capture variability among pitfall arrays with treatments. In deciduous sites, I predicted relative abundance would increase with retention level, with wood frog abundance expected to be limited by a lack of mature (60-80 year) deciduous canopy cover in sites with lower retention (20% and clearcuts with 0%). My results were not consistent with this prediction; early season capture rates in clearcut and 20% retention treatments were comparable to those in 50% retention and unharvested controls. In the late season, capture rates were actually higher in lower retention treatments relative to 50% retention and controls. In conifer sites, I predicted abundance would decrease with amount of retention, owing to early aspen regeneration that provided more suitable upland conditions relative to higher retention and mature (unharvested) conifer stands. Although there was no significant difference in capture rates among retention levels during early season, capture rates generally increased with retention level during the late season. Again, these observations were largely inconsistent with my predictions, although the observation of relatively high early season capture rates in lower retention treatments in conifer sites does provide some support for my initial hypothesis.

These results may be explained, in part, by the levels of forest regeneration considered in the study. Timber harvest treatments were applied at EMEND 17-years previous to measures of wood frog responses thus likely providing sufficient time for recovery of lost forest habitat features. Reduced abundance of wood frogs and other forest-associated amphibians following timber harvesting is often attributed to the loss of forest cover, and other forest elements, such as leaf litter, which provide shade and habitat for refuge and foraging (Demaynadier and Hunter 1995, 1998, 1999; Semlitsch et al., 2009). In deciduous sites, the greater percentage of mature deciduous trees in higher retention (50%) and unharvested stands, were expected to provide greater cover and inputs of leaf litter. Forest succession in the boreal mixedwood typically involves a transition from broadleaf species, to conifer species (Macdonald and Fenniak, 2007) and early forest succession following disturbance is usually dominated by shade-intolerant species such as trembling aspen and balsam poplar (Gradowski et al., 2010; Lieffers et al., 1996). These species are usually first to regenerate because they can propagate asexually through suckering (Frey et al., 2003). At EMEND, post-harvest clearcuts and lower retention treatment stands are dominated by trembling aspen in both deciduous and conifer-dominated forests (Craig and Macdonald, 2009; M. Robinson, *personal observation*). Deciduous leaf litter and canopy cover provided by 15+ year aspen in clearcut and lower retention stands may therefore have compensated for differences in these habitat elements between retention levels and forest types.

Forest type alone also had a significant effect on adult wood frog abundance, but only during the late season (July and August). While capture rates varied little between forest types during the early season, late season capture rates were significantly higher in the 2 conifer sites relative to the 2 deciduous sites. This result was somewhat novel given previous research findings that suggest wood frogs prefer deciduous forest over conifer forest (Browne et al., 2009; Roberts and Lewin, 1979). For example, working in Northeastern Alberta, Constible et al. (2001) found greater wood frog abundance at study lakes dominated by deciduous forests (Owl River) compared with those dominated by conifer forest (Mariana Lake), a difference the authors attributed to potential variation in breeding site quality between the two study areas.

Convergence of habitat in deciduous and conifer sites from mature trees (pre-harvest) to early successional stands dominated by young trembling aspen help explain observed densities of wood frogs among sites. Prior to harvesting, conifer-dominated stands consisted predominantly (>70%) of mature trees, such as white spruce (Macdonald and Fenniak, 2007; Volney et al., 1999). Macrohabitat conditions on the forest floor of conifer-dominated forests sharply contrast with those of deciduous forests. In conifer sites, the forest floor of control stands was dominated by moss and lichens, and did not have the leaf litter layer characteristic of control stands of deciduous sites (M. Robinson, *personal observation*). These observations are consistent with preharvest data at EMEND showing deeper litter layer in unharvested conifer-dominated sites relative to deciduous sites (Macdonald and Fenniak, 2007). The fact that late season capture rates were higher in my conifer sites suggests that aspen regrowth associated with early forest succession may help provide suitable upland habitat for wood frogs following timber harvest.

Soil Moisture

Habitat features other than those associated with forest harvest and regeneration may further explain seasonal variation in abundance of adult wood frogs at study sites. I found that soil moisture, as predicted by the Depth-to-Water (DTW) index, had a significant effect on capture rates for late, but not early season (Table A2-8 and A2-9). Although I did not directly measure soil moisture, adult wood frog captures were higher in areas predicted to have wetter soil conditions (i.e. lower DTW). Variation in soil moisture among study sites may also help explain the difference in abundance during the late season between deciduous and conifer forests. Sampling locations (pitfall arrays) at conifer study sites were wetter on average than deciduous sites based on lower average DTW values (Figure A2-2). Wood frogs and other amphibians have increased risk of desiccation in disturbed environments (DeMaynadier and Hunter, 1999; Semlitsch et al., 2009) and activity may therefore be limited by available moist refugia sites in forested uplands. Since the 2 conifer sites were predicted to be wetter than deciduous sites, higher late season capture rates there may reflect greater activity allowed by availability of wet areas near pitfall arrays.

These findings agree with my initial predictions and are not surprising given the association of wood frogs with moist microhabitats observed in other studies (Freidenfelds et al., 2011; Rittenhouse and Semlitsch, 2007; Roberts and Lewin, 1979). For example, Freidenfelds et al., (2011) used radiotelemetry to track adult wood frog movements through recent clearcuts in Maine, USA and found that although frogs freely traversed clearcuts, individuals were often located in pools, puddles, and other moist refugia (Freidenfelds et al., 2011). The authors suggested that availability of standing water and moist areas in clearcuts may benefit migrating amphibians, and that the absence of such features may help explain wood frog avoidance of clearcuts in other studies (Rittenhouse and Semlitsch, 2007; Rothermel and Semlitsch, 2002). The observed seasonal effects of soil moisture also make sense given the timing of movements associated with different life history activities of this species. Late spring and early summer, when adult capture rates were highest, correspond to post-breeding movements of wood frogs from breeding sites into upland foraging habitat. During these months (May and June in my study area), conditions at upland trapping sites were wetter overall (as observed on the ground), coinciding with early spring snowmelt. May and June also had the highest cumulative rainfall during 2015 (Figure A2-3); amphibian movements tend to be correlated with environmental variables, particularly rainfall and temperature (Mazerolle, 2001; Vasconcelos and Calhoun, 2004). Therefore, wood frog activity in these forests may not have been limited during early season months due to higher available soil moisture. Previous studies also suggest that wood frog movements may only be limited during certain times of their active season in post-harvest environments. In Maine, USA, Popescu et al. (2012) found higher captures of both adult and juvenile (YOY) wood frogs in unharvested and partial cut treatment stands relative to clearcuts over a 6-year post-harvest study period. However, differences in abundance were only observed during summer and fall months (June to September), but not during the spring migration period

(April to May) (Popescu et al., 2012).

In the boreal region of northwest Alberta, ephemeral wetlands and small streams, as well as temporary aquatic “non-wetland” features, such as ephemeral draws or pools, are highly variable with respect to hydrology and may contain standing water for only a brief period after spring snowmelt or heavy rainfall (ESRD, 2015; M. Robinson, *personal observation*. Wet Areas Mapping (WAM) is a static model, meaning that model outputs (such as DTW) do not vary among years and thus do not consider inter-annual or seasonal conditions that may influence the location, extent, and permanence, of wet areas within a forested landscape. Despite this limitation, the effectiveness of the DTW index has been verified in several regions of Alberta, including EMEND and the boreal mixedwood (White et al., 2012). Therefore, the DTW index my serve as a useful proxy for estimating wet areas that may be important for amphibians in post-harvest forests in Alberta’s boreal region.

Breeding site proximity

Abundance of adult wood frogs was predicted to be positively related to breeding site proximity, with capture rates expected to decline as the distance to the nearest breeding site increased. Contrary to expectations, there was no effect of breeding site proximity on wood frog abundance during either the early or late season. This result was unexpected given previous research findings in Alberta showing declining densities of wood frogs and other amphibians with increasing distance from wetlands, lakes, and other potential breeding habitats (Hannon et al., 2002; Macdonald et al., 2006; Okonkwo, 2011; Roberts and Lewin, 1979).

These results may be explained by variation in breeding site density and the availability of wet areas (discussed above) among the 4 study sites. Population studies for aquatic-breeding amphibians are often centered around a single focal breeding site (e.g. lake, wetland, vernal pool), with populations defined as the individuals sampled at the breeding site and a defined area of surrounding upland habitat. The amount of surrounding upland habitat considered as part of a local population’s range varies with species and the corresponding migration and dispersal distances of adults and post-metamorphic juveniles, respectively (Semlitsch and Bodie, 2003; Semlitsch, 2000). However, populations of many amphibian species, including the wood frog, may be spatially structured as metapopulations, where nearby breeding sites and breeding populations are connected by the movement of individuals among neighboring ponds (Marsh and Trenham, 2001; Petranka et al., 2004). I frequently captured frogs at large distances from breeding sites (range: 74.7 – 961.2 m), confirming that adult wood frogs may utilize forested upland habitat far removed from breeding wetlands. Two of my study sites (D1 and C1) had a relatively high number of breeding sites (8 at each site) compared to D2 and C2, each of which contained only one. Although most breeding habitats at D1 and C1 supported relatively small breeding populations (≤ 3 egg masses), and were not included in proximity analysis, the relatively high number of breeding habitats relative to upland trapping sites may have precluded any effect of breeding site distance on upland densities.

Variation in breeding habitat, reproductive effort, and YOY

Young-of-the-year (YOY) are an important life stage for wood frogs and other amphibian species as they represent recruitment to local populations. Due to the nature of the EMEND design, I was unable to control for the number, type, and location of breeding habitats at my study sites. This precluded a controlled comparison of YOY metrics (e.g. production, dispersal distances) among study sites. Despite this, YOY captures, in concert with the variation in breeding habitats and reproductive effort (egg masses), documented during this study, are informative for the conservation of local amphibian populations in managed forests of the boreal mixedwood.

I observed breeding at a variety of permanent and temporary aquatic habitats across my 4 study sites (Figure A2-1), and differences in YOY captures reflected variation in the size and permanency of breeding sites. The study sites with the highest YOY captures (the 2 conifer study sites: C1 and C2), both contained permanent breeding sites (2 beaver ponds in C1, and a single permanent wetland in C2). The presence of permanent breeding habitats allowed wood frog tadpoles to successfully metamorphose and emerge as YOY, representing relatively high YOY captures at these sites (201 in C1, and 110 in C2). In comparison, YOY captures were relatively low at the 2 deciduous sites (D1 and D2), which were supported by smaller, more temporary breeding habitats. At D1, I documented relatively high reproductive effort (88 total egg masses) across 8 breeding sites consisting of both natural ephemeral wetlands and small anthropogenic pools (i.e. water-filled ATV ruts, old harvest landings). Despite a relatively high number of breeding sites and considerable reproductive effort from resident breeding females, all breeding sites dried prior to tadpoles completing metamorphosis, resulting in only a single YOY capture. In comparison, D2 contained only a single breeding site (I1) with a relatively small breeding population (2 egg masses). Despite its small size (area = 33.7m^2; max depth = 70 cm), it retained water for the entire season (i.e. did not dry by August 31), allowing tadpoles to successfully reach metamorphosis and emerge as YOY. Although I did not quantify metamorph production at breeding sites, I captured a total of 23 YOY at upland trapping sites in D2. This information, combined with regular tadpole surveys showing rapid growth and development of larvae (see Chapter 3), suggests this population achieved high reproductive success and represents a sizable contribution to the local population considering the small size of the breeding site and the associated breeding population.

These findings underscore the importance of considering the number and type of potential breeding sites within harvest areas for maintaining local amphibian populations. Wood frogs are opportunistic breeders and can utilize a variety of lentic habitats - both natural and anthropogenic - for reproduction (DiMauro and Hunter, 2002; Eaton, 2004; M. Robinson, *personal observation*). An area may act as a "reproductive trap" in some years if wetlands and other potential breeding sites (both natural and man-made) do not have adequate size and depth to maintain standing water required for tadpoles to complete development and reach metamorphosis (DiMauro and Hunter, 2002). However, even a single ephemeral wetland can make considerable contribution to local populations through production of YOY.

Comparison with previous research

These results further highlight the disparity in responses of amphibian populations to timber harvesting and forest management in North America. While previous studies in Alberta have shown wood frogs are tolerant of recent disturbance from harvesting (Constible et al., 2001; Hannon et al., 2002; Macdonald et al., 2006), studies from other parts of North America have found that negative effects of harvesting can persist for several years. In Maine, USA, Popescu et al. (2012) observed higher captures of both adult and juvenile (YOY) wood frogs in unharvested and partial cut harvest treatments relative to clearcuts over a 6-year period following harvesting. This demonstrates that the negative effects on terrestrial habitat and abundance may persist even after considerable vegetative regrowth has occurred in the post-harvest environment.

My study examined abundance of wood frogs at the scale of retention harvest treatments at EMEND (~ 4-10 ha). Timber harvest blocks in the boreal mixedwood may be much larger (> 100 ha) than those studied at EMEND. Further, variable retention harvest stands in Alberta would be expected to reflect a variety of dispersed and clumped retention, depending on desired targets of the forest company. EMEND provided a unique opportunity to examine patterns in wood frog abundance across post-harvest forests that varied in breeding site distribution and ground moisture. Although previous research has been conducted in Alberta on wood frogs and other amphibians in relation to forest management (Constible et al., 2001; Hannon et al., 2002; Macdonald et al., 2006), these studies were centered on large wetlands and lakes, and did not explicitly consider ground moisture or variation in breeding sites, particularly small ephemeral wetlands. This study may represent a more accurate characterization of habitat heterogeneity reflective of early successional post-harvests forest in the boreal mixedwood. While large wetlands likely maintain regional populations, small wetlands can also make occasional contributions.

2.5 – Conclusions

My study demonstrated that retention harvesting had a weak effect on adult wood frog abundance of adult wood frogs 17-year post-harvest forests, and that the effect depended on season and forest type, with differences among retention treatments and forest types strongest during later summer months (July and August). My results suggest that habitat changes associated with early regeneration of aspen and other deciduous species may help provide suitable upland habitat for wood frogs in both deciduous- and (previously) conifer-dominated forests. Further, availability of wet areas may help mitigate the effects of habitat change associated with forest harvesting and subsequent regeneration, especially during later summer months when wood frog activity may be more limited by relative lack of moist refugia. Protection of potential breeding habitats (e.g. beaver ponds, permanent and ephemeral wetlands) with adequate depth and hydroperiod will help maintain local wood frog and other amphibian populations by providing a source of new recruits. Where possible, forest managers should balance retention between wet and dry upland areas to provide adequate shaded and moist refuge and foraging habitat for wood frogs. Retention should also be placed around small streams and ephemeral wetlands, as these are used by wood frogs and other boreal amphibians and may provide refuge and travel corridors between different habitats (Okonkwo, 2011). Future research should examine multi-year population dynamics of wood frogs and other amphibian species in more recent variable retention harvests.

2.6 - Tables

Table 2-1. Final GLMMs describing adult wood frog capture rates for early and late season sampling. Final models included only predictors and interactions that were statistically significant. Captures were converted to “Catch per Unit Effort “(CPUE) [(total adult frog captures at array/ # of trap nights) * 100] and used as the final response variable. CPUE values were Ln-transformed to meet assumptions of normality and equal variance. Individual pitfall arrays within each study area acted as independent units of observation. P-values in bold indicate statistical significance of predictors at α = 0.05.

Season	Final Model	Predictor	Coefficient Estimate	Standard Error	t-value	p-value
Early	**Retention + Forest**	Retention	0.001	0.001	0.598	0.550
		Forest	0.040	0.152	-0.263	0.794
Late	**Retention + Forest + (Retention*Forest)**	Retention	0.001	0.001	0.640	0.523
		Forest Type	-0.177	0.067	-2.660	**0.031**
		Retention * Forest	-0.084	0.035	-2.420	**0.025**

2.7 – Figures

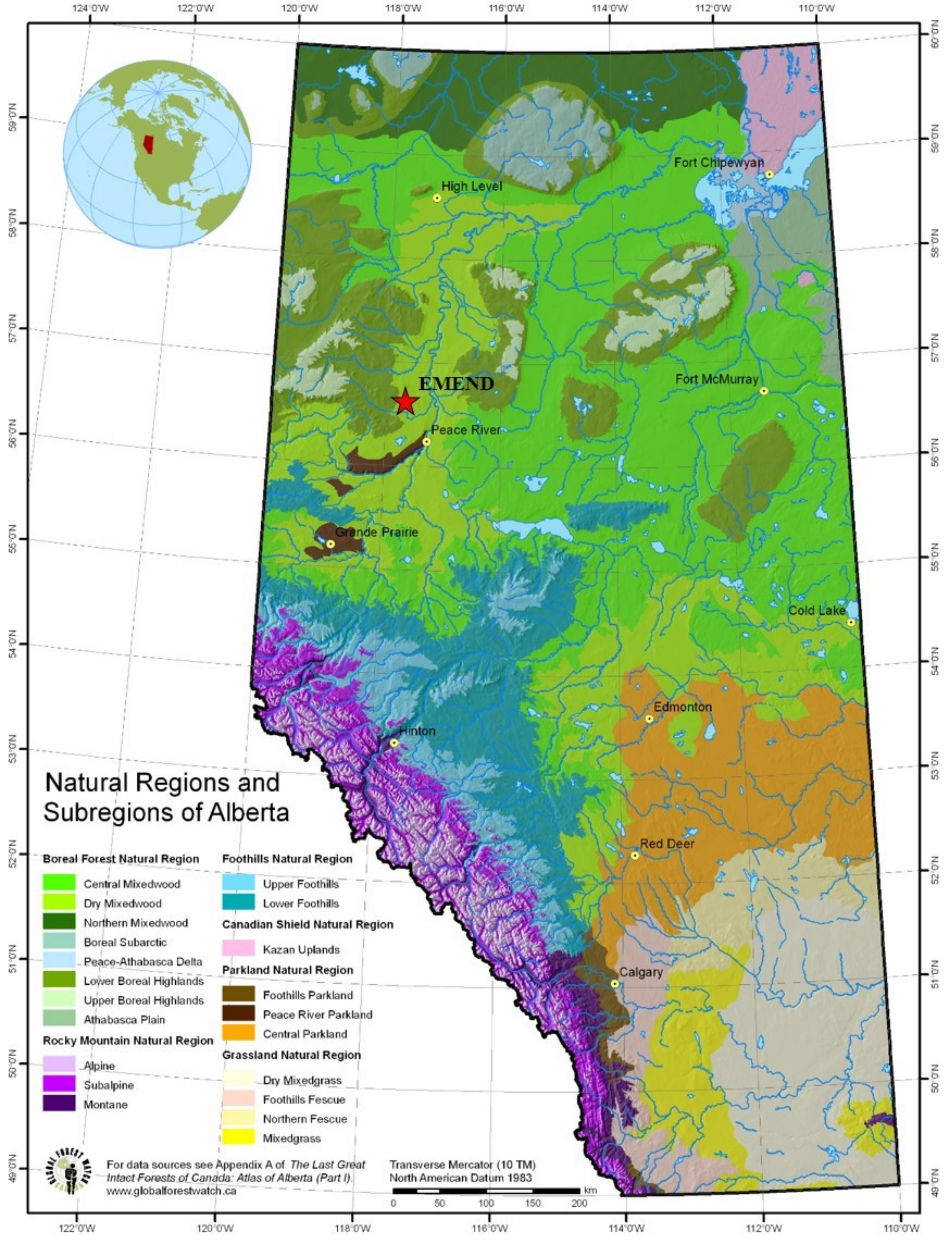

Figure 2-1. Map of natural subregions of Alberta, including the 3 subregions making up the boreal mixedwood (Central Mixedwood, Dry Mixedwood, Northern Mixedwood). Location of EMEND shown northwest of Peace River (red star). Map modified from: globalforestwatch.ca.

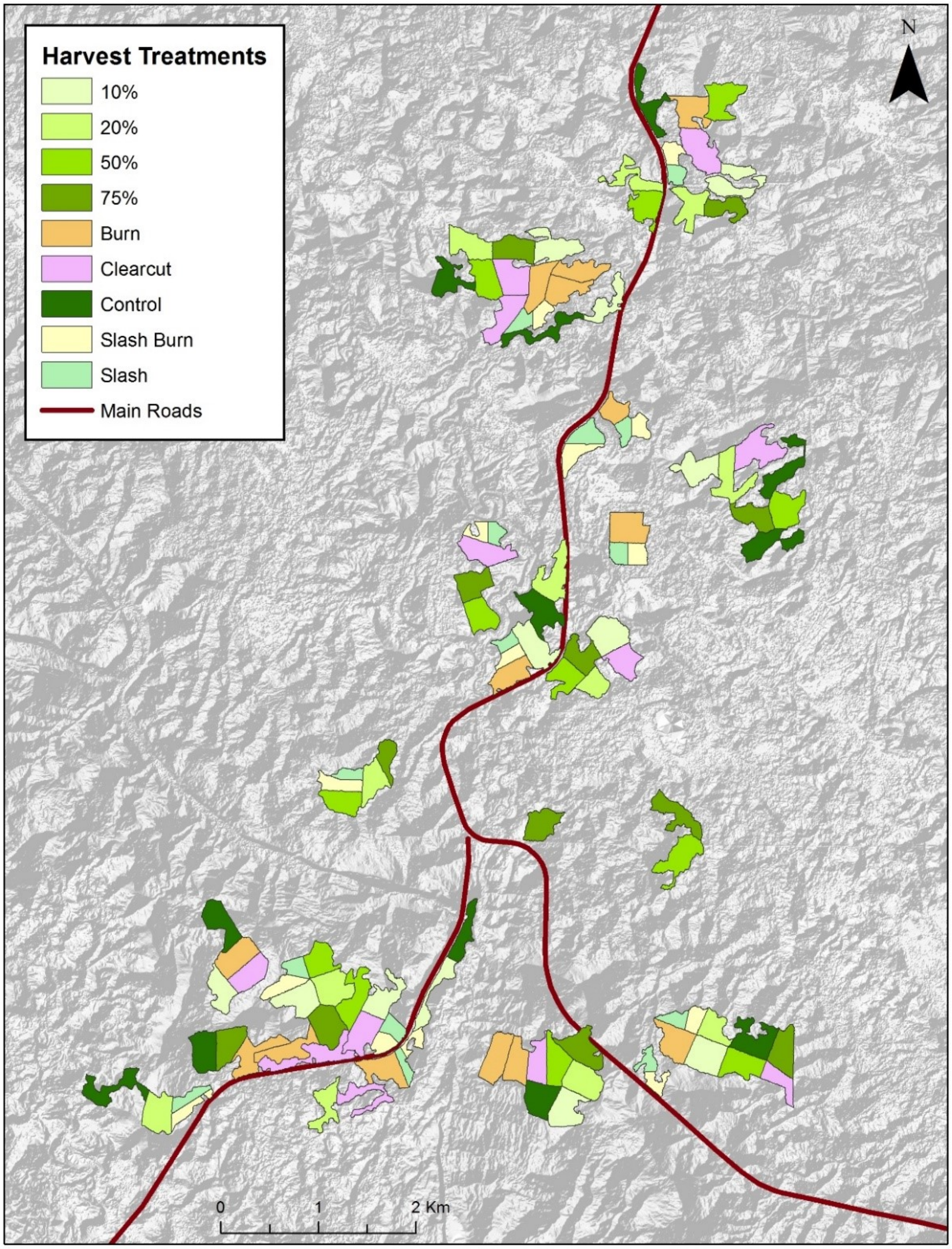

Figure 2-2. Map of EMEND study area including retention harvest treatments.

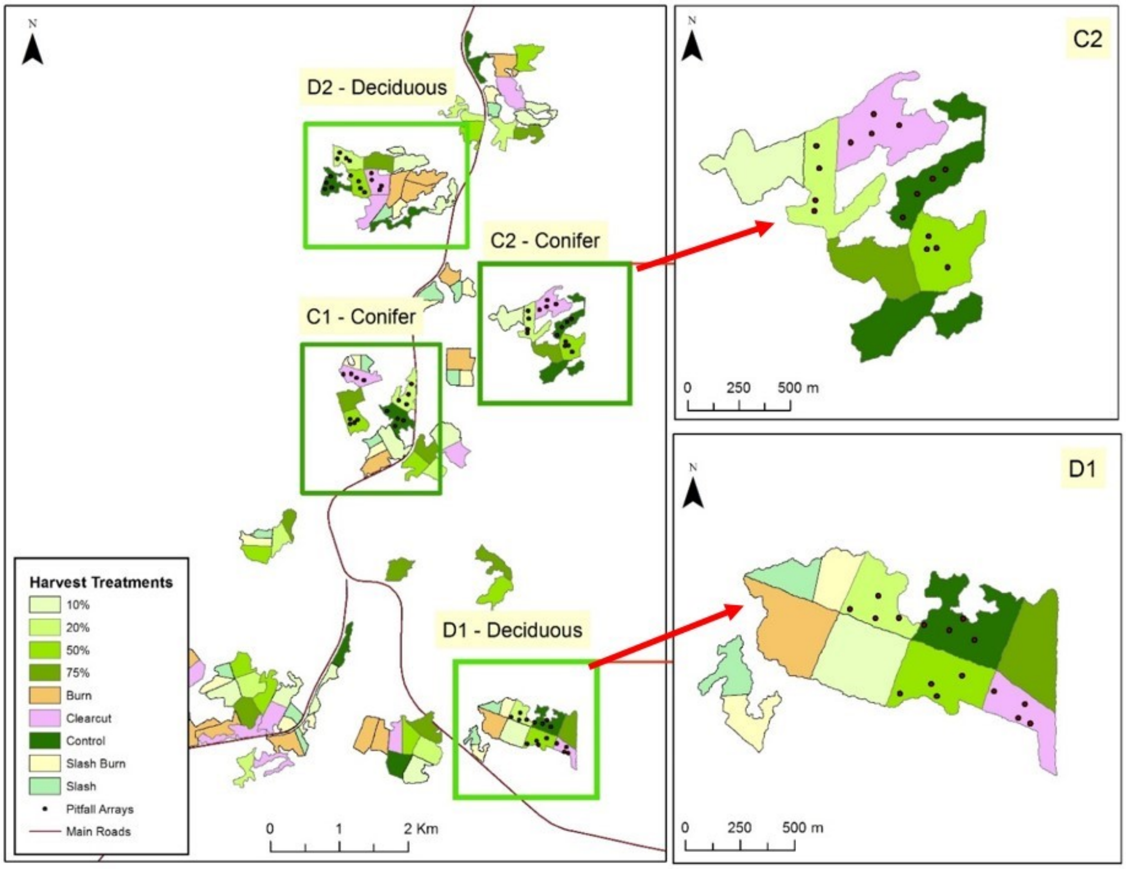

Figure 2-3. Map of pitfall array placement within retention harvest treatments at 4 study sites sampled at EMEND in 2015. Sites C2 (top right) and D1 (bottom right) shown at smaller scale for detail.

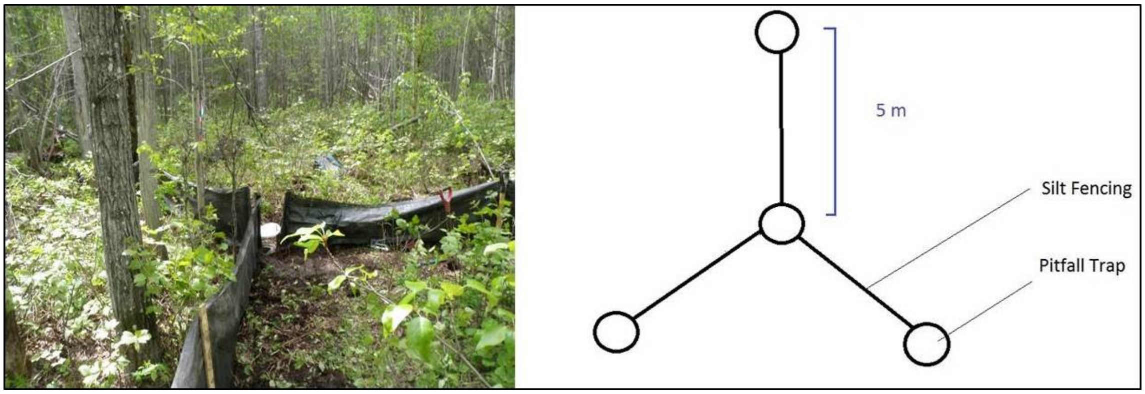

Figure 2-4. Pitfall trapping array design used to live capture wood frogs.

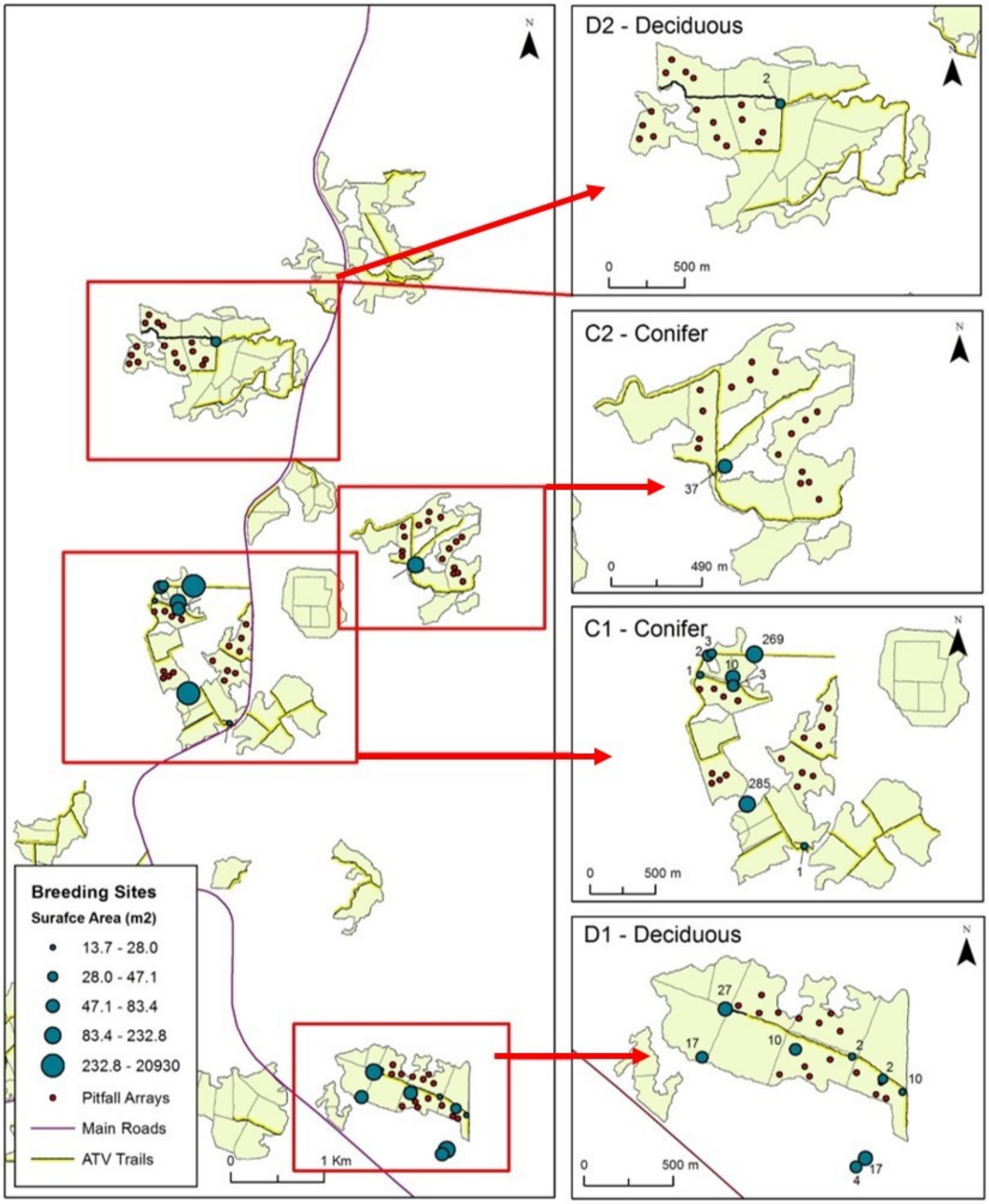

Figure 2-5. Location of breeding sites across 4 study sites sampled at EMEND in 2015. Marker size is proportional to wetland surface area. The number of egg masses counted at each breeding site is shown next to individual markers on 4 inset maps (right).

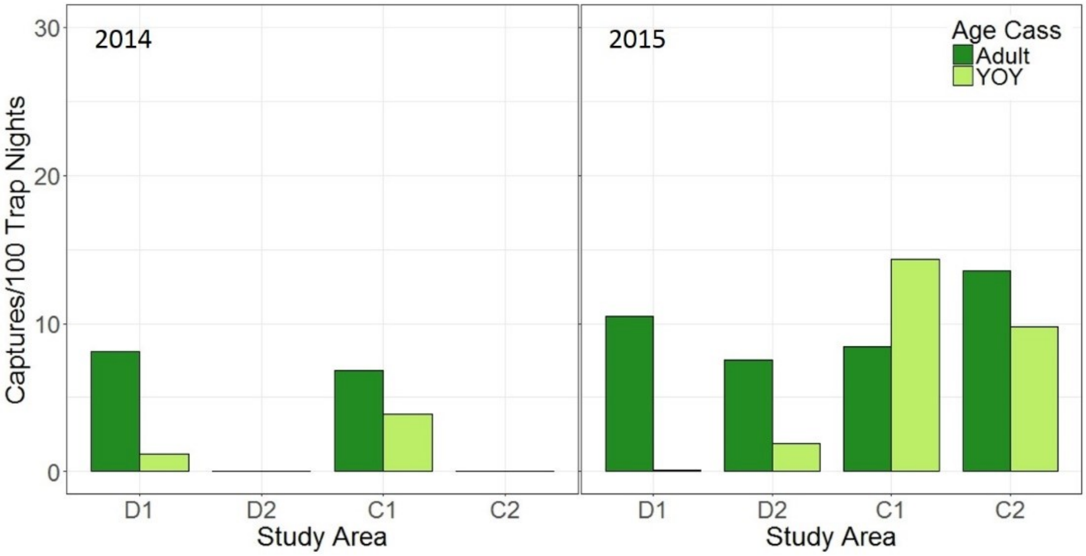

Figure 2-6. Capture rates for adult and YOY wood frogs in 2014 (left) and 2015 (right). Only 2 study sites (D1 and C1) were sampled in 2014 and over a shorter time period (July 15 – August 25). Two additional study sites (D2 and C2) were included in 2015 for a total of 4 study sites. In 2015, sampling was conducted for a longer period (approximately May to August) but trapping dates varied slightly among study sites and pitfall arrays. Bars represent standardized capture rates (captures/100 trap nights) totaled across all pitfall arrays (n=16) at each study site.

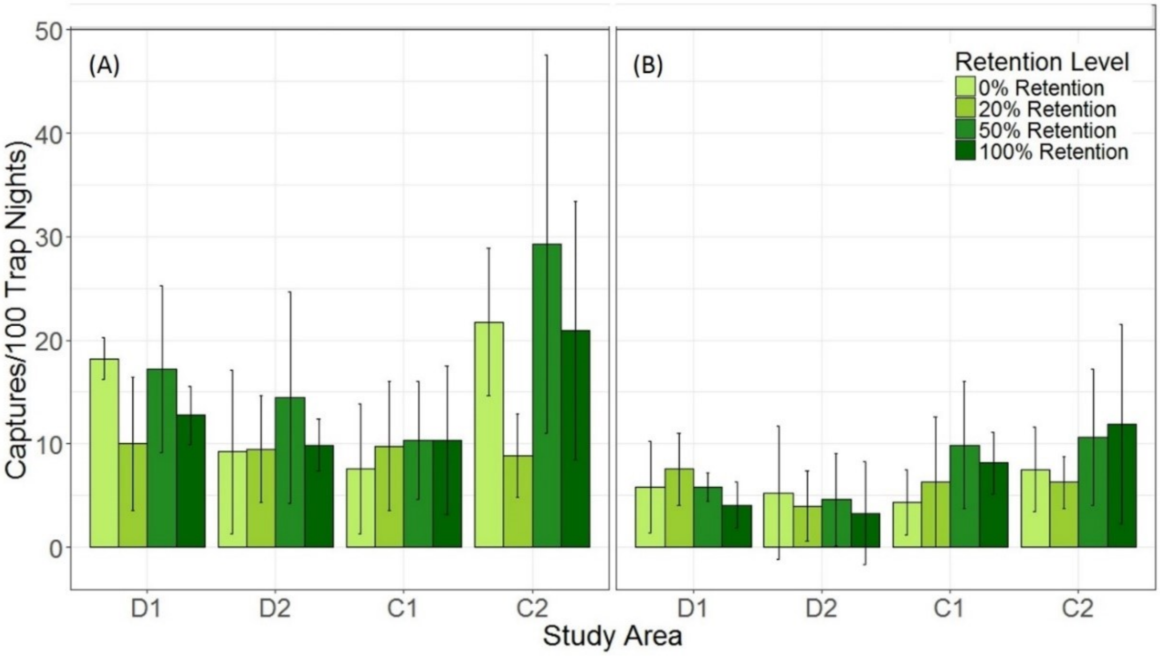

Figure 2-7. Comparison of adult wood frog capture rates across retention levels for (A) early season (May + June) and (B) late season (July + August) sampling at 4 study sites at EMEND in 2015. Captures at each array were converted to "Catch per Unit Effort "(CPUE) [(total adult frog captures at array/ # of trap nights) * 100]". Values shown are mean ± standard deviation.

2.8 – Appendices

Table A2-1. UTM coordinates (NAD 1983; Zone 11V) of pitfall arrays used to sample wood frogs at EMEND IN 2015. Shown also are EMEND Block, Compartment, Study Area, Forest Type, Retention Level, and Array ID (table continued on next page).

EMEND Block	EMEND Compartment	Study Site	Forest Type	Retention Level	Array ID	UTM Coordinates	
						Easting	Northing
A	850	D1	Deciduous	0	850_1	419166	6290255
A	850	D1	Deciduous	0	850_2	419136	6290190
A	850	D1	Deciduous	0	850_3	419025	6290312
A	850	D1	Deciduous	0	850_4	419191	6290167
A	854	D1	Deciduous	20	854_1	418363	6290690
A	854	D1	Deciduous	20	854_2	418493	6290751
A	854	D1	Deciduous	20	854_3	418481	6290648
A	854	D1	Deciduous	20	854_4	418588	6290650
A	853	D1	Deciduous	50	853_1	418877	6290385
A	853	D1	Deciduous	50	853_2	418736	6290346
A	853	D1	Deciduous	50	853_3	418762	6290290
A	853	D1	Deciduous	50	853_4	418594	6290303
A	852	D1	Deciduous	100	852_1	418819	6290593
A	852	D1	Deciduous	100	852_2	418704	6290617
A	852	D1	Deciduous	100	852_3	418883	6290646
A	852	D1	Deciduous	100	852_4	418935	6290548
I	946	D2	Deciduous	0	946_1	416336	6298571
I	946	D2	Deciduous	0	946_2	416342	6298472
I	946	D2	Deciduous	0	946_3	416477	6298385
I	946	D2	Deciduous	0	946_4	416451	6298323
I	949	D2	Deciduous	20	949_1	416021	6298747
I	949	D2	Deciduous	20	949_2	415970	6298788
I	949	D2	Deciduous	20	949_3	415875	6298871
I	949	D2	Deciduous	20	949_4	415837	6298784
I	947	D2	Deciduous	50	947_1	416237	6298297
I	947	D2	Deciduous	50	947_2	416175	6298353
I	947	D2	Deciduous	50	947_3	416150	6298454
I	947	D2	Deciduous	50	947_4	416039	6298536
I	948	D2	Deciduous	100	948_1	415662	6298343
I	948	D2	Deciduous	100	948_2	415756	6298359
I	948	D2	Deciduous	100	948_3	415683	6298433
I	948	D2	Deciduous	100	948_4	415743	6298526

EMEND Block	EMEND Compartment	Study Site	Forest Type	Retention Level	Array ID	UTM Coordinates	
						Easting	Northing
G	922	C1	Conifer	0	922_1	416044	6295663
G	922	C1	Conifer	0	922_2	416117	6295604
G	922	C1	Conifer	0	922_3	415932	6295659
G	922	C1	Conifer	0	922_4	416224	6295573
G	919	C1	Conifer	20	919_1	416734	6295285
G	919	C1	Conifer	20	919_2	416847	6295224
G	919	C1	Conifer	20	919_3	416870	6295370
G	919	C1	Conifer	20	919_4	416918	6295516
G	920	C1	Conifer	50	920_1	416026	6294936
G	920	C1	Conifer	50	920_2	416086	6294959
G	920	C1	Conifer	50	920_3	416029	6295009
G	920	C1	Conifer	50	920_4	416135	6294998
G	918	C1	Conifer	100	918_1	416717	6295016
G	918	C1	Conifer	100	918_2	416561	6295124
G	918	C1	Conifer	100	918_3	416801	6294989
G	918	C1	Conifer	100	918_4	416680	6294908
H	932	C2	Conifer	0	932_1	419012	6296676
H	932	C2	Conifer	0	932_2	418886	6296731
H	932	C2	Conifer	0	932_3	418876	6296635
H	932	C2	Conifer	0	932_4	418774	6296593
H	933	C2	Conifer	20	933_1	418595	6296259
H	933	C2	Conifer	20	933_2	418600	6296310
H	933	C2	Conifer	20	933_3	418619	6296465
H	933	C2	Conifer	20	933_4	418605	6296576
H	929	C2	Conifer	50	929_1	419147	6296070
H	929	C2	Conifer	50	929_2	419248	6295983
H	929	C2	Conifer	50	929_3	419156	6296133
H	929	C2	Conifer	50	929_4	419194	6296076
H	930	C2	Conifer	100	930_1	419029	6296225
H	930	C2	Conifer	100	930_2	419099	6296340
H	930	C2	Conifer	100	930_3	419174	6296416
H	930	C2	Conifer	100	930_4	419238	6296460

Table A2-2. Cumulative wood frog captures at study sites sampled at EMEND in 2014 and 2015. Captures are shown as raw counts as well as standardized capture rates (captures/100 trap nights) for adult, young-of-the year (YOY) and total captures (adults + YOY). Only 2 study sites (D1 and C1) were sampled in 2014 and sampling was restricted to later summer (July – August). In 2015, 2 additional study sites were added (D2 and C2) for a total of 4 study sites. Sampling was conducted throughout the spring and summer (May to August) in 2015. Trap nights denotes the cumulative number of nights all trapping arrays were open within each study site during study periods.

				Raw Captures			**Standardized Captures Rates (CPUE)**		
Year	**Study Site**	**Forest Cover**	**Trap Nights**	**Adult**	**YOY**	**Total**	**Adult**	**YOY**	**Total**
2014	D1	Deciduous	604	49	7	56	8.11	1.16	9.27
	C1	Conifer	544	37	21	58	6.80	3.86	10.66
2015	D1	Deciduous	1432	150	1	151	10.47	0.07	10.54
	D2	Deciduous	1212	91	23	114	7.51	1.9	9.41
	C1	Conifer	1400	118	201	319	8.43	14.36	22.79
	C2	Conifer	1126	153	110	263	13.59	9.77	23.36

Table A2-3. Seasonal captures rates for adult and young-of-the-year (YOY) wood frogs across 4 timber retention levels at 4 study sites sampled at EMEND in 2015. Captures were standardized as “Catch per Unit Effort “(CPUE) [(total frog captures at array/ # of trap nights) * 100]. Early season encompassed sampling over sessions 1 and 2 (May – June) whereas late season encompassed sampling over sessions 3 and 4 (July to August).

			Adults		YOY	
Study Site	**Forest Cover Type**	**Harvest Retention Level**	**Early Season**	**Late Season**	**Early Season**	**Late Season**
D1	Deciduous	0	18.2 ± 1.99	5.81 ± 4.45	0	0
		20	10.0 ± 6.42	7.56 ± 3.49	0	0.58 ± 1.16
		50	17.2 ± 8.05	5.81 ± 1.34	0	0
		100	12.8 ± 2.80	4.07 ± 2.23	0	0
D2	Deciduous	0	9.21 ± 7.89	5.26 ± 6.45	0	6.58 ± 2.63
		20	9.46 ± 5.18	3.95 ± 3.40	0	5.26 ± 3.04
		50	14.5 ± 10.2	4.61 ± 4.49	0	3.29 ± 3.31
		100	9.87 ± 2.52	3.29 ± 4.98	0	0
C1	Conifer	0	7.61 ± 6.28	4.38 ± 3.15	0	14.38 ± 10.48
		20	9.78 ± 6.28	6.25 ± 6.29	0	19.38 ± 3.75
		50	10.3 ± 5.72	9.88 ± 6.12	0	59.88 ± 14.38
		100	10.3 ± 7.18	8.14 ± 3.00	0	25.58 ± 11.07
C2	Conifer	0	21.8 ± 7.15	7.5 ± 4.08	0	11.88 ± 3.15
		20	8.87 ± 4.06	6.25 ± 2.5	0	18.8 ± 3.23
		50	29.3 ± 18.3	10.6 ± 6.57	0	20.0 ± 4.56
		100	21.0 ± 12.5	11.9 ± 9.66	0	16.2 ± 5.95

Table A2-4. Summary of all breeding sites identified at 4 study sites at EMEND in 2015, including coordinates (NAD 1983 - UTM Zone 11 V), wetland surface area, egg mass survey dates, total egg masses, drying date, permanency, and whether site was used in breeding site proximity analysis.

Study Site	Breeding Site	UTM Coordinates (Wetland Center)		Surface Area (m^2)	Survey Date 1	Survey Date 2	Total Masses	Drying Date	Permanency	Proximity Analysis (Yes/No)
		Easting	Northing							
D1	EA53	419002	6290403	16.5	May 8	May 22	2	May 30	Ephemeral	No
	CA4	419173	6290278	47.1	May 8	May 13	2	May 30	Ephemeral	No
	A1	419023	6289781	82.1	May 6	May 13	4	May 30	Ephemeral	Yes
	CA2	419284	6290202	13.7	May 8	May 13	10	May 30	Ephemeral	Yes
	EMD8	418684	6290444	74.9	May 8	May 15	10	June 10	Ephemeral	Yes
	A2	419076	6289830	175.1	May 6	May 13	17	May 30	Ephemeral	Yes
	EA1	418160	6290400	72.0	May 7	May 15	17	May 30	Ephemeral	Yes
	EMD7	418291	6290670	215.2	May 7	May 22	27	June 10	Ephemeral	Yes
D2	I1	416594	6298577	33.7	May 9	May 25	2	-	Ephemeral	Yes
C1	EA115	416735	6294448	27.5	May 13	-	1	May 25	Ephemeral	No
	EA144	415935	6295772	28.0	May 14	-	1	May 25	Ephemeral	No
	G2	415997	6295921	73.5	May 14	-	2	May 25	Ephemeral	No
	EA148	416190	6295686	83.4	May 14	-	3	May 25	Ephemeral	No
	G3	416026	6295936	43.4	May 14	-	3	May 25	Ephemeral	No
	EA152	416186	6295753	201.5	May 14	-	10	June 15	Ephemeral	Yes
	GBN	416351	6295932	16,750	May 14	-	269	-	Permanent	Yes
	GBS	416296	6294772	20,930	May 14	-	285	-	Permanent	Yes
C2	* HP1	418739	6296163	232.8	-	-	* 37	-	Permanent	Yes

* Egg mass survey was not possible at the single breeding site in C2 in 2015. Total egg mass count shown was from the following year (2016) and used in concert with pool permanency as basis of inclusion in proximity analysis.

Table A2-5. Data from early season sampling (May – June) used for GLMMs explaining adult wood frog capture rates across 4 study sites at EMEND IN 2015. Adult captures at each array are shown as raw counts and as "Catch per Unit Effort "(CPUE) [(total adult captures at array/ # of trap nights) * 100]. Trap nights denotes the number of nights a pitfall arrays were open and actively trapping. (table continued on next page).

Pitfall Array	Study Site	Forest Type	Retention Level	Trap Nights	Adult Count	Adult CPUE	Ln(CPUE)	Breeding Distance (m)	DTW (8 ha)
850T1	D1	Deciduous	0	48	8	16.67	3.28	129.4	2.014
850T2	D1	Deciduous	0	48	8	16.67	3.28	148.5	2.801
850T3	D1	Deciduous	0	48	10	20.83	3.43	281.5	0.436
850T4	D1	Deciduous	0	48	9	18.75	3.36	99.4	1.943
854T1	D1	Deciduous	20	45	4	8.89	2.94	74.7	2.513
854T2	D1	Deciduous	20	45	1	2.22	2.50	217.7	2.577
854T3	D1	Deciduous	20	45	8	17.78	3.32	191.3	2.924
854T4	D1	Deciduous	20	45	5	11.11	3.05	227.3	1.880
853T1	D1	Deciduous	50	48	11	22.92	3.49	201.9	1.093
853T2	D1	Deciduous	50	48	6	12.50	3.11	111	1.287
853T3	D1	Deciduous	50	48	12	25	3.56	172.7	0.472
853T4	D1	Deciduous	50	48	4	8.33	2.91	167.3	4.667
852T1	D1	Deciduous	100	45	4	8.89	2.94	201.1	8.093
852T2	D1	Deciduous	100	45	7	15.56	3.24	174.2	6.977
852T3	D1	Deciduous	100	45	6	13.33	3.15	283.6	7.957
852T4	D1	Deciduous	100	45	6	13.33	3.15	271.8	8.742
946T1	D2	Deciduous	0	38	2	5.26	2.73	258.2	1.679
946T2	D2	Deciduous	0	38	2	5.26	2.73	273.1	3.736
946T3	D2	Deciduous	0	38	8	21.05	3.44	224.9	3.444
946T4	D2	Deciduous	0	38	2	5.26	2.73	291.6	3.567
949T1	D2	Deciduous	20	37	4	10.81	3.04	597.9	1.778
949T2	D2	Deciduous	20	37	2	5.41	2.73	658.9	1.779
949T3	D2	Deciduous	20	37	6	16.22	3.27	777	2.357
949T4	D2	Deciduous	20	37	2	5.41	2.73	785	0.892
947T1	D2	Deciduous	50	38	4	10.53	3.02	453.8	2.277
947T2	D2	Deciduous	50	38	5	13.16	3.14	475.3	4.017
947T3	D2	Deciduous	50	38	2	5.26	2.73	460.9	2.725
947T4	D2	Deciduous	50	38	11	28.95	3.66	556.7	0.871
948T1	D2	Deciduous	100	38	3	7.89	2.88	961.2	3.466
948T2	D2	Deciduous	100	38	4	10.53	3.02	866.2	4.041
948T3	D2	Deciduous	100	38	3	7.89	2.88	922.6	3.989
948T4	D2	Deciduous	100	38	5	13.16	3.14	852.8	4.306
918T1	C1	Conifer	0	46	3	6.52	2.80	351.3	1.554
918T2	C1	Conifer	0	46	0	0	2.30	248.6	2.684

Pitfall Array	**Study Site**	**Forest Type**	**Retention Level**	**Trap Nights**	**Adult Count**	**Adult CPUE**	**Ln(CPUE)**	**Breeding Distance (m)**	**DTW (8 ha)**
918T3	C1	Conifer	0	46	3	8.70	2.93	428.6	2.492
918T4	C1	Conifer	0	46	7	15.22	3.23	304	0.638
919T1	C1	Conifer	20	46	5	10.87	3.04	484.1	0.108
919T2	C1	Conifer	20	46	7	17.39	3.31	545.9	0.221
919T3	C1	Conifer	20	46	4	8.70	2.93	622.3	1.095
919T4	C1	Conifer	20	46	1	2.17	2.50	555.7	0.165
920T1	C1	Conifer	50	46	0	2.17	2.50	183.1	1.238
920T2	C1	Conifer	50	46	4	13.04	3.14	171.9	1.337
920T3	C1	Conifer	50	46	7	15.22	3.23	243.3	1.507
920T4	C1	Conifer	50	46	3	10.87	3.04	186.2	1.598
922T1	C1	Conifer	100	46	4	8.70	2.93	168.2	0.828
922T2	C1	Conifer	100	46	5	10.87	3.04	164.3	0.165
922T3	C1	Conifer	100	46	1	2.17	2.50	270.9	0.259
922T4	C1	Conifer	100	46	9	19.57	3.39	184	0.309
932T1	C2	Conifer	0	31	4	12.90	3.13	581.3	0.772
932T2	C2	Conifer	0	31	8	25.81	3.58	586.9	0.040
932T3	C2	Conifer	0	31	4	19.35	3.38	491.6	0.216
932T4	C2	Conifer	0	31	8	29.03	3.66	431.6	0.352
933T1	C2	Conifer	20	31	3	9.68	2.98	173.1	0.157
933T2	C2	Conifer	20	31	3	9.68	2.98	202.4	0.294
933T3	C2	Conifer	20	31	3	12.90	3.13	325.1	1.517
933T4	C2	Conifer	20	31	1	3.23	2.58	434.3	0.139
929T1	C2	Conifer	50	21	7	42.86	3.97	418.6	0.220
929T2	C2	Conifer	50	31	1	6.45	2.80	540.1	0.515
929T3	C2	Conifer	50	31	6	22.58	3.48	418.2	0.252
929T4	C2	Conifer	50	31	12	45.16	4.01	463.4	0.663
930T1	C2	Conifer	100	31	6	32.26	3.74	296.6	1.224
930T2	C2	Conifer	100	31	0	3.23	2.58	401.3	1.071
930T3	C2	Conifer	100	31	4	22.58	3.48	503.4	1.419
930T4	C2	Conifer	100	31	3	25.81	3.58	580.9	1.481

Table A2-6. Data from late season sampling (July – August) used for GLMMs explaining adult wood frog capture rates across 4 study sites at EMEND IN 2015. Adult captures at each array are shown as raw counts and as "Catch per Unit Effort "(CPUE) [(total adult captures at array/ # of trap nights) * 100]. Trap nights denotes the number of nights a pitfall arrays were open and actively trapping. (table continued on next page).

Pitfall Array	**Study Site**	**Forest Type**	**Retention Level**	**Trap Nights**	**Adult Count**	**Adult CPUE**	**Ln(CPUE)**	**Breeding Distance (m)**	**DTW (8 ha)**
850T1	D1	Deciduous	0	43	1	2.33	2.51	129.4	2.014
850T2	D1	Deciduous	0	43	1	2.33	2.51	148.5	2.801
850T3	D1	Deciduous	0	43	3	6.98	2.83	281.5	0.436
850T4	D1	Deciduous	0	43	5	11.63	3.07	99.4	1.943
854T1	D1	Deciduous	20	43	2	4.65	2.68	74.7	2.513
854T2	D1	Deciduous	20	43	2	4.65	2.68	217.7	2.577
854T3	D1	Deciduous	20	43	5	11.63	3.07	191.3	2.924
854T4	D1	Deciduous	20	43	4	9.30	2.96	227.3	1.880
853T1	D1	Deciduous	50	43	3	6.98	2.83	201.9	1.093
853T2	D1	Deciduous	50	43	3	6.98	2.83	111	1.287
853T3	D1	Deciduous	50	43	2	4.65	2.68	172.7	0.472
853T4	D1	Deciduous	50	43	2	4.65	2.68	167.3	4.667
852T1	D1	Deciduous	100	43	1	2.33	2.51	201.1	8.093
852T2	D1	Deciduous	100	43	1	2.33	2.51	174.2	6.977
852T3	D1	Deciduous	100	43	2	4.65	2.68	283.6	7.957
852T4	D1	Deciduous	100	43	3	6.98	2.83	271.8	8.742
946T1	D2	Deciduous	0	38	5	13.16	3.14	258.2	1.679
946T2	D2	Deciduous	0	38	0	0	2.30	273.1	3.736
946T3	D2	Deciduous	0	38	0	0	2.30	224.9	3.444
946T4	D2	Deciduous	0	38	3	7.89	2.88	291.6	3.567
949T1	D2	Deciduous	20	38	2	5.26	2.73	597.9	1.778
949T2	D2	Deciduous	20	38	3	7.89	2.88	658.9	1.779
949T3	D2	Deciduous	20	38	1	2.63	2.54	777	2.357
949T4	D2	Deciduous	20	38	0	0.00	2.30	785	0.892
947T1	D2	Deciduous	50	38	2	5.26	2.73	453.8	2.277
947T2	D2	Deciduous	50	38	1	2.63	2.54	475.3	4.017
947T3	D2	Deciduous	50	38	0	0	2.30	460.9	2.725
947T4	D2	Deciduous	50	38	4	10.53	3.02	556.7	0.871
948T1	D2	Deciduous	100	38	4	10.53	3.02	961.2	3.466
948T2	D2	Deciduous	100	38	0	0	2.30	866.2	4.041
948T3	D2	Deciduous	100	38	1	2.63	2.54	922.6	3.989
948T4	D2	Deciduous	100	38	0	0	2.30	852.8	4.306
918T1	C1	Conifer	0	40	3	7.50	2.86	351.3	1.554
918T2	C1	Conifer	0	40	0	0	2.30	248.6	2.684

Pitfall Array	Study Site	Forest Type	Retention Level	Trap Nights	Adult Count	Adult CPUE	Ln(CPUE)	Breeding Distance (m)	DTW (8 ha)
918T3	C1	Conifer	0	40	2	5.00	2.71	428.6	2.492
918T4	C1	Conifer	0	40	2	5.00	2.71	304	0.638
919T1	C1	Conifer	20	40	2	5.00	2.71	484.1	0.108
919T2	C1	Conifer	20	40	6	15.00	3.22	545.9	0.221
919T3	C1	Conifer	20	40	2	5.00	2.71	622.3	1.095
919T4	C1	Conifer	20	40	0	0	2.30	555.7	0.165
920T1	C1	Conifer	50	43	3	6.98	2.83	183.1	1.238
920T2	C1	Conifer	50	43	4	9.30	2.96	171.9	1.337
920T3	C1	Conifer	50	43	8	18.60	3.35	243.3	1.507
920T4	C1	Conifer	50	43	2	4.65	2.68	186.2	1.598
922T1	C1	Conifer	100	43	4	9.30	2.96	168.2	0.828
922T2	C1	Conifer	100	43	5	11.63	3.07	164.3	0.165
922T3	C1	Conifer	100	43	2	4.65	2.68	270.9	0.259
922T4	C1	Conifer	100	43	3	6.98	2.83	184	0.309
932T1	C2	Conifer	0	40	5	12.50	3.11	581.3	0.772
932T2	C2	Conifer	0	40	3	7.50	2.86	586.9	0.040
932T3	C2	Conifer	0	40	3	7.50	2.86	491.6	0.216
932T4	C2	Conifer	0	40	1	2.50	2.53	431.6	0.352
933T1	C2	Conifer	20	40	3	7.50	2.86	173.1	0.157
933T2	C2	Conifer	20	40	1	2.50	2.53	202.4	0.294
933T3	C2	Conifer	20	40	3	7.50	2.86	325.1	1.517
933T4	C2	Conifer	20	40	3	7.50	2.86	434.3	0.139
929T1	C2	Conifer	50	40	4	10.00	3.00	418.6	0.220
929T2	C2	Conifer	50	40	3	7.50	2.86	540.1	0.515
929T3	C2	Conifer	50	40	2	5.00	2.71	418.2	0.252
929T4	C2	Conifer	50	40	8	20.00	3.40	463.4	0.663
930T1	C2	Conifer	100	40	10	25.00	3.56	296.6	1.224
930T2	C2	Conifer	100	40	1	2.50	2.53	401.3	1.071
930T3	C2	Conifer	100	40	3	7.50	2.86	503.4	1.419
930T4	C2	Conifer	100	40	5	12.50	3.11	580.9	1.481

Table A2-7. Results of GLMMs comparing 7 different Flow-Initiation Threshold (FIT) values for Depth-to-Water on adult wood frog capture rates across 4 study sites at EMEND in 2015. Captures were converted to "Catch per Unit Effort "(CPUE) [(total adult captures at array/ # of trap nights) * 100] and used as the final response variable. Individual pitfall arrays at each study site acted as independent units of observation. CPUE values were Ln-transformed to meet regression assumptions of normality and equal variance. DF = Degrees of Freedom; LogLik = Log Likelihood Ratio; AICc = Akaike Information Criteria corrected for Small Sample Size; ΔAIC_c = Delta AIC_c; w_i = Akaike Weight.

Season	**DTW Model**	**DF**	**logLik**	**AICc**	**ΔAICc**	w_i
Early	DTW 0.5	4	-22.421	53.521	0	0.232
	NULL	3	-23.890	54.180	0.659	0.167
	DTW 16	4	-22.840	54.358	0.837	0.153
	DTW 1	4	-23.195	55.068	1.547	0.107
	DTW 8	4	-23.213	55.104	1.584	0.105
	DTW 2	4	-23.326	55.329	1.809	0.094
	DTW 4	4	-23.501	55.681	2.160	0.079
	DTW 12	4	-23.715	56.109	2.588	0.064
Late	DTW 8	4	-6.194	21.066	0	0.315
	DTW 4	4	-6.810	22.299	1.233	0.170
	DTW 0.5	4	-7.062	22.803	1.736	0.132
	DTW 12	4	-7.346	23.370	2.304	0.099
	NULL	3	-8.496	23.391	2.325	0.098
	DTW 2	4	-7.548	23.774	2.708	0.081
	DTW 16	4	-7.854	24.385	3.319	0.060
	DTW 1	4	-8.161	25.000	3.933	0.044

Table A2-8. Results of initial GLMMs explaining early season adult wood frog capture rates at 4 study sites sampled at EMEND in 2015. Captures were converted to “Catch per Unit Effort “(CPUE) [(total adult captures at array/ # of trap nights) * 100] and used as the final response variable. Individual pitfall arrays within each study site acted as independent units of observation. CPUE values were Ln-transformed to meet assumptions of normality and equal variance.

Model	**Predictor**	**Coefficient Estimate**	**Standard Error**	**t-value**	**p-value**
Retention	Retention	0.001	0.001	0.600	0.550
Forest	Forest	-0.040	0.152	-0.263	0.794
Moisture	Moisture	-0.057	0.049	-1.17	0.245
Breeding	Breeding	0.011	0.052	0.220	0.830
Retention*Forest	Retention	0.001	0.002	0.791	
	Forest	0.009	0.180	0.052	
	Retention*Forest	-0.001	0.002	-0.519	0.875
Retention*Moisture	Retention	0.001	0.001	1.19	
	Moisture	-0.186	0.114	-1.63	
	Retention *Moisture	0.001	0.001	1.02	0.289
Forest*Moisture	Forest	0.096	0.180	0.536	
	Moisture	-0.183	0.173	-1.057	
	Forest*Moisture	0.134	0.182	0.739	0.590
Breeding*Moisture	Breeding	0.015	0.053	0.280	
	Moisture	-0.060	0.052	-1.160	
	Breeding*Moisture	-0.008	0.054	-0.150	0.696
Forest*Breeding	Forest	-0.042	0.130	-0.320	
	Breeding	0.096	0.092	1.040	
	Forest*Breeding	-0.125	0.109	-1.140	0.761
Retention*Breeding	Retention	0.001	0.001	0.590	
	Breeding	0.032	0.082	0.400	
	Retention*Breeding	-0.0004	0.001	-0.420	0.909

Table A2-9. Results of initial GLMMs explaining late season adult wood frog capture rates at 4 study sites sampled at EMEND in 2015. Captures were converted to "Catch per Unit Effort "(CPUE) [(total adult captures at array/ # of trap nights) * 100] and used as the final response variable. Individual pitfall arrays within each study area acted as independent units of observation. CPUE values were Ln-transformed to meet assumptions with normality and equal variance. P-values in bold indicate statistical significance of a predictor at α = 0.05.

Model	Predictor	Coefficient Estimate	Standard Error	t-value	p-value
Retention	Retention	0.001	0.001	0.640	0.522
Forest	Forest	-0.177	0.067	-2.660	**0.031**
Moisture	Moisture	-0.084	0.035	-2.420	**0.032**
Breeding	Breeding	-0.033	0.039	-0.850	0.407
Retention*Forest	Retention	0.002	0.001	1.960	
	Forest	0.025	0.097	-0.260	
	Retention*Forest	-0.004	0.002	-2.100	**0.025**
Retention*Moisture	Retention	0.002	0.001	1.680	
	Moisture	-0.140	0.081	-1.730	
	Retention*Moisture	0.0004	0.001	0.440	0.058
Forest*Moisture	Forest	-0.126	0.105	-1.199	
	Moisture	-0.029	0.133	-0.222	
	Forest*Moisture	-0.027	0.140	-0.196	0.093
Breeding*Moisture	Breeding	-0.036	0.035	-1.030	
	Moisture	-0.095	0.035	-2.730	
	Breeding*Moisture	-0.022	0.041	-0.520	0.095
Forest*Breeding	Forest	-0.176	0.066	-2.670	
	Breeding	0.006	0.068	0.080	
	Forest*Breeding	0.006	0.068	0.080	0.095
Retention*Breeding	Retention	0.001	0.001	0.830	
	Breeding	-0.008	0.063	-0.030	
	Retention*Breeding	-0.001	0.001	-0.750	0.604

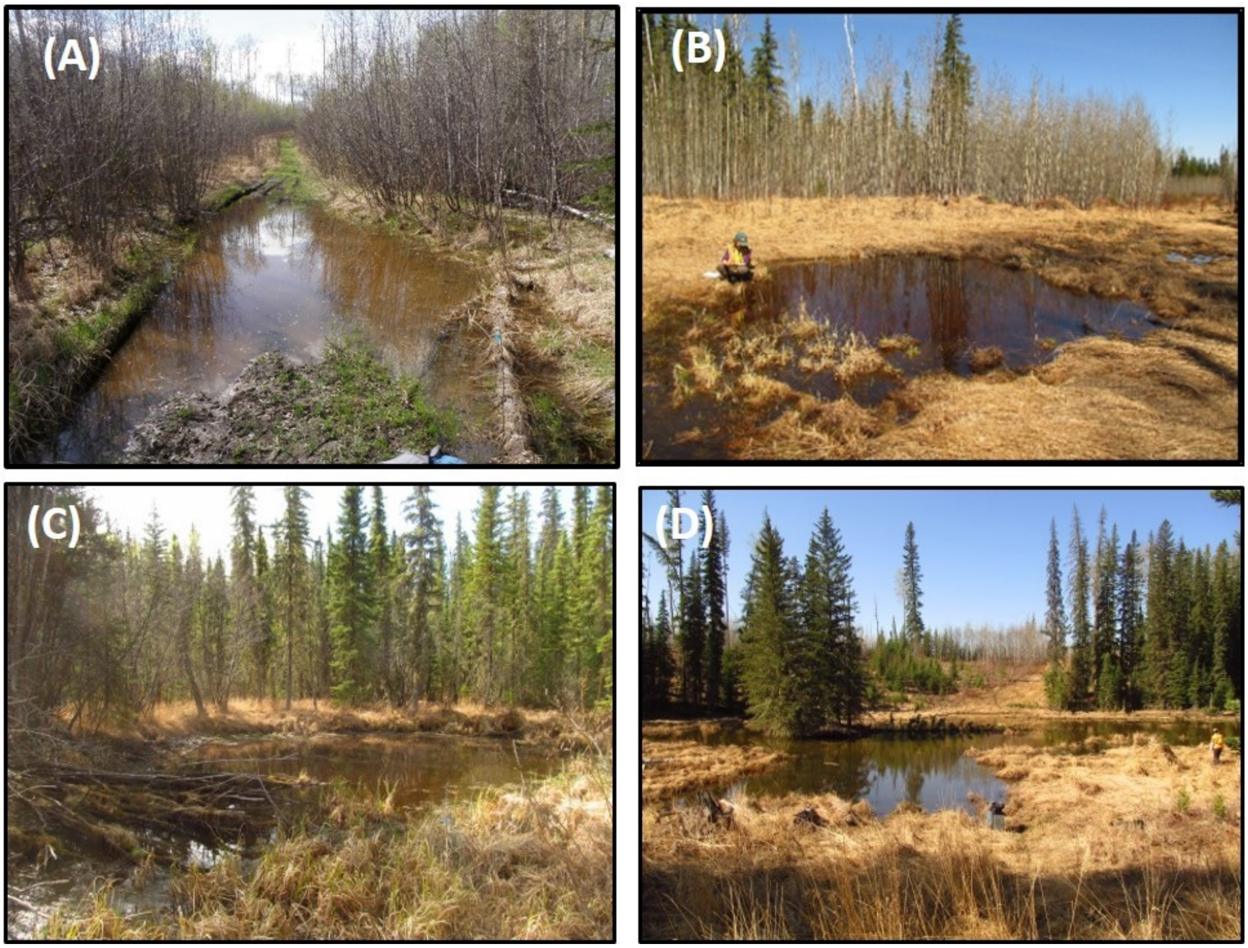

Figure A2-1. Variation in breeding habitats across 4 terrestrial study sites at EMEND (A) Anthropogenic [ATV ruts] – EA53; Study Site D1, (B) Ephemeral Wetland - I1; Study Site D2, (C) Permanent Wetland [HP1 – Study Site C2, (D) Permanent Wetland [Beaver Pond] – B920; Study Site C1.

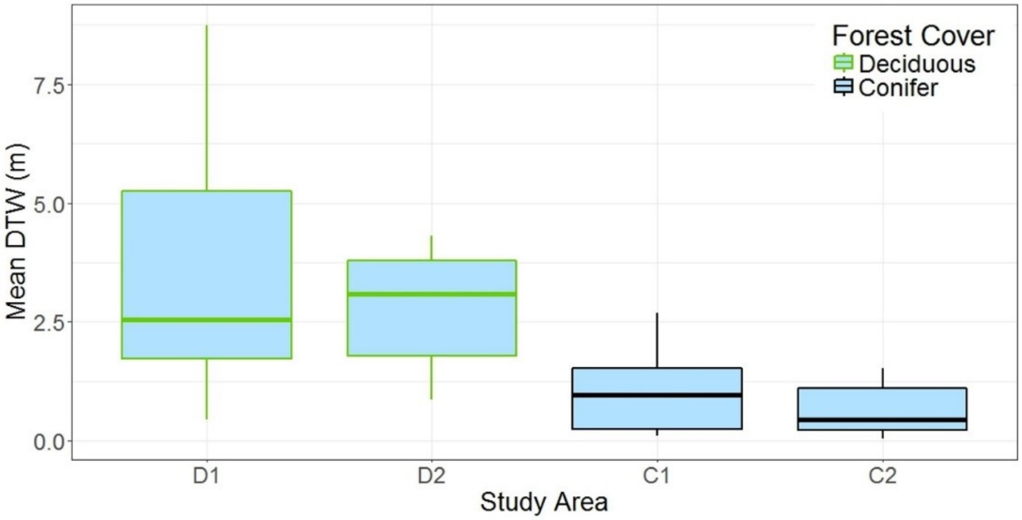

Figure A2-2. Comparison of predicted moisture among 4 study sites sampled at EMEND in 2015. Soil moisture was estimated based on the Depth-to-Water (DTW) obtained from the Wet Area Mapping (WAM) model. Shown are mean Depth-to-Water (DTW) among 4 study sites sampled for wood frogs at EMEND in 2015. DTW describes the predicted distance to the water table and so lower values indicate greater predicted wetness.

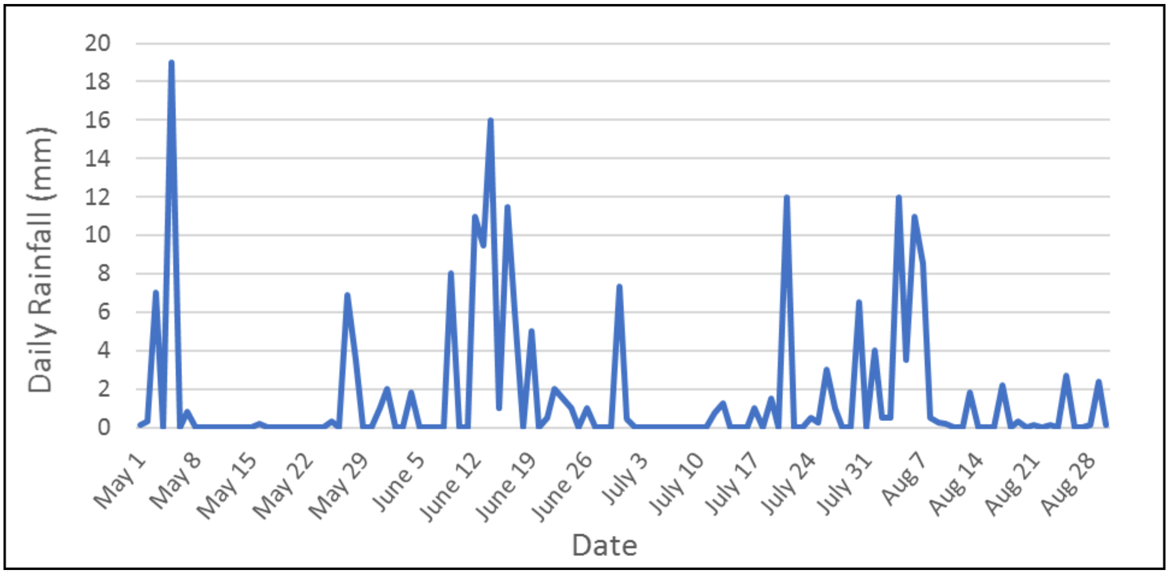

Figure A2-3. Daily rainfall for the 2015 study period (May 1 – August 31). Daily rainfall data were obtained from a single rain gauge placed approximately central to study area (EMEND "Old Camp" parking location - UTM Zone 11V; 417846, 6289708).

Chapter 3 - Influence of wetland size and forest canopy on hydroperiod and tadpole performance in small ephemeral wetlands

3.1 - Introduction

Complex life cycles involve a transition between distinct life stages that allows species to utilize resources in different environments (Wilbur and Collins, 1973; Wilbur, 1980). Many aquatic-breeding amphibians have complex, multi-stage life histories that necessitate the use of both aquatic and terrestrial habitat during different parts of their life cycle (Semlitsch, 2000). For amphibians occurring in Alberta, successful reproduction is dependent on aquatic habitat. Adults lay eggs in freshwater, where they hatch into aquatic larvae which grow, develop, and metamorphose into terrestrial juveniles. Two of the primary determinants of amphibian population success are the number and quality of larvae completing metamorphosis (Semlitsch, 2000). Regulation of amphibian populations therefore occurs, in part, at the aquatic larval stage (Altwegg, 2003; Berven, 2009; Vonesh and De la Cruz, 2002). Given the necessity of aquatic habitat for larval development (Blomquist and Hunter, 2010), it is important to understand the effects of land management activities on aquatic breeding habitats to ensure persistence of local amphibian populations.

Ephemeral wetlands, also called vernal pools, are small, temporary wetlands characterized by seasonal cycles of filling and drying (Burne and Griffin, 2005; Colburn, 2004; Zedler, 2003). Depending on the region, they typically fill with snowmelt, rainfall, or groundwater in the spring or fall, then dry in later spring or summer (Calhoun et al., 2003; DiMauro and Hunter, 2002). Ephemeral wetlands are typically isolated from other wetlands and lack permanent inlets or outlets (Burne and Griffin, 2005; DiMauro and Hunter, 2002). They vary considerably in size, vegetation, length of inundation, and connection with other wetlands (Burne and Griffin, 2005; Tiner, 2003; Zedler, 2003). Ephemeral wetlands support unique biological communities whose species are adapted to their temporary hydrology (De Meester et al., 2005; Tiner, 2003; Zedler, 2003). Further, annual drying prevents establishment of many aquatic predators, most notably fish, making ephemeral wetlands ideal breeding habitat for many amphibian species (Gibbs, 1993; Semlitsch and Bodie, 1998).

Hydroperiod – the length of time a wetland retains surface water – is a key determinant of amphibian reproductive success (Babbitt et al., 2003; Herrmann et al., 2005; Skelly et al., 1999; Snodgrass et al., 2000), influencing both larval development (Halverson et al., 2003; Skelly et al., 2002) and production of juveniles (Karraker and Gibbs, 2009). Amphibian larvae have a limited time to complete development, undergo metamorphosis, and emerge from the wetland before it dries. As wetlands dry, amphibian larvae must either remain in the aquatic environment to maximize growth prior to metamorphosis (risking mortality by desiccation) or avoid drying events by completing metamorphosis at a smaller size (Skelly, 1996; Wilbur, 1987). Provided a wetland retains water, faster growth, combined with greater time in the aquatic environment, enables tadpoles to metamorphose at a larger body size (Wilbur and Collins, 1973) which has positive implications to fitness of juvenile amphibians throughout their lives. Individuals that metamorphose at larger body size experience greater survival, and are typically younger and larger at the time of first reproduction (Berven, 1990; Semlitsch et al., 1988). Faster development and earlier metamorphosis may allow more time for juveniles to accrue resources on land and increase body mass prior to overwintering, provided growing conditions in the terrestrial environment (e.g. food resource availability) are more favorable relative to the wetland.

The hydrologic cycles of ephemeral wetlands are highly dynamic, with hydroperiod often varying dramatically among years depending on a number of factors (Calhoun et al., 2003; ESRD, 2015). Although the hydrology of small wetlands is not completely understood (Kirkman et al., 1999), when isolated from other water bodies, filling and drying is regulated primarily by a balance between precipitation, groundwater exchange, and evaporation rates (Brooks and Hayashi, 2002). Wetland size is another important factor influencing hydroperiod (Brooks and Hayashi, 2002) and is commonly used as management criterion for assigning protective status to water bodies (Babbitt, 2005; Snodgrass et al., 2000; Zedler, 2003). Physical dimensions, such as surface area and depth, dictate the volume of water a wetland can hold at capacity. In southern Maine, USA, ephemeral wetlands with shallower basins and less surface area, dried earlier than larger, deeper wetlands (Brooks and Hayashi, 2002). Variation in annual precipitation is also an important factor affecting hydroperiod (Brooks, 2004; Semlitsch et al., 1996); years with little rainfall can result in extensive larval mortality or complete reproductive failure, whereas high rainfall years can lead to very high metamorph production (Berven, 1990).

The amount of forest canopy surrounding wetlands can alter conditions important for growth and development of amphibian larvae. Surrounding vegetation alters the light environment experienced by aquatic organisms (Halverson et al., 2003) with closed-canopy wetlands receiving less solar radiation, resulting in lower water temperatures relative to open-canopy wetlands (Halverson et al., 2003; Schiesari, 2006; Skelly et al., 2002; Werner and Glennemeier, 1999). Growth and development rates of amphibian larvae are slower at lower ambient temperatures (Berven and Gill, 1983; Newman, 1998), but temperatures beyond a species' thermal optima may adversely impact growth, development, and mobility (Duarte et al., 2012). Provided adequate food availability, the effects temperature on tadpole performance are asymmetric, with development rates showing a greater proportional reduction in response to lower temperature compared to growth rates (Smith-Gill and Berven, 1979). Density of conspecifics is another factor that may affect tadpole performance in the aquatic environment. Studies have shown that larval growth and development are negatively related with larval density (Wilbur, 1976; Smith, 1983; Petranka, 1989) with increases in larval density resulting in slower individual growth and development, as well as a reduction in the number of individuals completing metamorphosis (Semlitsch, 2000).

Canopy-mediated light conditions also affect aquatic macrophyte growth and primary productivity. Periphyton - a biofilm of algae, bacteria, and fungi - constitutes an important food source for tadpoles that can limit growth and development (Kupferberg et al., 1994; Skelly et al., 2002). Wetlands with open-canopy environments are characterized by greater periphyton production and aquatic plant diversity (Schiesari, 2006; Skelly et al., 2002). Greater food resources in open-canopy pools may result in faster larval growth (Newman, 1998; Skelly et al., 2002) whereas slower growth in closed-canopy pools may increase the probability of larval mortality due to drying events (DiMauro and Hunter, Jr., 2002; Skelly, 1995). The effects of canopy-mediated light regimes are expected to be especially pronounced in small breeding wetlands, where canopy vegetation may cover the entire basin (Halverson et al., 2003). In addition, trees and other surrounding vegetation may reduce evaporation by blocking solar radiation and wind, potentially extending wetland hydroperiod.

Some amphibian species are considered open-canopy specialists and experience poor performance and survivorship in closed-canopy wetlands (Skelly et al., 1999). Wood frog tadpoles, however, appear to be tolerant of shaded wetlands, with research in eastern North America demonstrating that the species can reproduce in both open- and closed-canopy ponds (Schiesari, 2006; Skelly et al., 2005, 2002; Werner and Glennemeier, 1999). Previous studies have found that growth of wood frog tadpoles is more rapid in open-canopy sites (Skelly et al., 2002; Werner and Glennemeier, 1999) with metamorphs tending to emerge at earlier dates and smaller sizes in ephemeral wetlands relative to permanent ponds (DiMauro and Hunter, Jr., 2002; Karraker and Gibbs, 2009). Timber harvesting and vegetation removal adjacent to ephemeral breeding wetlands may therefore affect reproductive success of wood frogs and other amphibians by altering within-pool conditions, as well as reducing the time available for development to metamorphosis. Given that shorter hydroperiods may result in increased mortality and/or reduced size and fitness of emerging metamorphs, understanding the factors affecting wetland hydroperiod is essential for protection and management of ephemeral breeding habitats for amphibians.

Small ephemeral wetlands are a common feature in Alberta's boreal mixedwood, and are important features for amphibians (Eaton, 2004; Okonkwo, 2011). Despite their prevalence in the boreal mixedwood, wetlands smaller than 4 ha have no legislated buffer zone requirements during harvest operations (ESRD, 2016). However, some forest companies voluntarily retain some forest vegetation around the perimeter of ephemeral wetlands as part of their timber retention strategy to help protect wetlands from sun and wind, potentially extending hydroperiods (DMI, 2016; Jim Witiw, *personal communication*). This strategy is also intended to provide suitable riparian and adjacent upland habitat for resident adult and juvenile amphibians.

The effects of surrounding forest canopy cover on the breeding suitability of ephemeral wetlands remains largely unstudied in Alberta's boreal mixedwood. Specifically, it is unknown how the amount of surrounding canopy, in concert with wetland size, influences wetland hydroperiod and performance of larval amphibians. The objectives of this study were to (1) investigate the influence of wetland size and forest canopy on the permanence (hydroperiod) of small ephemeral wetlands and (2) evaluate tadpole performance (growth and development) in small ephemeral wetlands of various wetland sizes and forest canopy conditions. To address these questions, I sampled populations of wood frog tadpoles in a representative set of ephemeral wetlands in the boreal mixedwood forest from early spring (egg deposition) until metamorphosis or until wetlands dried, and measured tadpole growth and development over regular sampling intervals. I measured hydroperiod by documenting the drying date of each wetland and determined if tadpoles successfully completed metamorphosis. Pool size (surface area and maximum depth) as well a percent canopy cover, were measured at each wetland to evaluate the relationship between these variables and hydroperiod. In wetlands that did not dry prematurely, I also measured the time to, and size at metamorphosis of emerging young-of-the-year (YOY) froglets. In addition, within each wetland I measured physical, chemical, and biological variables shown in previous studies to be important for tadpole growth and development.

Predictions

I predicted that larval performance in ephemeral wetlands would be mediated by forest canopy cover, wetland size (volume), and tadpole density. Specifically, I predicted that growth and development of wood frog tadpoles would be slower, and that tadpoles would reach metamorphosis at later dates, in wetlands with greater surrounding forest canopy cover. Shading provided by trees and other vegetation should result in both lower water temperatures and lower primary productivity (e.g. algal food resources for tadpoles) limiting growth and development. I also predicted the effects of canopy cover would depend on wetland size; canopy effects should be more negative on growth and development in smaller wetlands since surrounding trees and riparian vegetation would be able to cover a greater percentage of smaller wetland basins, resulting in relatively higher levels of shading. Since tadpole growth is also strongly density-dependant (Petranka, 1989; Smith, 1983; Wilbur, 1976), I expected tadpole growth and development to be reduced in wetlands with greater tadpole density. I also expected density dependence to be strongest in smaller wetlands since tadpoles in smaller and shallower wetlands would experience greater density-dependant resource limitation, particularly as wetlands dried and water volume decreased.

With respect to hydroperiod, I predicted both canopy cover and wetland size would be related to wetland drying date. Specifically, I predicted that wetlands with more forest canopy cover and greater maximum depth would have longer hydroperiods than shallower wetlands with less forest canopy cover. Wetlands with deeper basins (greater maximum depth) should have a greater water holding capacity than shallower wetlands and thus take longer to dry. Further, greater surrounding forest canopy cover should reduce the evaporative effects of solar radiation and wind on wetland surface water, resulting in longer hydroperiods.

By determining the size and canopy conditions best suited for pool permanence and tadpole performance, information from this study can be used to guide forest managers in protecting and managing ephemeral breeding wetlands during harvest operations and thus help maintain local amphibian populations in managed forests.

3.2 – Methods

Selection of study wetlands

A total of 15 breeding sites (hereafter, wetlands) were selected for sampling out of 41 candidate wetlands in the study area. Wetlands were identified in spring and summer of 2014 and 2015 using ground searches and were located within the EMEND study area (Volney et al., 1999), as well as the surrounding area (Figure 3-1). Wood frog breeding in wetlands was confirmed by the presence of egg masses or tadpoles. Wetlands were selected that encompassed a variation in wetland size (depth and surface area) and amount (percentage) of surrounding forest canopy cover. Wetlands were excluded from study if they were (1) unoccupied (no wood frog breeding) and/or (2) deemed too difficult to access for regular sampling.

Wetland classification

Wetlands were defined using the Alberta Wetland Classification System (ESRD, 2015). Under this system, wetlands are classified as mineral wetlands or peatlands depending on whether benthic organic accumulation is greater or less than 40 cm. All wetlands were classified as *Seasonal–Shallow Open Water Mineral Wetlands* based on having a maximum depth $\leq$ 2m and benthic organic accumulation < 40cm. They were further classified as *Form A Wetlands* based on the presence of submersed aquatic vegetation in the deepest part of the basin that cover > 25% of the total area (ESRD, 2015). Benthic substrates consisted of clay (grey luvisols) and/or relatively decomposed organic peat deposits. A single site (EMD7) was an old harvest landing where compacted clay created a shallow pool supporting submersed aquatic vegetation; this pool functioned as a breeding site for wood frogs. Human-made pools are common in timber harvest blocks in the area and are often used by amphibians for breeding (M. Robinson, *personal observation*). Pool permanency for all wetlands was defined as *seasonal* where surface water is present for the majority of the growing season, but usually dry by the end of the summer (ESRD, 2015).

Dominant forest cover and wetland vegetation

Dominant forest cover was assessed visually in the field and defined by the forest vegetation type within 10 m of each wetland's shore. Forest cover type was placed in one of 4 categories: (1) Mature Deciduous (≥ 70% mature deciduous trees), (2) Mature Conifer (≥ 70% mature conifer trees), (3) Regeneration (10-15-year old saplings and/or woody shrubs dominate), or (4) Open (few to no trees or woody shrubs surrounding the wetland). Although several of these vegetation types may have been present in the area surrounding a wetland, dominant cover was based on the forest vegetation type providing the most cover (i.e. shading) around a wetland's basin. Mature tree species included trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*). In sites with few to no mature trees, vegetative cover was provided by saplings of the above species, as well as woody shrubs, predominantly Willow (*Salix* spp*.)* and/or Alder (*Alnus* spp*.)*.

The vegetation community (emergent and submergent vegetation) of each wetland was also assessed visually in the field. Dominant emergent vegetation included cattails (*Typha* spp.), sedges (*Carex* spp.), and horsetails (*Equisetum* spp.). Dominant submergent vegetation usually consisted of common yellow crowfoot (*Ranunculus* spp.).

Wetland size (depth and surface area)

Maximum pool depth was measured at the deepest potion of each wetland (R. . F. Baldwin et al., 2006) during the first surveys that occurred in May 2015. This location was marked with a stake and flagging tape with depth measured at the same location in every survey to monitor changes in water levels. Wetland boundaries were flagged in early May during high water period, and were defined by the extent of hydric soils and wetland vegetation (Pillsbury and Miller, 2008).

Most study wetlands were approximately elliptical in shape, therefore pool length and width were measured with a measuring tape and the surface area estimated based on the area of an ellipse (Calhoun et al., 2003).

Percent canopy cover

Overstory canopy cover was estimated with a spherical densiometer (in August 2015 during leaf out) at 5 locations within the pool basin; these included the 4 cardinal directions from the wetland center at a distance of 3 m from the shoreline, and at the wetland center (Skelly et al., 2002). The 5 measurements were averaged with wetlands thereafter classified as open-canopy (< 40% canopy cover) or closed-canopy (> 60% canopy cover) (Werner and Glennemeier, 1999). Classification of study wetlands, including vegetation, size, and canopy cover, are summarized in Table 3-1.

Wetland drying (hydroperiod)

Wetland depth was measured during every survey to monitor changes in depth and to define the wetland hydroperiod. If a wetland was close to drying (maximum depth 5-10 cm), wetland visits were more frequent (every 2-3 d) to ensure an accurate drying date. Wetland drying dates were defined as the day a wetland no longer contained surface water. Hydroperiod was defined as the number of days a wetland contained standing water measured from May 1, 2015. If a wetland contained water for the duration of the season (did not dry) it was assigned a hydroperiod of the full growing season of 122 days (May 1 – August 31).

Wetland physiochemistry

Water temperature (°C), pH, and conductivity (mS) were measured in every survey session using a multi-parameter probe (Hanna Instruments®, USA). Water chemistry was measured (1) during tadpole and egg mass surveys (2) during periphyton collection (see below), and (3) on independent site visits where only physiochemistry and depth were measured. During each visit, measurements were taken at 4 permanent sample locations around the wetland perimeter (one at each cardinal direction) and averaged. Measurements were taken 1-3 m from shore in at least 10 cm of water, with the probe approximately 5 cm below the water surface. Permanent sample locations were adjusted if necessary to coincide with receding water levels as wetlands dried.

Physiochemistry measurements were taken until young-of-the-year (YOY) froglets (hereafter, metamorphs) began to emerge or until wetlands had insufficient water to allow readings (< 10 cm). For physiochemistry sampling, I attempted to visit each study wetland an equal number of times and to restrict sampling times to between 12:00 – 17:00 to standardize water temperature for time of day among wetlands. Due to differences in drying date, shorter hydroperiod wetlands had fewer sampling dates than those with longer hydroperiods. Not all physiochemistry sample data were used in subsequent analyses (see *Statistical analysis –Physiochemistry and chlorophyll-a*).

Primary productivity – periphyton assays

Periphyton growth was assayed in a sub-sample of breeding wetlands (n=7) as an index of primary productivity and potential food resources for tadpoles. Six representative wetlands (2 open- and 4 closed-canopy) were selected for sampling based on surface area and depth; wetlands chosen for periphyton assays were larger and deeper relative to other wetlands. This increased likelihood that water would persist long enough to maintain meter emersion (see below).

Periphyton was sampled using “periphyton meters” consisting of a cylindrical acrylic rod (5 cm long, 1 cm in diameter) suspended from a float using fishing line (Figure 3-2). Rods were enclosed in galvanized steel caging (mesh size: 1mm^2) to prevent grazing by macro-invertebrates and tadpoles. Meters were deployed at wetlands in the shallow-water (littoral) zone in at least 30 cm of water for two, 2-wk periods in early June (June 2 – June 17) and late June (June 17 – July 2). Sampling periods roughly coincided with timing of the 2nd and 3rd tadpole surveys (see *Tadpole Surveys*). Meters (4 per site) were placed at the north, south, east, and west corners of the wetland approximately 3 m from shore, in at least 30 cm of water, and away from dense aquatic vegetation to avoid competition for light. Following the incubation period (i.e. period during which rods were in place in the wetland), rods were carefully removed from floats and replaced with new rods. Algae-covered rods were then placed in 50 mL centrifuge tubes (Corning®), covered in aluminum foil to protect the samples from light, and placed in a cooler on ice. Within 6 h of collection, periphyton samples were frozen at -20° C until processing.

Periphyton processing (chlorophyll-a)

Periphyton samples were analyzed for chlorophyll-a using direct extraction with buffered ethanol, followed by measuring light absorbance with a spectrophotometer (Steinman et al., 2007). Chlorophyll-a gives a measure for the total amount of autotrophic material in a sample (Biggs and Kilroy, 2000). To perform extraction, 20 mL of 90% buffered ethanol (1 g magnesium carbonate + 950 mL 95% ethanol + 50 mL deionized water) was added directly to rods in original centrifuge tubes (so rod was just covered). Samples were placed in a water bath of 78° C (the boiling point of ethanol) for 5 min. Samples were then placed in a dark refrigerator at 4° C to extract overnight (8 h). The following morning, an aliquot of each sample (2 mL) was read on a spectrophotometer at 665 nm (turbidity reading) and then at 750 nm (chlorophyll-a reading). Following initial readings, each aliquot was treated with 0.1 M hydrochloric acid (0.06 mL per aliquot) and allowed to sit for 5 minutes. The samples were then re-read at 665 and 750 nm on the spectrophotometer. Acidification with HCl degrades chlorophyll-a leaving only non-photosynthetic contents so the difference in pre- and post-acid readings gives an accurate measure of the photosynthetic material in the sample (Steinman et al., 2007). Chlorophyll-a concentration was calculated using the formula: 29.6 (constant) x (E665 pre-acid - E665 post-acid)*extract volume*(total sample volume/subsample volume)/area sampled (cm^2 or m^2)* 1 cm and expressed as $\mu g/cm^2$.

Precipitation

Annual precipitation data for a 10 y period (2007 to 2016) were obtained from the Alberta Climate Information Service's (ACIS) historical weather station viewer (Alberta Agriculture and Forestry, 2016). Data for Alberta township T089R03W6 (location of the wetlands) was estimated by an interpolation procedure using nearby weather stations (Alberta Agriculture and Forestry, 2016). These data were used to calculate average precipitation and compare previous year's precipitation with that of the sampling year (2015). A single rain gauge was installed in a central location of the study area and checked daily to obtain total daily precipitation.

Wood frog sampling

Egg mass surveys

Egg mass surveys were conducted at each wetland in early May to assess reproductive effort and timing of breeding (Baldwin et al., 2006). During surveys, 2 observers waded around the wetland and visually identified masses. The 2 observers started at the same location and searched in opposite directions around the perimeter of the pool until they met. After meeting, observers searched the opposing member's side of the wetland to ensure masses had not been missed. Masses were marked with flagging tape to avoid recounting during subsequent surveys. Search time for egg mass counts was commensurate with wetland size. After the wetland had been searched, egg masses were counted by visual inspection or feeling beneath the water surface if masses were layered (Baldwin et al., 2006). I estimated egg mass counts at all sites to avoid inconsistencies due to different observer experience levels. Two egg mass counts were conducted at each wetland between May 6 and May 21, 2015 (Table 3-2); this ensured masses from later breeding individuals were not missed. Egg mass counts were not possible at 3 wetlands (P217, P208, and WSRW01) as these sites were not identified until after May 21; by this date most eggs had hatched.

Tadpole surveys

To monitor tadpole growth and development, tadpole surveys were conducted at regular intervals at 13 of the 15 wetlands (Table A3-1). Tadpole surveys began in late-May, about two weeks after eggs had hatched. During initial surveys, tadpoles were in an early free-swimming stage (field stage 1; see Table A3-2 for description of stages). Tadpoles were sampled using timed-continuous dipnet surveys (Halverson et al., 2003). Two observers systematically waded around the wetland, dipnetting continuously through all available microhabitats until a sufficient sample of tadpoles (target 20 to 40) were captured (range: 10 - 39; $\mu = 25.7 \pm 7.1$). After capture, tadpoles were held in water-filled plastic containers in the shade until surveys were complete. Once a complete sample was obtained, individual photographs were taken of each tadpole to measure body size and assess developmental stage. Individual tadpoles were placed in a transparent rectangular container (5 x 10 x 4 cm) with a 4-cm section of ruler for scale. The container was placed on a level surface and 1-3 dorsal photographs were taken from a set distance (10 cm) with a Cannon Powershot SX150® (Figure 3-3). Container edges were used as a reference and kept in line with the camera's view finder to keep photo distance consistent. Additionally, 1-3 lateral photographs were taken of each tadpole, focusing on the junction of the body and tail, to determine developmental stage (see *Developmental stage*). Processing of an individual tadpole usually took one minute or less. Once all tadpoles had been photographed, they were released at the wetland of capture. Tadpole density was estimated for each survey as "catch per unit effort" (number of wood frog tadpoles captured/total time dipnetting/number of observers).

Tadpole surveys were performed until metamorph emergence was complete or until the site dried. Between 1 and 5 tadpole surveys were conducted at each wetland, depending on wetland drying date. Tadpole surveys were also done during metamorph surveys (see below) to assess development of any remaining tadpoles. The number of days between surveys varied, but were usually in range of 10 – 14 d. In a few cases, intervals were longer due to logistical constraints preventing access to some wetlands (i.e. road and trail closures from heavy rain).

Image analysis - tadpole body size

Image analysis was used to measure body size of tadpoles (Davis et al., 2008). Images were processed using the software ImageJ©. A single dorsal image of each tadpole was used to measure 4 size dimensions as defined by Altig (2007): (1) Total Length – tip of snout to end of tail, (2) Body Length - tip of snout to junction of body and tail musculature, (3) Tail Length – Junction of body and tail to tip of tail, and (4) Body Width –width at widest portion of the body (Figure 3-4). Each image was individually calibrated using a line drawn along a set length (10 mm) of the scale ruler in each photograph. Calibration in this manner allowed pixels to be converted to a distance in millimeters.

Developmental stage

Gosner (1960) divides tadpole development into 46 stages. It was not feasible to assign development stage at this precision since many diagnostic features could not be reliably assessed in the field. Tadpoles were instead assigned to 1 of 7 "field identifiable stages" based on morphological features readily visible in lateral photographs (Table A3-2). Field stages included:

Stage 0 (hatchling), Stage 1 (free swimming, no rear limb buds), Stage 2 (free-swimming with rear limb buds), Stage 3 (rear limb buds "paddle-shaped"), Stage 4 (all digits on rear limb developed), Stage 5 (front limb buds present but not emerged), and Stage 6 (one or both front limb buds emerged).

Larval period

At wetlands where at least some larvae reached metamorphosis, larval period was estimated as a proxy for development rate. Larval period was defined as the number of days from May 21 until the date when the first terrestrial metamorphs were observed (emergence start date). May 21 was chosen as the start of the larval period since it coincided with final egg mass surveys and start of tadpole surveys. In addition, visual inspection of masses during final egg mass surveys and of tadpole development during the earliest tadpole surveys in May, confirmed that tadpoles were at early hatchling stages (Field Stage 0; Gosner 21-24) across study wetlands. A single wetland (EMD7) was known to have an earlier hatch date (~ May 10) and so was out of synchrony with other study wetlands (see *Statistical analysis – tadpole growth models*).

Metamorph surveys

To determine the metamorph emergence period, area-constrained visual encounter surveys were conducted at wetlands every 2-4 d once metamorph emergence had begun. Visual encounter surveys were initiated once the first terrestrial metamorph was observed at a wetland. During visual-encounter surveys, two researchers systematically walked around the wetland searching 3 m of the shoreline and 3 m of adjacent water for newly emerged metamorphs. In the case that a breeding pool had nearly dried, the entire basin of the exposed pool was searched. Metamorphs were captured, weighed, and measured (SUL). Emergent vegetation was thoroughly searched, as were any other available cover objects (e.g. woody debris, rocks). Newly emerged metamorphs would often take refuge in aquatic vegetation or other microhabitats, especially if weather conditions were unfavorable for activity (e.g. cool and overcast conditions).

Searches alternated between groups of sites depending on timing of metamorph emergence at different wetlands. I attempted to conduct an equal number of metamorph surveys at all wetlands to ensure standardization of search effort among sites. Due to logistical constraints, it was not possible to conduct intensive searches at one site (I1), although it was possible to confirm emergence at this site through reduced surveys/searches. Of the remaining 6 wetlands which produced metamorphs, 4-5 visual encounter surveys were performed, where metamorphs were captured, weighed, and measured.

Metamorph emergence period was defined as the number of days between the first observation of a terrestrial metamorph at a wetland (Start Emergence Date) to the date metamorphs were no longer found during visual encounter surveys and no tadpoles were captured during simultaneous dipnet sampling of remaining water (End Emergence Date). Metamorphs were defined as fully-formed froglets with tail buds ≤ 1mm (Gosner Stages 45-46) (Gustafson et al., 2015).

Statistical analysis

Physiochemistry and chlorophyll-a

Of the 15 study wetlands sampled, 12 were used to compare physiochemistry; 11 of these wetlands were where tadpole performance was assessed (see *Tadpole Growth Models*). Physiochemistry measurements were divided into 4 sampling periods, approximately coinciding with tadpole survey times: (1) May 22 – May 31, (2) June 12 – June 17, (3) June 21 – June 23, and (4) July 9 – July 11. A single sampling date was selected for each wetland and sampling period. Sample dates were selected that allowed the shortest time intervals (number of days) separating different wetlands within a sampling period. Due to differences in drying dates, the number of open- and closed-canopy wetlands varied in each sampling period. Mean wetland physiochemistry parameters (temperature, pH, conductivity) were compared between open and closed-canopy wetlands for each sampling period using Welsh's t-test tests. Similarly, periphyton productivity (mean chlorophyll-a) was compared between the subset of open and closed-canopy wetlands for which periphyton was sampled using Welsh's t-test.

Relationships between hydroperiod, wetland size, and canopy cover

Quantile regression was used to assess the relative strength of relationships between wetland permanence (hydroperiod) and wetland size and canopy variables. Since hydroperiod (Julian day of pool drying) was not normally distributed, quantile regression was chosen since it makes no assumptions about normality or homogeneity of variance of the dependent variable (Cade and

Noon, 2003). The Julian day of wetland drying was regressed against two wetland size variables (maximum depth and surface area) and against percent canopy cover. The strength of the relationships between hydroperiod and predictor variables was evaluated using pseudo R^2 values.

Tadpole size models

Tadpole body size on a given survey date was used as a proxy for growth. Generalized linear mixed models (GLMMs) with a Gaussian response were used to test which habitat variables had the greatest influence on tadpole body size among wetlands. Average tadpole body length at each wetland and survey date was the response variable. Tadpole body length was chosen due to its use in similar studies (Halverson et al., 2003; Whiting, 2010) and because it was the most reliable body size measurement among tadpoles sampled (e.g. total length was not reliable since tadpoles were occasionally missing potions of their tails). Mean tadpole body length was Ln-transformed to meet model assumptions of normality and homogeneity of variance. All models included Julian day (days since May 1) as a fixed effect to account for date of sampling. Wetland (site) was included as a random effect in all models to account for any unmeasured variation among study wetlands. Wetlands were included in size analysis only if the site persisted long enough to allow for at least 2 tadpole surveys. A total of 11 wetlands were selected for body size analysis. One wetland was excluded (EA9) due to insufficient tadpole surveys and one wetland (EMD 7) was excluded due to asynchronous breeding (oviposition) relative to other wetlands (i.e. eggs were laid, and subsequently hatched, at an earlier date). Final sampling sessions from late in the development period were excluded from analysis when most tadpoles captured were undergoing metamorphosis (Field Stages 5 and 6). As tadpole undergo metamorphosis, they decrease in body size as a result of morphological changes associated with the transition from tadpole to frog (McDiarmid and Altig, 1999). As such, I excluded sampling events that included metamorphosing tadpoles to ensure body size changes were reflective of pre-metamorphosis development stages (Gosner stages 25-39). In addition, the final sampling events for two wetlands (EA1 and EA91) were excluded since tadpoles were sampled during final stages of wetland drying and the reduced water volume had resulted in a marked reduction in growth for each wetland’s tadpole cohort.

A global model was constructed that best explained variation in tadpole body size among study wetlands across survey dates. Inclusion of predictors – percent canopy cover, wetland volume, and tadpole density - as well as their interaction terms, were first examined as univariate GLMMs to assess their individual significance. Significance of individual predictors was determined using log-likelihood ratio tests where candidate models were compared to a null model without the predictor of interest. Models were evaluated as having good fit if they explained significantly more variation in tadpole body size compared to the null model without the predictor term.

3.3 - Results

Wetland drying and hydroperiod

Hydroperiod ranged from 30 to 122 days ($\mu = 77.5 \pm 36.5$; Table 3-3). Of the 15 wetlands, 8 of 15 (53%) dried prior to any animals metamorphosing successfully, resulting in complete tadpole mortality. Hydroperiod among unsuccessful wetlands ranged from 30 to 71 d ($\mu = 47.0 \pm 15.6$).

The remaining 7 wetlands (47%) retained water long enough to allow successful metamorphosis. Hydroperiod among these wetlands ranged from 88 to 122 d ($\mu = 112.3 \pm 13.4$). Two of the longer hydroperiod sites (EA68, P217) were dry by mid-August after completion of metamorph emergence. One closed-canopy wetland, P208, was subject to very low water levels in the second half of July, and the site was completely dry by July 27; tadpole performance (growth and development) was lower at this site compared to open-canopy counterparts. As a result, metamorphs emerged early, and at a smaller body size. The remaining 4 successful wetlands (I1, FP1, FP2, FP3) never dried during surveys, with water retained until the end of August.

Relationships between hydroperiod wetland size and canopy

Maximum water depth was most related to wetland hydroperiod ($R^2 = 0.66$, $p < 0.001$), while wetland surface area and percent canopy cover had comparatively weak relationships with hydroperiod (Figure 3-5). All wetlands, except one (WSRW01) with maximum depths ≥ 50 cm had hydroperiods sufficient for tadpoles to reach metamorphosis prior to drying.

Tadpole Growth and Development

The final model explaining tadpole body size at wetlands included percent canopy, wetland volume, and an interaction between canopy cover and volume (Table 3-4). In the final model, percent canopy cover had a significant effect on average tadpole growth ($p < 0.001$); on a given survey date, tadpoles tended to be larger at wetlands with less surrounding forest canopy. Although wetland volume alone was not significant ($p = 0.67$), there was a significant interaction between canopy cover and volume ($p < 0.001$). Based on the negative interaction coefficient ($ß = -0.082 \pm 0.026$), this indicates that the effect of canopy on body size became stronger (more negative) as wetland volume increased. No other variables or interaction terms were significant in initial models (Table A3-4) and so were not included in the final model.

Among the 7 wetlands with successful metamorphosis, tadpole development was faster in open-canopy wetlands relative to closed-canopy wetlands, as indicated by the length of larval periods Wood frog tadpoles in the 3 open-canopy wetlands (P217, I1, EA68) had shorter larval periods (51, 52, and 54 days) with metamorph emergence occurring about 10 d earlier (start of emergence between July 11 – 14) than in closed-canopy wetlands. At these latter sites (P208, FP1, FP2, and FP3), wood frog tadpoles experienced longer larval periods (range: 60 - 64 days).

Wetland physiochemistry and chlorophyll-a

For all 4 sampling sessions combined, mean water temperature was significantly different ($p = 0.032$) between closed-canopy and open-canopy wetlands. On average, water temperature was 3° C higher in open-canopy wetlands relative to closed-canopy wetlands. When examined individually, differences in water temperature were significant between these wetland types for sampling sessions 1 and 4, but not for sessions 2 or 3 (Table 3-5). For the subset of wetlands sampled for periphyton, mean chlorophyll-a was higher in closed-canopy wetlands compared to open-canopy wetlands, but the difference was not statistically significant for either collection period (Table 3-6). There was no significant difference in pH or conductivity between open- and closed-canopy wetlands.

Metamorph emergence

Heavy riparian and emergent vegetation made locating metamorphs during surveys problematic at some wetlands. Captures were not sufficient to compare metamorph production or body size confidently across the 7 wetlands that saw successful metamorph emergence. See supplemental appendix for metamorph capture data (Table A3-7).

Annual and monthly precipitation

With respect to annual precipitation, 2015 was drier on average relative to last 10 years. Annual precipitation in 2015 was 313.8 mm, more than 100 mm lower than the 10-year average (441.2 ± 84.0 mm) for the study area (Figure 3-6). In terms of seasonal precipitation patterns during the 2015 sampling period (May – August), June had the highest monthly rainfall (85.2 mm), followed by August (50.8 mm) (Table 3-7). In comparison, the months of May and July were much drier with total monthly precipitation of 39.1 and 28.2 mm respectively.

3.4 - Discussion

Hydroperiod, wetland size and canopy Cover

I found that wetland size, but not canopy cover, was related to hydroperiod and that maximum depth had a better relationship with hydroperiod than surface area (Figure 3-5). Of the 7 'successful' wetlands (those retaining water long enough to allow tadpole metamorphosis), all but one (WSRW01), had maximum depths of 50 cm or greater. These results align with previous research from eastern North America that found a relationship between wetland size and hydroperiod. For example, DiMauro and Hunter (2002) found that surface area and depth were among the variables that best explained hydroperiod of natural and anthropogenic temporary wetlands in managed forests of Maine, USA. Similarly, in central Massachusetts, USA, Brooks and Hayashi (2002) found that vernal pools with maximum depths and surface areas greater than 50 cm and 1000 m^2, respectively, had the longest hydroperiods, containing surface water over 80% of times surveyed over a 3-year period. However, the authors of the latter study noted that several pools were large in area but also shallow, and as a result had relatively short hydroperiods. In the current study, surface area and depth were positively related (Figure A3-2).

Generally, wetlands with larger surface areas were also deeper, but this pattern did not always hold. For example, one wetland (I1) had a small surface area (33.7 m^2) but was relatively deep (0.70 m), and another (FP2) had a large surface area (542 m^2) but was relatively shallow (0.55 m). These results suggest that depth may be a more reliable predictor of hydroperiod of ephemeral wetlands than surface area alone.

Contrary to expectations, there was no relationship between hydroperiod and percent canopy cover. Wetlands with greater canopy cover were predicted to have longer hydroperiods based on the assumption that surrounding trees and vegetation would reduce water evaporation by blocking wind and solar radiation. The lack of a canopy-hydroperiod relationship may be due to the small sample size of wetlands (n = 15) and sampling over only a single year. Difficultly locating sites, as well as logistical constraints, limited the number of wetlands that could be sampled intensively. Since I included a range of sizes and depths in my sample of wetlands (area: 33.7 – 542.7 m^2; maximum depth: 8 – 75 cm), and since depth and surface area were both related to hydroperiod, small sample size effects may have obscured any further relationship between hydroperiod and canopy cover. Further, hydroperiods of ephemeral wetlands vary annually, and one year of study is unlikely to capture the range of hydroperiods expected across multiple years.

Trees and surrounding vegetation may influence drying rates of ephemeral wetlands through other mechanisms that were not measured. For example, evapotranspiration - the combination of surface evaporation and transpiration from catchment vegetation (Leibowitz and Brooks, 2007) - is often the main mechanism of water loss from geographically isolated wetlands (Brooks, 2005, 2004). Water loss from transpiration usually peaks during spring and summer months when trees and vegetation are in full foliage and rates of transpiration exceed precipitation (Brooks, 2005; Leibowitz and Brooks, 2007). Transpiration from surrounding vegetation can contribute significantly to water loss from small wetlands. For example, vegetation surrounding prairie pothole wetlands in Saskatchewan create a drawdown zone that results in visible water loss during the day (Hayashi et al., 1998; Winter, 2000). In addition to size and vegetation cover, hydroperiod of ephemeral wetlands may be influenced by several other factors including land use, topographic position, and soil porosity (Sun et al., 2002; Tsai et al., 2007). Further research is required to better understand the hydrology of ephemeral wetlands in the boreal mixedwood.

Annual precipitation is another important consideration when examining hydroperiod. Following spring snowmelt, rainfall is often the primary source of water for ephemeral wetlands (Brooks, 2005, 2004). Based on annual rainfall data, 2015 was a drier year at 414.7 mm compared to previous years and the 10-year average of 441.1 ± 84.0 mm (Figure 3-6). By comparison, the annual precipitation in 2014 was about 100 mm higher (416.0 mm) than 2015, and about 200 mm higher in 2013 (526.3 mm). Wetter years, with greater winter snowfall and/or higher rain during spring and summer would be expected to result in longer hydroperiods, fewer drying events, and ultimately greater reproductive success of wood frogs at ephemeral breeding wetlands. The range of hydroperiods observed in my study (30 – 122 d) would be expected to vary between years.

Tadpole Performance

Canopy had a negative effect on the performance of wood frog tadpoles. Among the 11 wetlands where performance was measured, both growth and development were faster in wetlands with less surrounding canopy cover. These findings are consistent with similar studies in eastern North America (Halverson et al., 2003; Schiesari, 2006; Skelly et al., 2002; Werner and Glennemeier, 1999) and Alberta (Stevens et al., 2006) showing reduced performance of anuran tadpoles in response to greater canopy cover surrounding breeding wetlands. Provided hydroperiod is sufficient (i.e. wetland does not dry prematurely), wetlands with less canopy cover may benefit wood frog tadpoles by allowing them to reach a larger body size and develop more rapidly. If faced with high mortality risks within a wetland, such as predators (Smith, 1983) or the threat of wetland drying (Semlitsch, 1987; Smith, 1983), faster development allows tadpoles to escape the aquatic environment more quickly and thus avoid mortality. Larger body size may improve tadpole survival by decreasing predation risk as tadpoles (Brodie et al., 1983; Semlitsch, 1990; Tejedo, 1993), and increasing survival in the terrestrial environment following metamorphosis (Berven, 1990; Semlitsch et al., 1988). Despite the difference in performance, wood frogs still reproduced successfully at closed-canopy wetlands, provided they retained water long enough. Metamorphosis of tadpoles was confirmed at all 4 ‘successful’ closed-canopy wetlands (Table A3-7). My findings show that wood frogs can successfully reproduce in both open- and closed-canopy ephemeral wetlands in the boreal mixedwood, but that reproduction in closed-canopy wetlands may come at a cost to growth and development, and subsequent fitness of tadpoles and metamorphs.

The effect of canopy on tadpole growth also depended on wetland volume, as indicated by a significant interaction term in my models (ß = -0.082 ± 0.026, p = 0.001; Table 3-4). This indicates that the effect of canopy on tadpole growth became more negative as wetland volume increased. This was counter to my initial predictions that canopy effects on tadpole growth would become stronger (more negative) with decreasing wetland volume, owing to greater shading effects of canopy around shrinking basins (as wetlands dried), combined with increased density-dependant interactions among tadpoles in reduced volumes. If slower tadpole growth in more shaded wetlands is primarily a function of lower water temperatures (discussed below) this result may be due to reduced water temperatures that would be expected to accompany large increases in water volume of wetlands (e.g. during periods of heavy rain). In my study, water volumes decreased steadily between early-May and early June as initial wetland volumes provided by snowmelt were gradually depleted but were not replaced since rainfall events were infrequent (Figure 3-7). However, wetland volumes increased to near capacity in mid-June (approximately June 7 – 19) coinciding with several large rainfall events. Although these heavy rain events prevented premature drying of several wetlands, sudden decreases in water temperature may have temporarily dampened tadpole growth.

Density

Contrary to expectation, there was no effect of density on tadpole growth. Although individual growth of tadpoles is reduced in response to higher larval density (Petranka, 1989; Smith, 1983; Wilbur, 1976), my study design may have precluded the isolation of this effect. I sampled tadpoles in natural wetlands, where tadpoles could move freely throughout the wetland and seek out favorable microhabitats and resources throughout the day and growing season. Other studies (e.g. Skelly et al. 2002; Stevens et al., 2006) have used within-pond enclosures, where tadpole density can be explicitly controlled. Our measurement of density (catch per unit effort) may not have been insufficient to quantify actual tadpole density at wetlands. Density-dependent effects from other anuran species present in wetlands may be important as well. Boreal chorus frog tadpoles were present in 5 of the 11 wetlands used in growth analysis;

previous research from Alberta has shown that interspecific competition is an important factor affecting tadpole performance in breeding wetlands (Whiting, 2010). Although not quantified in my study, density-dependent effects between wood frog and other anuran tadpoles may be an important mechanism affecting larval performance in ephemeral wetlands of the boreal.

Wetland physiochemistry

Temperature

My study focused on comparing tadpole performance among ephemeral wetlands that varied in size and canopy cover, but did examine other possible causal factors including water temperature and primary productivity. On average, water temperature was 3.1° C higher in open-canopy wetlands relative to closed-canopy wetlands (Table 3-5). These findings are consistent with research in eastern North America that found higher water temperatures in ponds with less surrounding forest canopy cover (Halverson et al., 2003; Schiesari, 2006; Skelly et al., 2002; Werner and Glennemeier, 1999). The positive relationship between water temperature and the growth and development of amphibian larvae is well-established (Berven and Gill, 1983; Smith-Gill and Berven, 1979). My comparisons were based on a relatively small number of sampling dates and therefore likely did not fully characterize the variability in daily water temperatures expected to occur in small wetlands. Small wetlands, particularly those with shallow depths and lower water volumes, may experience high daily fluctuations in water temperature due to lower heat storage capacity (Dupuis and Hann, 2009; Losordo and Piedrahita, 1991). Sheffers (2010) noted that daily water temperatures were more variable in smaller, shallower natural and artificial stormwater wetlands relative to larger, deeper sites in Edmonton, Alberta. I addressed this challenge by controlling the time of day when selecting sampling dates for analysis, and thus my results should reasonably reflect average temperature differences between open- and closed-canopy wetlands in my study.

Primary Productivity

The availability of food resources can potentially limit growth of amphibian larvae. In addition, resource gradients associated with forest canopy, such as primary productivity, have frequently been cited as a potential factor limiting the distribution and performance of amphibian larvae (Schiesari, 2006; Skelly et al., 2005). I quantified periphyton growth using chlorophyll-a as an index of primary productivity and a potential food resource for wood frog tadpoles. Contrary to expectations, chlorophyll-a concentrations were actually higher in closed-canopy wetlands (Table 3-6). I predicted that higher light levels associated with reduced canopy shading would correspond with increased primary productivity and periphyton growth. Some studies have found greater abundance and diversity of periphyton in open-canopy wetlands (e.g. Skelly et al., 2002). However, similar to my results, Stevens et al., (2006) reported no significant difference in chlorophyll-a between older and newer beaver ponds that differed in canopy cover, and suggested that high phosphorus concentrations in newer ponds (with greater canopy cover) compensated for reduced light availability for primary production. This may explain chlorophyll-a differences observed in my wetlands, although organic nutrients, such as nitrogen and phosphorous, were not measured.

Anuran tadpoles, including wood frog tadpoles, can have diverse omnivorous diets that may include periphyton, aquatic plants, carrion, and leaf litter, and detritus (Altig et al., 2007; Schiesari, 2006; Skelly and Golon, 2003; Stoler and Relyea, 2013). Research has shown that differences in food quality, such as the type of leaf litter, influences tadpole performance (Stoler and Relyea, 2013; Williams et al., 2008), as well as tadpole and metamorph morphology (Stoler and Relyea, 2013; Stoler et al., 2015). Availability and quality of food resources may also vary among breeding wetlands with different amounts and types of forest canopy cover and thus influence performance of tadpoles (Schiesari, 2006; Stolar and Reylea, 2013). For instance, Schiesari (2006) found that quality of food resources (detritus, periphyton, and phytoplankton), as measured by carbon to nitrogen (C: N) ratio, was lower (lower C: N) in closed-canopy wetlands. The author demonstrated in a lab experiment that increasing food quality in a range representative of gradients found in open- and closed-canopy ponds increased growth of wood frog and leopard frog tadpoles. Similarly, Stolar and Reylea (2013) found that exposure of wood frog tadpoles to different species of broadleaf and conifer litter resulted in differences in performance (growth and development), as well as differences in body morphology (e.g. tail dimensions, intestinal length). Other studies, however, have challenged the contribution of food resources to canopy-driven performance differences in tadpoles. In Alberta, Stevens et al. (2006) found that growth and development of wood frog tadpoles was faster in older beaver ponds, which had less canopy cover and higher water temperatures than newer ponds. However, addition of food did not significantly improve tadpole performance in either pond type, suggesting that physiochemical properties like temperature and dissolved oxygen were driving differences in tadpole performance. Given this knowledge, it is likely that my periphyton measurements did not adequately represent all potential food resources available to tadpoles. Further research is needed to evaluate the diets of amphibian larvae, food resource gradients in ephemeral wetlands in the boreal mixedwood, and their potential effects on tadpole performance.

Dissolved oxygen (DO) is another unmeasured property that may have varied among wetlands affecting tadpole performance. Previous research has suggested that lower DO concentrations in closed-canopy wetlands may reduce growth and development of wood frog larvae (Werner and Glennemeier, 1999; Stevens et al., 2006; Schiesari, 2006). Lower DO in closed-canopy wetlands may increase stress and lead to increased “bobbing behavior”, where tadpole gulp air at the surface to supplement respiration through gills (Schiesari, 2006; Wassersug and Seibert, 1975). I observed frequent bobbing behavior, as well as bloated (stressed) and dead tadpoles at 2 of my closed canopy wetlands (FP2 and FP3) during final surveys in late July. This period coincided with high air and water temperatures and low water levels at these and other study wetlands (M. Robinson, *personal observation*). It is conceivable that increased water temperature and low water levels exacerbated low DO levels resulting in high tadpole mortality during this period, and may explain why so few metamorphs were found during visual-encounter surveys (Table A3-7).

Variation in breeding (oviposition) date

Although hatching dates among wetlands were similar, and tadpoles were at the same developmental stages when tadpole surveys began, I did not obtain exact breeding (oviposition) dates at all wetlands. Oviposition may have varied slightly among wetlands, which may have resulted in an advanced start in embryonic and larval development at wetlands with earlier oviposition and hatching dates. Wood frogs are synchronous breeders (Berven and Grudzien, 1990; Petranka and Thomas, 1995), gathering at breeding sites at first opportunity in spring (Russell and Bauer, 2000). This species is also selective when choosing oviposition sites (Hopey and Petranka, 1994), preferring shallow waters with warmer temperatures, often near the north end of the breeding ponds (Russell and Bauer, 2000; Stevens and Paszkowski, 2004). Wood frogs may therefore colonize and breed at open-canopy wetlands at earlier dates due to faster snow melting near forested uplands (Metcalfe and Buttle, 1998) were breeding adults overwinter. In addition, faster ice melting and warmer water temperatures may offer more favorable oviposition conditions at these sites. Despite not obtaining precise oviposition dates at my wetlands, visual assessment of egg mass (embryonic) development and development stages of tadpoles in May suggest that breeding was approximately synchronous among the wetlands included in growth analysis and therefore any differences in tadpole performance due to variation in oviposition and hatching dates were likely minimal.

Importance of ephemeral wetlands

The relative importance of small ephemeral wetlands for amphibian reproduction likely varies regionally across Alberta's boreal region. In the southeastern portion of the boreal mixedwood, shallow lakes are abundant and provide suitable breeding habitat for amphibians (Eaton, 2004; Eaton et al., 2005), but farther to the northwest, in my study area, small seasonal wetlands may be much more important due to relative scarcity of larger, more permanent water bodies (Eaton, 2004; M. Robinson, *personal observation*). The density of potential breeding habitats, both permanent and ephemeral, and the connection between adjacent uplands, should be considered when allocating timber retention in harvest blocks. Smaller ephemeral wetlands may be less critical for supporting local populations in recent harvest areas if the density of potential breeding wetlands is high.

Protection of ephemeral wetlands is also likely to benefit other amphibian species. Several other boreal amphibian species co-occur at small ephemeral wetlands, including boreal chorus frogs (*Pseudacris maculata*) and boreal toads (*Anaxyrus boreas*), with both species using these habitats for reproduction (Okonokwo, 2011; M. Robinson, *personal observation*). During larval surveys, I found boreal chorus frog tadpoles at 5 of 15 of my study wetlands in 2015. Although wood frogs and boreal chorus frogs have different breeding phonologies and non-breeding habitat requirements, maintenance of ephemeral wetlands in areas of timber harvest would likely benefit local populations of both species.

Limitations and future research

This study contributes to our understanding of ephemeral wetlands as amphibian breeding habitat in Alberta's boreal mixedwood, but there remains a need for future research. The current study investigated broad-scale effects of forest canopy cover and wetland size on hydroperiod and tadpole performance. I did not, however, examine effects of different types of forest canopy on tadpole performance (e.g. coniferous vs. deciduous). Due to differences in crown density, light transmission is lower in canopies formed by white spruce relative to aspen canopies of similar stem size (Stadt and Lieffers, 2000), and since they don't defoliate, conifer canopies block light equally year-round (Constabel and Lieffers, 1996). Different types of forest canopy would also alter organic matter inputs (i.e. leaf litter, conifer needles) into ephemeral water bodies, which would may alter tadpole growth, development, and survival by affecting water chemistry or available food resources (Stoler and Relyea, 2013). This study likely did not encompass the full spectrum of wetland types in the boreal mixedwood, as it focused on mineral wetlands and thus excluded peatlands (fens or bogs). Further research should explore amphibian reproduction in a broader range of wetland types.

Management implications

Results obtained from this study have important implications for conservation and management of small ephemeral wetlands during variable retention harvesting, as well as the local amphibian populations they support. Given that maximum wetland depth had a better relationship with hydroperiod than did surface area, wetland depth may serve as a useful criterion for prioritizing protection of small ephemeral wetlands during timber harvest. In years with below average rainfall, deeper wetlands will be more likely to retain water long enough for tadpoles to reach metamorphosis, whereas shallower wetlands may be more likely to dry prematurely. Large but shallow wetlands may act as reproductive traps for wood frogs during years with lower than average rainfall (DiMauro and Hunter, 2002). However, shallower wetlands (< 50 cm in this study) may have hydroperiods sufficient to allow tadpole metamorphosis during wetter years. Smaller and shallower ephemeral wetlands also function as hydration sites for wood frogs and other amphibians (Okonkwo, 2011) and may help facilitate movements within and between local populations (Gibbs, 2000, 1993; Semlitsch, 2000). As such, the protection of smaller and shallower wetland habitat should not be overlooked by forest managers.

Forested buffers around ephemeral wetlands have been proposed as a management strategy to maintain suitable breeding and upland habitat for amphibian populations (Freidenfelds et al., 2011), with their value as a conservation tool being well-supported in other parts of North America (Semlitsch and Bodie, 2003; Semlitsch, 2000, 1998). In Alberta, water bodies < 4 ha do not currently require any vegetated buffers under Alberta's timber harvesting ground rules (ESRD, 2016). However, some companies employ voluntary protection of these features, such as retaining a ring of trees around the wetland perimeter (DMI, 2016, 2010). Although I found no evidence of a relationship between canopy cover and hydroperiod, shading provided by trees and surrounding vegetation is still likely to influence water evaporation and drying rates. Further, I found that percent canopy cover influences growth and development of wood frog tadpoles, likely by mediating water temperature and possibly other mechanisms. By these means, canopy management around ephemeral wetlands through variable retention harvesting is likely to influence the suitability of ephemeral wetlands as breeding habitat for wood frogs and other amphibian species in the boreal mixedwood. The basin and riparian areas of ephemeral wetlands should be avoided during harvest operations - and at a minimum - riparian vegetation and woody shrubs, such as alder and willow species, should be retained, as these will provide shade and cover around wetland basins. In addition to protecting aquatic breeding habitat, mature trees and other vegetation will provide shaded refuge and foraging habitat for adult and YOY wood frogs.

3.5 - Conclusions

My study demonstrated that wetland size, but not canopy cover was related to hydroperiod of small ephemeral wetlands, and that maximum depth had a better relationship with hydroperiod than surface area. Maximum depth may therefore serve as a useful criterion for prioritizing the protection of ephemeral breeding wetlands during variable retention timber harvesting. I also found that canopy cover had a negative effect on wood frog tadpole performance, with tadpoles experiencing slower growth and development in wetlands with greater surrounding canopy cover. However, tadpoles still successfully completed metamorphosis in closed-canopy wetlands, provided they did not dry prematurely. Performance differences may be explained, in part, by variation in water temperature, which was higher in open-canopy wetlands relative to closed-canopy wetlands. Identification and protection of ephemeral wetlands during timber harvesting and other land-use activities is important to the conservation of local wood frog and other amphibian populations. Retention of trees and other vegetation around ephemeral wetlands and associated wet areas, combined with connections to upland forest habitat, will benefit local populations by maintaining suitable conditions in the aquatic environment for larval growth and development, providing cover and refuge for adult and young-of-the-year amphibians, and providing travel corridors to facilitate movements between habitat types and nearby populations.

3.6 - Tables

Table 3-1. Summary of habitat features used in classification of wetlands; these included dominant forest cover type, surface area, maximum depth, and percent canopy cover. All 15 wetlands were classified as *Form A - Seasonal Shallow Open Water Mineral Wetlands* based on the Alberta Wetland Classification System (ESRD, 2015). Canopy closure was classified as open (< 40% canopy cover) or closed-canopy (> 60% canopy cover) based on Werner and Glennemeier (1999).

Wetland	**Forest Cover Type**	**Surface Area (m^2)**	**Maximum Depth (cm)**	**% Canopy Cover**	**Canopy Closure**
I1	Open	33.7	70	2.9	open
EA91	Open	39.4	31	7.4	open
WSRW01	Regeneration	46	51	80.9	closed
EA9	Open	47.3	23	3.8	open
EA1	Mature Deciduous	72.1	40	82.1	closed
EMD8	Mature Deciduous	75	23	85.3	closed
A1	Regeneration	82.1	8	21.8	open
P217	Regeneration	170.9	75	9.4	open
A2	Regeneration	175.1	14	4.4	open
P208	Regeneration	199.6	50	68.8	closed
EMD7	Open	215.5	20	7.1	open
FP3	Mature Conifer	262.1	60	78.8	closed
EA68	Regeneration	314.5	75	22.1	open
FP1	Mature Deciduous	431.8	70	61	closed
FP2	Mature Conifer	542.7	55	73.8	closed

Table 3-2. Summary of egg mass survey dates and egg mass counts at 15 wetlands in 2015.

		Survey 1		Survey 2		
Wetland	**Block**	**Date**	**Egg Masses**	**Date**	**Egg Masses**	**Total Masses**
A1	A	May 6	3	May 13	1	4
A2	A	May 6	14	May 13	3	17
EA1	A	May 7	17	May 15	0	17
EA68	C	May 6	0	May 15	29	29
EA9	C	May 4	6	May 15	1	7
EA91	C	May 4	23	May 15	17	40
EMD7	A	May 7	27	May 13	0	27
EMD8	A	May 8	9	May 15	1	10
FP1	F	May 12	8	May 21	0	8
FP2	F	May 12	0	May 21	14	14
FP3	F	May 12	0	May 21	9	9
I1	I	May 9	2	May 20	0	2
P217	P2-200*	-	-	-	-	-
P208	P2-200*	-	-	-	-	-
WSRW01	P2-200*	-	-	-	-	-

*P2-200 denotes wetlands not located at EMEND; egg mass counts were not possible at these wetlands since they were identified after May 21, when eggs had already hatched.

Table 3-3. Drying dates, hydroperiod, metamorph emergence dates (start and end), and larval period for 15 wetlands sampled in 2015. Hydroperiod was calculated as the number of days since May 1st to the date when the wetland dried. Metamorph emergence start date was defined as the day when wood frog metamorphs (Gosner Stage 45-46) were first observed at a wetland; similarly, end date was the day when metamorphs were no longer observed during visual encounter surveys. Larval period for each wetland was calculated as the number of days since May 21st until the start date of metamorph emergence.

Wetland	Drying Date	Hydroperiod	Emergence Start Date	Emergence End Date	Larval Period (days)
A1	May 30	30	-	-	-
A2	May 30	30	-	-	-
EMD7	June 10	41	-	-	-
EMD8	June 10	41	-	-	-
EA9	June 12	43	-	-	-
WSRW01	June 21	52	-	-	-
EA1	July 7	68	-	-	-
EA91	July 10	71	-	-	-
P208	July 27	88	July 20	July 27	60
EA68	August 12	104	July 14	July 22	54
P217	August 14	106	July 11	July 27	51
* FP1	August 31	122	July 24	July 31	64
* FP2	August 31	122	July 24	July 31	64
* FP3	August 31	122	July 24	July 31	64
* I1	August 31	122	July 12	July 19	52

* Wetlands that never completely dried during study period were assigned a drying date and hydroperiod of August 31 and 122 days, respectively.

Table 3-4. Final model describing tadpole growth (body size on a given sampling date) in 11 ephemeral wetlands sampled in 2015. Final model includes only predictors and interactions that were statistically significant. Average tadpole body length at each wetland and survey date was the response variable and was Ln-transformed to meet model assumptions of normality and homogeneity of variance. All models included Julian day (days since May 1) as a fixed effect to account for date of sampling and wetland (site) as a random effect to account for any unmeasured variation among wetlands. P-values in bold indicate significance of predictor terms at $\alpha = 0.05$. Wetlands were included in body size analysis only if the site retained water long enough to allow for at least 2 tadpole surveys.

Predictor	**Coefficient Estimate**	**Standard Error**	**t-value**	**p-value**
Canopy	-0.191	0.024	-8.020	**< 0.001**
Volume	-0.026	0.022	-1.190	0.670
Canopy*Volume	-0.082	0.026	-3.200	**0.01**
Julian Day	0.496	0.022	22.590	**< 0.001**

Table 3-5. Results of Welsh's t-test comparing mean water temperature between open and closed-canopy breeding wetlands sampled in 2015. Comparisons are made over 4 discrete sampling sessions from late May to early July, as well as for all 4 sessions combined. Sampling sessions were as follows: (1) May 21 - May 31, (2) June 11 – June 17, (3) June 21 – June 23 and (4) July 9 – July 11. Due to differences in drying dates, the number of wetlands in each group varied among sampling session. Canopy closure was classified as open (< 40% canopy cover) or closed-canopy (> 60% canopy cover) based on Werner and Glennemeier (1999). P-values in bold indicate a significant difference in water temperature at α = 0.05.

Sampling Session	Canopy Closure	n	Mean Temperature (°C)	Standard Deviation	t-value	Degrees of Freedom	p-value
1	Closed	7	21.7	2.5	-2.518	7.509	**0.038**
	Open	5	26.4	3.8			
2	Closed	6	19.7	1.2	-0.808	3.403	0.472
	Open	4	21.5	3.9			
3	Closed	6	22.2	0.8	-0.984	3.114	0.395
	Open	4	25.0	5.4			
4	Closed	4	27.7	1.2	-2.687	4.656	**0.047**
	Open	3	29.7	0.7			
All Sessions	Closed	7	22.3	3.1	-2.263	25.477	**0.032**
	Open	5	25.4	4.6			

Table 3-6. Results of Welsh's t-test comparing mean chlorophyll-a between a subset of open and closed-canopy ephemeral wetlands sampled in 2015. Comparisons for 2 collection periods in which periphyton was sampled: (1) June 2 - June 17 and (2) June 17 – July 2. Canopy closure classified as open (< 40% canopy cover) or closed-canopy (> 60% canopy cover) based on Werner and Glennemeier (1999).

Collection Period	Canopy Closure	n	Mean Chlorophyll-a (µg/cm^3)	Standard Deviation	t-value	Degrees of Freedom	P-value
1	Closed	4	0.018	0.009	0.747	3.128	0.507
	Open	2	0.015	0.001			
2	Closed	4	0.017	0.002	2.524	3.841	0.068
	Open	2	0.014	0.001			
Combined	Closed	4	0.018	0.006	1.564	7.552	0.159
	Open	2	0.014	0.001			

3.7 - Figures

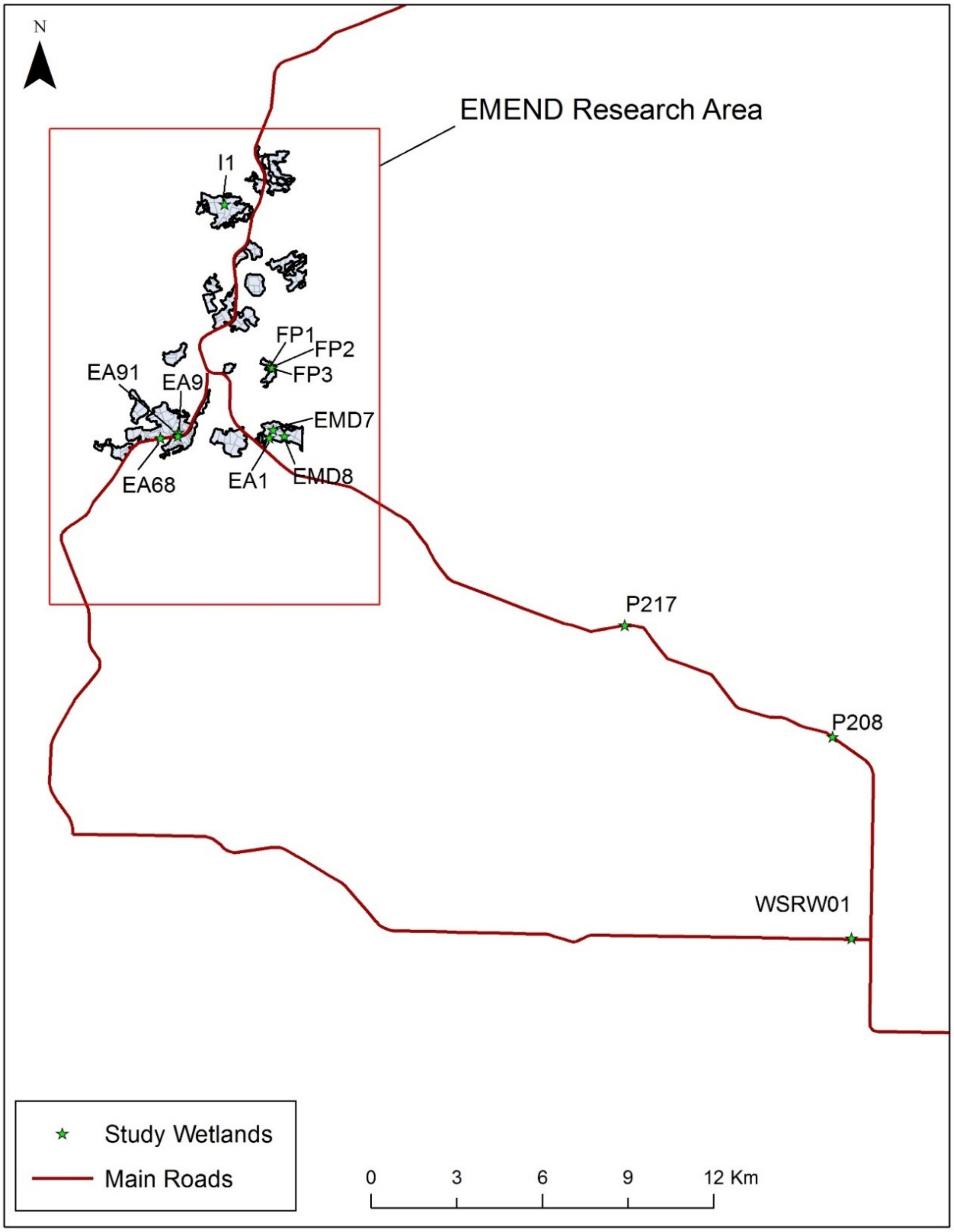

Figure 3-1. Map of breeding wetlands surveyed in 2015 at EMEND and surrounding area.

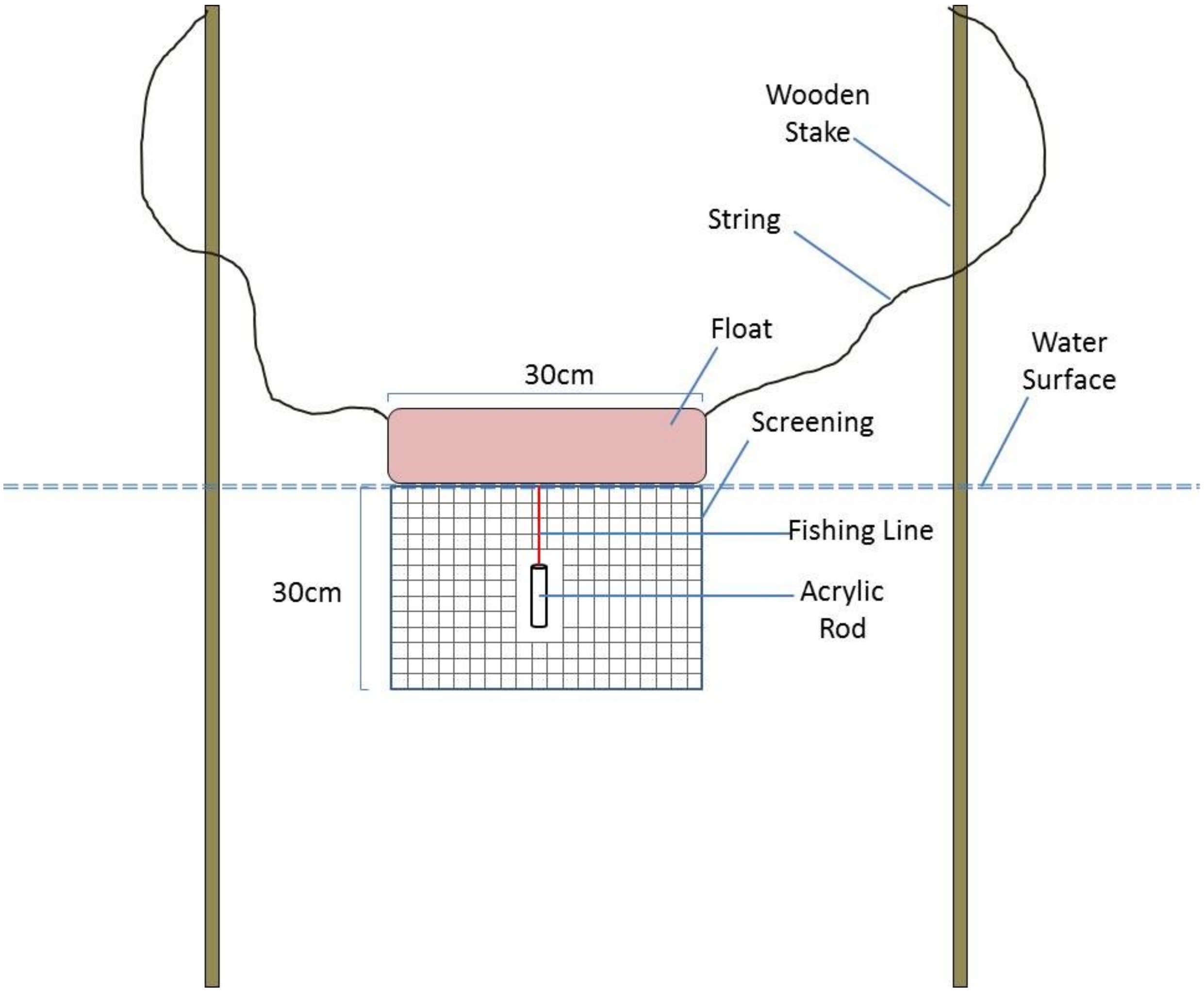

Figure 3-2. Diagram of apparatus ("periphyton meter") used to sample periphyton at study wetlands in 2015. Acrylic rods were suspended approximately 10 cm below the water surface.

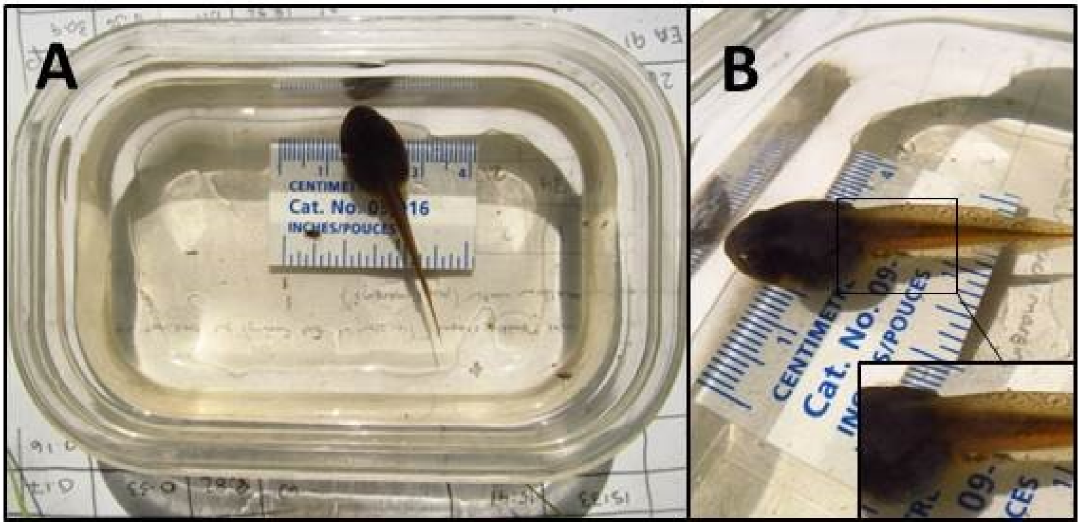

Figure 3-3. Example of photographs used to assess individual tadpole size and developmental stage. (A) Dorsal perspective photo used to measure body size and (B) Lateral perspective photo with magnified rear limbs (inset – bottom right) to assess developmental stage.

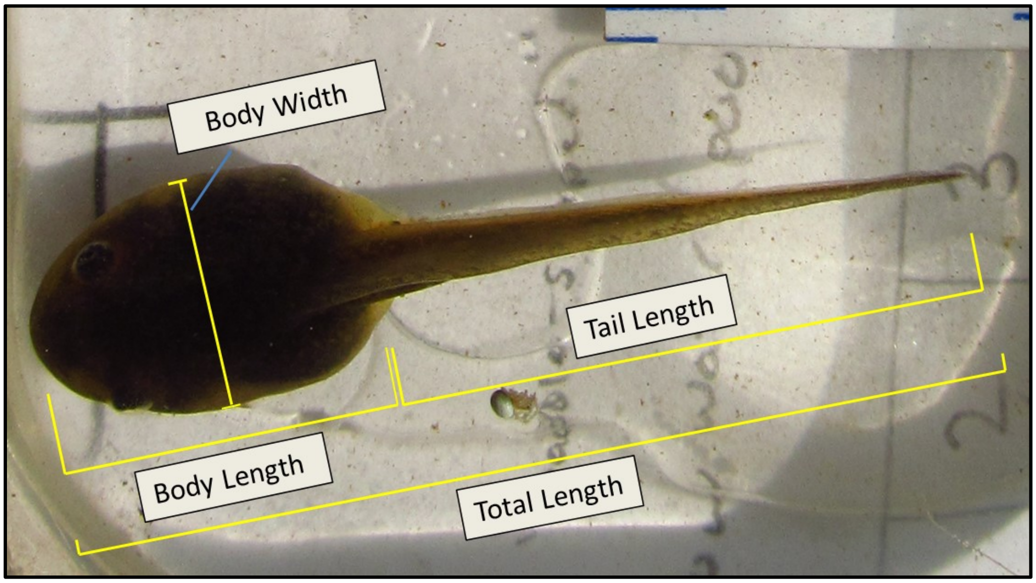

Figure 3-4. Diagram showing 4 tadpole size measurements taken using during image analysis: (1) total length, (2) body length, (3) tail length, and (4) body width. Note only body length was used in statistical analysis.

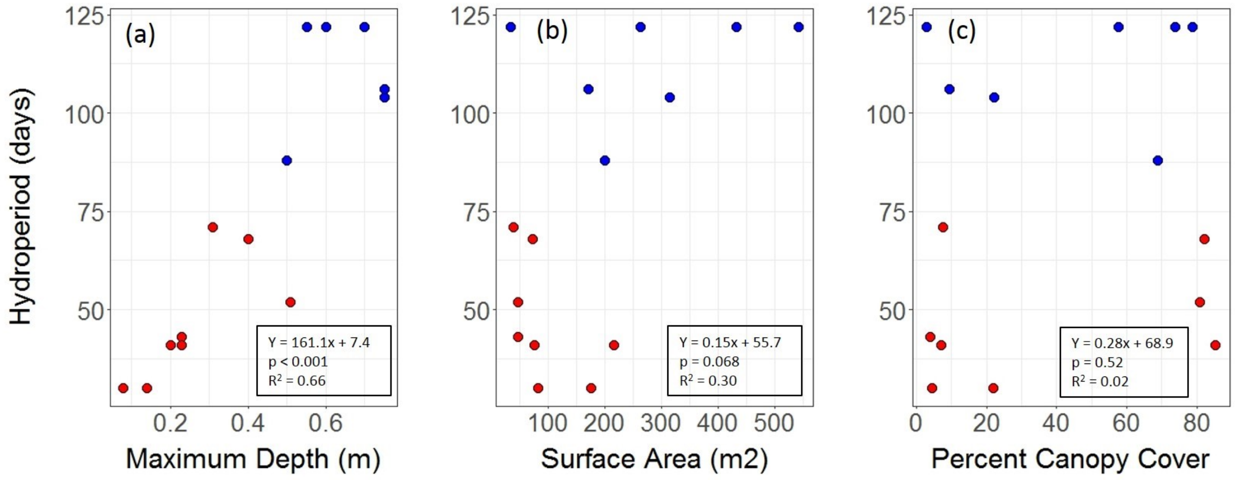

Figure 3-5. Relationships between wetland hydroperiod and (a) maximum depth (b) surface area and (c) percent canopy cover. Shown at bottom right of each panel are the regression equation, p-value, and pseudo-R^2 of quantile regression of each predictor. **Red** circles denote 'unsuccessful' wetlands (those that dried prematurely resulting in complete tadpole mortality), whereas **blue** circles denote 'successful' wetlands (those where tadpoles completed metamorphosis).

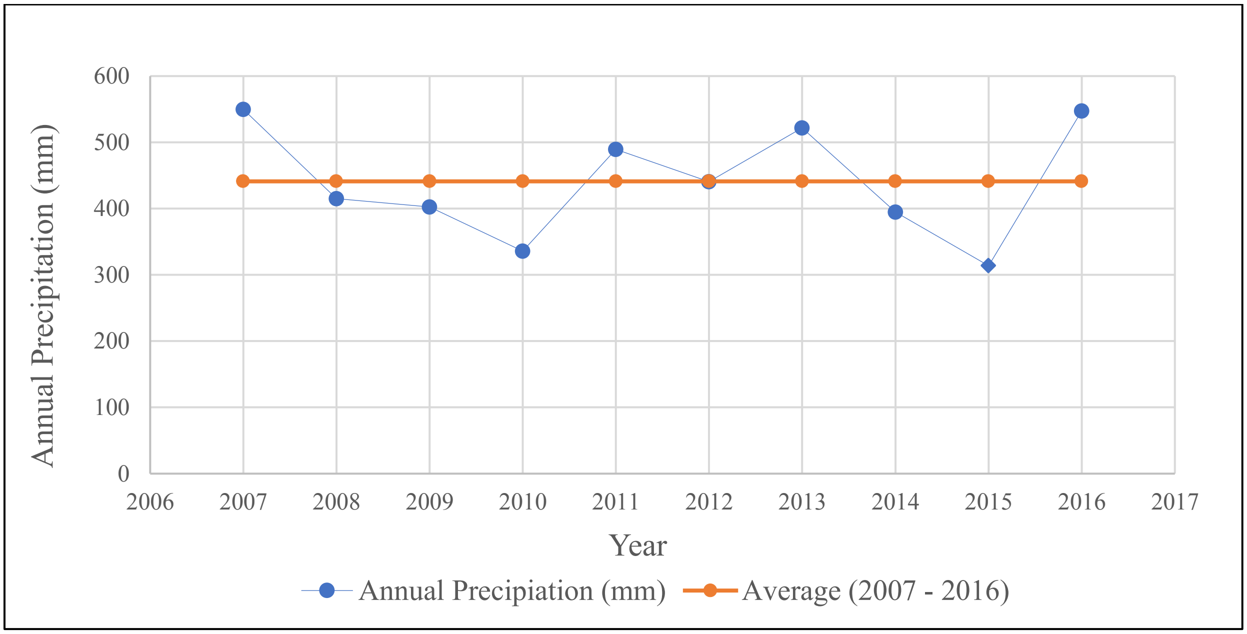

Figure 3-6. Annual precipitation for study area in each year between 2007 and 2016. Data were obtained from Alberta Climate Information Service's (ACIS) historical weather station viewer (Alberta Agriculture and Forestry, 2017). Annual precipitation for Alberta township T089R03W6 (location of study wetlands) estimated by interpolation procedure using nearby weather stations. These data were used to calculate the average annual precipitation over a 10-year period (2007 to 2016) to allow comparisons with precipitation from the year of sampling (2015)

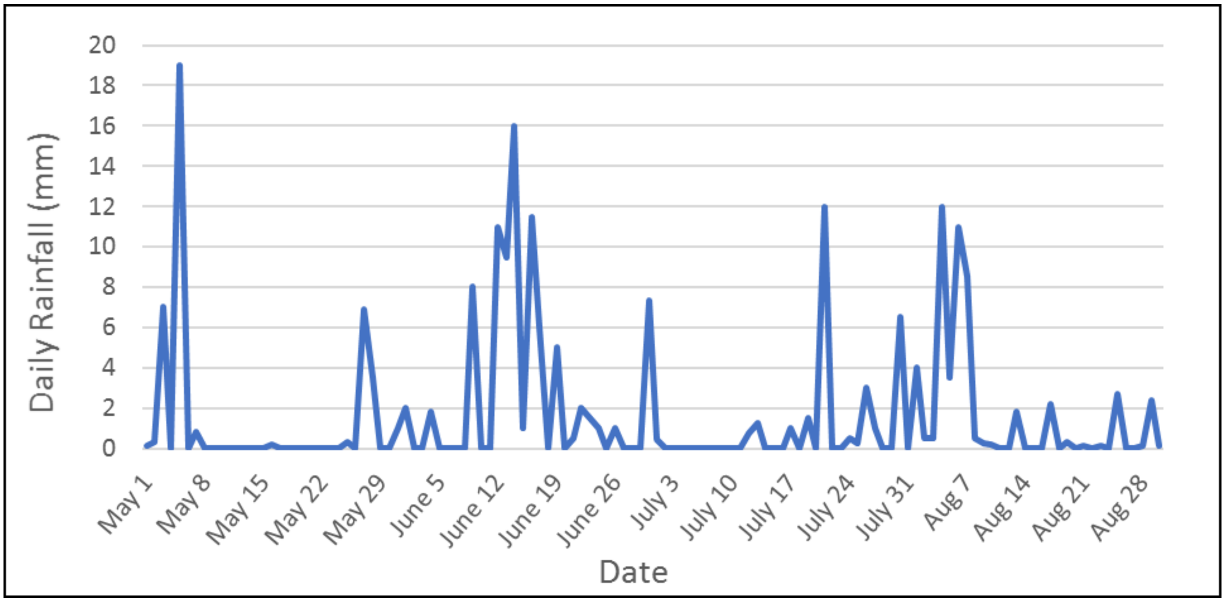

Figure 3-7. Daily rainfall for the 2015 study period (May 1 – August 31). Daily rainfall data were obtained from a single rain gauge placed approximately central to study wetlands (EMEND "Old Camp" parking location - UTM Zone 11V; 417846, 6289708)

3.8 – Appendices

Table A3-1. Tadpole survey dates for 13 wetlands sampled for tadpoles in 2015.

Wetland	Tadpole Survey Dates					
	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Total Surveys
*EA9	May 25	---	---	---	---	1
EMD8	May 26	June 10				2
WSRW01	May 31	June 14	---	---	---	2
*EMD7	May 22	May 30	June 10	---	---	3
EA91	May 25	June 12	June 26	Jul 10	---	4
I1	May 25	June 11	June 23	July 10	---	4
EA1	May 22	May 30	June 13	June 26	July 7	5
EA68	May 25	June 2	June 16	June 28	July 7	5
FP1	May 29	June 12	June 26	July 7	July 23	5
FP2	May 29	June 12	June 26	July 7	July 23	5
FP3	May 29	June 12	June 26	July 7	July 24	5
P208	May 23	June 12	June 27	July 11	July 20	5
P217	May 21	June 2	June 16	June 28	July 7	5

* Wetlands not included in tadpole growth analysis due to too few (< 2) tadpole surveys (EA9) or asynchronous breeding (oviposition) with other breeding wetlands (EMD7).

Table A3-2. Field stage, associated Gosner stages, and morphological features used to assign developmental stage to tadpoles.

Field Stage	**Gosner Stage(s)**	**Description**
0	21 - 24	Early hatchling. External gills and/or adhesive organs still present. Not yet free-swimming; usually still attached to egg mass
1	25	Free-swimming; no rear limb buds present. Usually dispersed from egg mass site
2	26 - 30	Free-swimming with rear limb buds present. No toe differentiation apparent
3	31 - 36	Early toe development on rear limb bud. Includes "paddle-shaped" rear limb buds (Gosner 31 - 33) and early stages of toe differentiation (Gosner 34 - 36). If toe cleavage present, apparent only between *some but not all toes*.
4	37 - 40	All toes on rear limbs fully developed and cleavage present between all 5 toes
5	41	Onset of metamorphosis as indicated by presence of front limb buds
6	42	Later metamorphosis as indicated by emergence of one or both front limbs

Table A3-3. Data collected during tadpole surveys at 13 ephemeral wetlands and used for tadpole size models at 11 of 13 wetlands in 2015 (see below). Data include: canopy cover, Julian day (days since May 1), surface area, maximum depth, volume (surface area x depth), sampling effort (elapsed time spent dipnetting for tadpoles), number of observers (# Obs.), number of wood frog tadpoles captured (# tadpoles), CPUE ("catch per unit effort" = # tadpoles/sampling effort/# obs), and average tadpole body length (mean ± standard deviation). Canopy cover and surface area were only measured once during study year (2015). Table continued next page.

Wetland	Survey Date	Julian Day	Canopy Cover (%)	Surface Area (m^2)	Depth (cm)	Vol (m^3)	Sampling Effort (min)	# Obs.	# Tadpoles	CPUE	Mean Body Length ± SD (mm)
EA1	May 22	22	82.1	72.1	38	27.4	5	2	21	2.100	3.88 ± 0.31
	May 30	30	82.1	72.1	40	28.8	25	2	30	0.600	6.17 ± 0.50
	June 13	44	82.1	72.1	30	21.6	6	2	30	2.500	10.56 ± 0.99
	June 26	57	82.1	72.1	35	25.2	8	2	25	1.563	15.58 ± 1.35
	*July 7	68	82.1	72.1	5	3.6	4	2	14	1.750	16.65 ± 1.04
EA68	May 25	25	22.1	314.5	75	235.8	9	2	29	1.611	6.79 ± 0.80
	June 2	33	22.1	314.5	62	195.0	20	1	21	1.050	10.00 ± 1.18
	June 16	47	22.1	314.5	60	188.7	9	2	30	1.667	13.92 ± 1.70
	June 28	59	22.1	314.5	54	169.8	10	2	35	1.750	17.24 ± 2.14
	*July 10	71	22.1	314.5	42	132.1	12	2	35	1.458	17.62 ± 1.81
EA91	May 25	25	7.4	39.4	31	12.2	8	2	26	1.625	6.01 ± 1.81
	June 12	43	7.4	39.4	26	10.2	6	2	18	1.500	13.10 ± 2.43
	June 26	57	7.4	39.4	29	11.4	11	2	21	0.955	16.21 ± 2.35
	*July 10	71	7.4	39.4	5	2.0	11	2	6	0.273	16.31 ± 1.35
EMD8	May 26	26	85.3	75.0	23	17.3	19	2	28	0.737	5.00 ± 0.26
	June 10	41	85.3	75.0	5	3.8	5	2	27	2.700	7.29 ± 0.58
FP1	May 29	29	61	431.8	60	259.1	18	2	30	0.833	4.78 ± 0.51
	June 12	43	61	431.8	44	190.0	12	2	46	1.917	8.06 ± 1.17
	June 26	57	61	431.8	49	211.6	11	2	27	1.227	12.52 ± 1.35
	July 10	71	61	431.8	29	125.2	11	2	25	1.136	18.91 ± 1.68
	*July 23	84	61	431.8	15	64.8	6	2	31	2.583	17.45 ± 0.98
FP2	May 29	29	73.8	542.7	50	271.3	15	2	25	0.833	4.14 ± 0.38
	June 12	43	73.8	542.7	45	244.2	19	2	34	0.895	7.87 ± 0.83
	June 26	57	73.8	542.7	48	260.5	11	2	25	1.136	12.61 ± 1.49
	July 10	71	73.8	542.7	37	200.8	6	2	26	2.167	18.90 ± 1.48

	Survey Date	Julian Day	Canopy Cover (%)	Surface Area (m^2)	Depth (cm)	Vol (m^3)	Sampling Effort (min)	# Obs.	# Tadpoles	CPUE	Mean Body Length ± SD (mm)
	*July 23	84	73.8	542.7	31	168.2	12	2	10	0.417	19.43 ± 0.93
FP3	May 29	29	78.8	262.1	57	149.4	19	2	21	0.553	3.96 ± 0.41
	June 12	43	78.8	262.1	55	144.1	12	2	29	1.208	7.15 ± 0.82
	June 26	57	78.8	262.1	55	144.1	11	2	23	1.045	10.47 ± 1.67
	July 10	71	78.8	262.1	42	110.1	6	2	25	2.083	18.07 ± 1.51
	*July 24	85	78.8	262.1	34	89.1	10	2	14	0.700	17.65 ± 1.98
I1	May 25	25	2.9	33.7	70	23.6	11	2	20	0.909	4.69 ± 0.32
	June 11	42	2.9	33.7	61	20.6	10	2	25	1.250	12.45 ± 0.83
	June 23	54	2.9	33.7	56	18.9	6	2	30	2.500	17.87 ± 1.01
	*July 10	71	2.9	33.7	47	15.9	7	2	26	1.857	19.28 ± 0.95
P208	May 23	23	68.8	199.6	50	99.8	24	2	26	0.542	4.87 ± 0.36
	June 12	43	68.8	199.6	44	87.8	9	2	16	0.889	10.10 ± 1.29
	June 27	58	68.8	199.6	36	71.8	4	2	30	3.750	14.13 ± 2.36
	July 11	72	68.8	199.6	26	51.9	4	2	25	3.125	15.92 ± 2.46
	*July 20	81	68.8	199.6	8	16.0	47	2	38	0.404	15.96 ± 0.88
P217	May 21	21	9.4	170.9	75	128.2	5	2	12	1.200	4.59 ± 0.48
	June 2	33	9.4	170.9	70	119.6	9	2	24	1.333	8.40 ± 0.76
	June 16	47	9.4	170.9	70	119.6	15	2	29	0.967	14.38 ± 1.53
	June 28	59	9.4	170.9	55	94.0	13	2	27	1.038	19.47 ± 1.10
	*July 11	72	9.4	170.9	42	71.8	9	2	31	1.722	19.31 ± 1.28
WSRW01	May 31	31	80.9	46.0	51	23.4	6	2	30	2.500	5.81 ± 0.76
	June 14	45	80.9	46.0	33	15.2	6	2	29	2.417	8.60 ± 1.27
**** EA9**	May 25	25	3.8	47.3	23	10.9	9	2	26	1.444	6.40 ± 0.50
**** EMD7**	May 22	22	7.1	215.5	18	38.8	8	2	12	0.750	6.83 ± 0.823
	May 30	30	7.1	215.5	20	43.1	3	2	30	5.000	11.25 ± 1.12
	June 10	41	7.1	215.5	5	10.8	5	2	15	1.500	12.78 ± 1.27

* Survey dates not included in tadpole size analysis since tadpoles were undergoing metamorphosis

** Wetlands not included in tadpole size analysis due to too few (< 2) tadpole surveys (EA9) or asynchronous breeding (oviposition) with other breeding wetlands (EMD7).

Table A3-4. Results of initial GLMMs for tadpole growth (body size on a given sampling date) at 11 ephemeral wetlands in 2015. Average tadpole body length at each wetland and survey date was the response variable and was Ln-transformed to meet model assumptions of normality and homogeneity of variance. All models included Julian day (days since May 1) as a fixed effect to account for date of sampling and wetland (site) as a random effect to account for any unmeasured variation among wetlands. P-values in bold indicate significance of predictor terms at $\alpha = 0.05$. Wetlands were included in body size analysis only if the site retained water long enough to allow for at least 2 tadpole surveys.

Model	Predictor	Coefficient	Standard Error	t-value	p-value
Canopy	Canopy	-0.159	0.031	-5.16	**<0.001**
	Julian Day	0.496	0.023	21.92	**<0.001**
Volume	Volume	-0.023	0.050	-0.45	0.667
	Julian Day	0.501	0.0245	20.44	**<0.001**
Density	Density	-0.026	0.029	-0.920	0.372
	Julian Day	0.519	0.027	19.040	
Canopy*Volume	Canopy	-0.191	0.024	-8.020	
	Volume	-0.026	0.022	-1.190	
	Canopy*Volume	-0.082	0.026	-3.200	**0.01**
	Julian Day	0.496	0.022	22.590	**<0.001**
Canopy*Density	Canopy	-0.159	0.031	-5.200	
	Density	0.023	0.030	0.770	
	Canopy*Density		0.031	-1.370	0.177
	Julian Day	0.491	0.025	19.270	**<0.001**
Volume*Density	Volume	-0.026	0.054	-0.490	
	Density	-0.022	0.035	-0.640	
	Volume*Density	0.012	0.036	0.370	0.722
	Julian Day	0.512	0.029	17.660	**<0.001**

Table A3-5. Survey dates, start and end times, search times, and metamorph captures for wood frogs and boreal chorus frogs, from metamorph surveys (area-constrained visual encounter surveys) at 7 ephemeral wetlands in 2015. Metamorph surveys were only performed at wetlands that retained water long enough for tadpoles to complete metamorphosis. Canopy closure defined as either 'open' (< 40% canopy cover) or 'closed' (> 60% canopy cover) based on Werner and Glennemeier (1999).

Site	**Canopy Closure**	**Date**	**Start Time**	**Finish Time**	**Search Time (min)**	**Metamorphs**	
						Wood Frogs	**Boreal Chorus Frogs**
EA68	Open	July 10	16:35	16:47	12	-	-
		July 14	14:17	15:02	45	25	15
		July 18	13:38	14:23	45	30	20
		July 22	13:44	14:29	45	4	1
P217	Open	July 11	15:34	16:19	45	4	6
		July 14	18:20	19:05	45	5	3
		July 18	18:14	18:59	45	7	0
		July 20	15:42	16:27	45	30	6
		July 22	15:30	16:15	45	24	2
		July 24	15:10	16:59	45	34	5
		July 27	16:30	17:15	45	32	3
I1	Open	July 10	10:29	10:44	15	0	-
		July 12	19:00	19:15	15	5	-
		July 19	15:50	16:05	15	3	
P208	Closed	July 20	18:45	19:30	45	4	0
		July 24	17:45	18:30	45	42	0
		July 27	19:00	19:45	45	65	3
FP1	Closed	July 24	13:44	14:29	45	2	-
		July 27	11:30	12:15	45	0	-
		July 29	13:30	14:15	45	3	-
		July 31	10:00	10:45	45	2	-
FP2	Closed	July 24	12:20	13:05	45	2	-
		July 27	12:40	13:25	45	7	-
		July 29	15:45	16:30	45	2	-
		July 31	11:50	12:35	45	0	-
FP3	Closed	July 24	11:18	11:58	45	0	-
		July 27	14:25	15:10	45	1	-
		July 29	17:00	17:45	45	0	-
		July 31	12:26	13:11	45	0	-

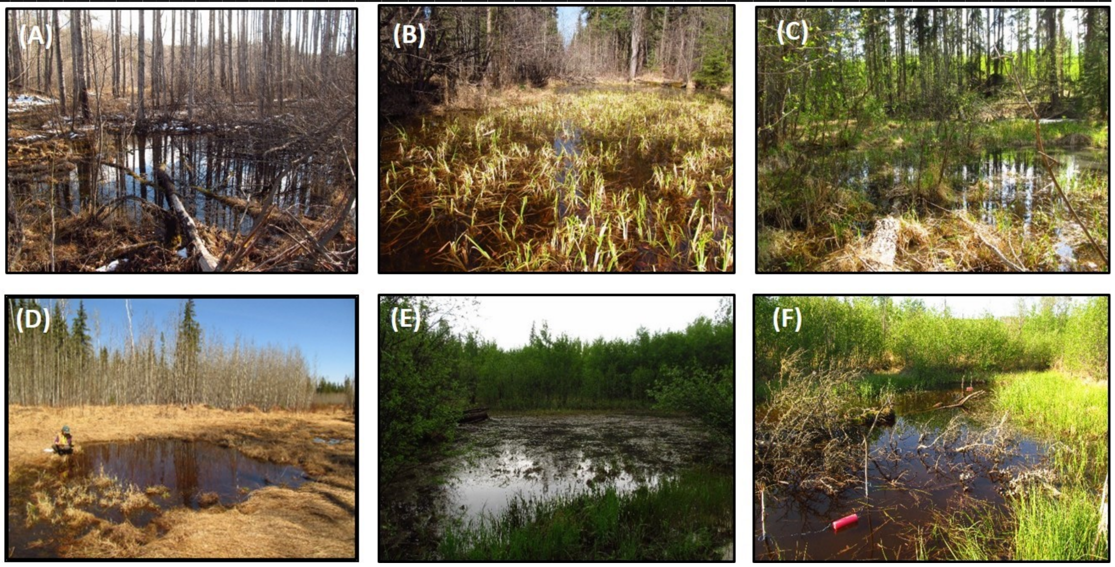

Figure A3-1. Examples of closed-canopy (top row; A - C) and open-canopy (bottom row; D – F) study wetlands sampled in 2015. (A) EA1, (B) FP1, (C) FP2, (D) I1, (E) EA68 and (F) P217.

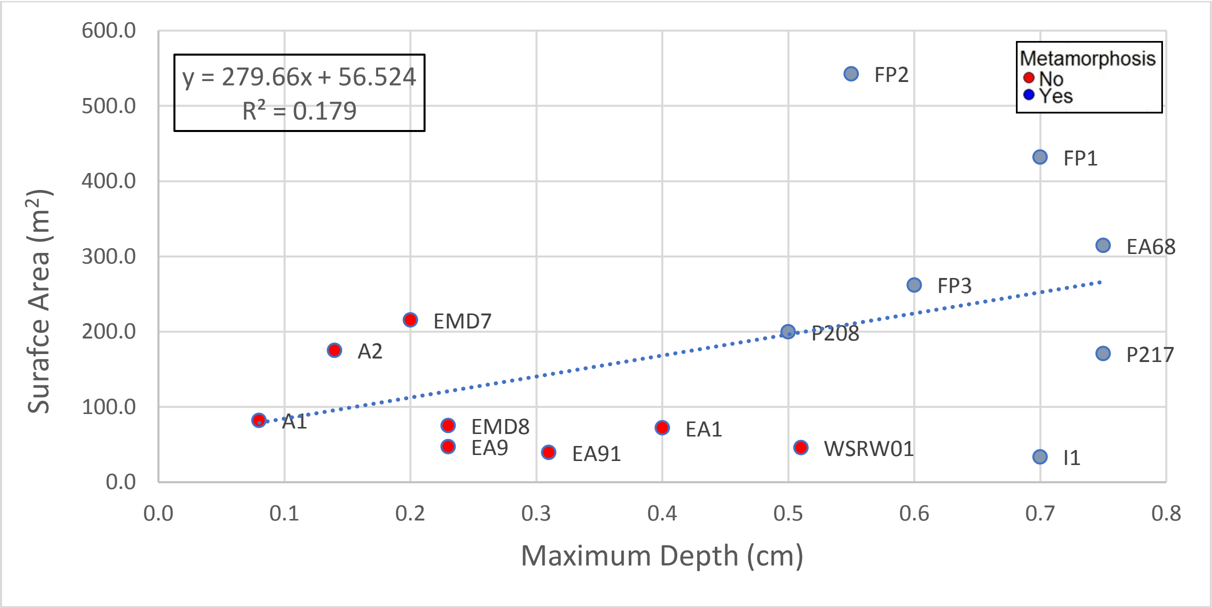

Figure A3-2. Relationship between maximum depth and surface area of 15 ephemeral wetlands surveyed in 2015. Identification (site ID) of each wetland is shown next to each marker. Marker color differentiates 'successful' (blue) and 'non-successful' (red) wetlands, based on whether wetland retained water long enough for tadpole to reach metamorphosis. Linear regression equation is given at top left.

Chapter 4 – General Conclusions and Management Implications

4.1 - General Conclusions

In chapter 2, I found that retention harvesting alone did not affect abundance of adult wood frogs in17-year post-harvest forests during either early or late season sampling. In late season, however, there was a significant interaction between retention and forest type; adult wood frog abundance generally decreased with retention level in deciduous sites, whereas in conifer sites, relative abundance increased with retention level. The interaction effect, however, was weak, and differences in capture rates between retention levels were relatively small. Forest type had a significant effect on adult wood frog abundance, but only during late season months (July and August), with capture rates significantly higher in conifer forests compared to deciduous forests. Aspen regrowth associated with early forest succession may partially explain observed variation in abundance between retention levels and forest types. In both deciduous and coniferous forests, leaf litter and canopy cover provided by 15+ year aspen in clearcut and lower retention stands may help provide suitable upland habitat for wood frogs following timber harvest.

I also found that soil moisture, as predicted by Depth-to-Water (DTW) index, was significantly related to adult wood frog abundance during late season, with higher capture rates at sampling sites with higher predicted soil moisture (lower DTW). Given that wood frogs, like other amphibians, are vulnerable to desiccation (DeMaynadier and Hunter, 1999; Semlitsch et al., 2009) and are often associated with moist habitats within forested uplands (Freidenfelds et al., 2011; Rittenhouse and Semlitsch, 2007; Roberts and Lewin, 1979), a greater availability of wet areas may have allowed increased wood frog activity during late season months when seasonal conditions were drier. Overall, convergence of habitat in deciduous and conifer forests from mature trees (pre-harvest) to early successional stands dominated by young trembling aspen, combined with availability of wet areas, may explain observed densities of adult wood frogs.

I did not observe an effect of breeding site proximity on upland abundance, which may be explained by the high number of breeding sites relative to pitfall arrays at some study sites, combined with availability of wet areas. Differences in young-of-the-year (YOY) captures reflected variation in the number and type of breeding habitats among study sites. The two study sites with the highest YOY captures, also had larger, more permanent breeding habitats which allowed tadpoles to reach metamorphosis. At my third study site, a single ephemeral wetland, with a relatively small breeding population, resulted in modest YOY captures at upland pitfall arrays, demonstrating that even very small wetlands may be important to local populations through recruitment. Finally, my fourth study site acted as a reproductive trap where, despite a relatively high number of breeding sites and reproductive effort (egg masses), all breeding sites dried prior to tadpoles completing metamorphosis. These findings underscore the importance of considering the number and type of potential breeding habitats within harvest areas for maintaining local amphibian populations in post-harvest forests.

Timber harvest in the boreal mixedwood blocks may be much larger (> 100 ha) than those studied at EMEND (~4-10 ha). EMEND provided a unique opportunity to examine seasonal patterns in wood frog abundance in post-harvest forests that varied in breeding site distribution and ground moisture. Although previous research has been conducted in Alberta on wood frogs and other amphibians in relation to forest management (Hannon et al., 2002; MacDonald et al., 2006; Browne et al., 2009; Constible et al., 2001), these studies were centered on large wetlands and lakes, and did not explicitly consider ground moisture or variation in breeding sites, particularly small ephemeral wetlands. This study may represent a more accurate characterization of habitat heterogeneity reflective of early successional post-harvests forests in the boreal mixedwood. Future research should examine multi-year population dynamics of wood frogs and other amphibian species in more recent variable retention harvest blocks.

In chapter 3, I found that wetland size was related to hydroperiod of ephemeral wetlands; larger and deeper wetlands generally had longer hydroperiods than smaller, shallower ones. However, maximum depth had a better relationship with hydroperiod than surface area, suggesting depth may be a more reliable predictor of hydroperiod than surface area alone. I found no relationship between hydroperiod and canopy cover. This was counter to my initial prediction that wetlands with greater canopy cover would have longer hydroperiods due to trees and vegetation reducing evaporation rates by blocking wind and solar radiation. My sample size of wetlands was small and included a range of sizes (depth and surface area); therefore, size effects may have obscured any effects of canopy cover on hydroperiod. Further, hydroperiods of ephemeral wetlands vary annually and a single year of sampling is unlikely to capture the range of hydroperiods expected across multiple years. To build on this research and better understand the hydrology of ephemeral wetland in the boreal, future studies should examine a larger sample of wetlands across multiple years, and investigate other possible factors influencing hydroperiod such as land-use, soil type, and topographic position.

Canopy cover had a negative effect on the performance of wood frog tadpoles; both growth (body size on a given date) and development (larval period) were faster in wetlands with less surrounding canopy cover; these results are consistent with studies in eastern North America (Halverson et al., 2003; Schiesari, 2006; Skelly et al., 2002; Werner and Glennemeier, 1999) and Alberta (Stevens et al., 2006). However, tadpoles successfully metamorphosed in both open- and closed-canopy wetlands, provided wetlands did not dry prematurely. Provided hydroperiod is sufficient, wetlands with less canopy cover may benefit wood frog tadpoles by allowing them to reach a larger body size and develop more rapidly, which may allow tadpoles to avoid mortality from drying ponds and increase survival in the terrestrial environment following metamorphosis.

Water temperature was higher in open-canopy wetlands relative to closed-canopy wetlands, which may help explain differences in tadpole performance. There was no significant difference in periphyton growth between open- and closed-canopy wetlands. Given the potential diversity of tadpole diets (Altig et al., 2007; Schiesari, 2006; Skelly and Golon, 2003; Stoler and Relyea, 2013), it is likely that my periphyton measurements did not adequately represent all potential food resources available to tadpoles in my study wetlands. Since previous studies have found that canopy-related gradients in food resource availability and quality can influence tadpole performance (Schiesari, 2006; Stoler and Relyea, 2013) future research is needed to evaluate variation in the abundance, distribution, and quality of potential food resources in ephemeral wetlands in the boreal mixedwood, as well as their potential effects on tadpole performance.

The current study was intended to investigate broad-scale effects of forest canopy cover and wetland size on hydroperiod and tadpole performance. Future research should examine effects of different types of forest canopy (e.g. conifer vs. deciduous) on tadpole performance. Differences in light transmission through conifer and deciduous canopies (Constabel and Lieffers, 1996; Stadt and Lieffers, 2000), as well as differences in carbon and nutrient inputs (e.g. leaf litter, conifer needles) (Stoler and Relyea, 2013), could potentially influence the growth, development, and survival of amphibian larvae by affecting seasonal water temperatures, water chemistry, and availability of food resources. In addition, this study likely did not encompass the full spectrum of wetland types in the boreal mixedwood, focusing only on mineral wetlands and excluding peatlands (fens and bogs). Further research should explore amphibian reproduction in a broader range of wetland types.

4.2 - Management Implications

My results suggest that habitat changes associated with early regeneration of aspen and other deciduous species may provide suitable upland habitat for wood frogs, in post-harvest deciduous and conifer forests. Further, availability of wet areas may help mitigate the effects of habitat change associated with forest harvesting and subsequent regeneration, especially during later summer months when wood frog activity may be more limited. Protection of potential breeding habitats (e.g. beaver ponds, permanent and ephemeral wetlands) with adequate depth and hydroperiod will help maintain local wood frog and other amphibian populations by providing a source of new recruits. Where possible, forest managers should balance retention between wet and dry upland areas to provide adequate shaded and moist refuge and foraging habitat for wood frogs. Retention should also be placed around small streams and ephemeral wetlands, as these are used by wood frogs and other boreal amphibians and may provide refuge and travel corridors between different habitats (Okonkwo, 2011).

Identification and protection of ephemeral wetlands during timber harvesting and other land-use activities is important to the conservation of wood frog and other amphibian populations. Wetland depth may serve as a useful criterion for prioritizing protection of small ephemeral wetlands during timber harvest. In years with below average rainfall, deeper wetlands will be more likely to retain water long enough for tadpoles to reach metamorphosis, whereas shallower wetlands may be more likely to dry prematurely. However, shallower breeding wetlands (< 50 cm in my study) may have hydroperiods sufficient to allow tadpole metamorphosis during wetter years. Smaller and shallower ephemeral wetlands also function as hydration sites for wood frogs and other amphibians (Okonkwo, 2011) and may help facilitate movements within and between local populations (Gibbs, 2000, 1993; Semlitsch, 2000). As such, the protection of smaller and shallower wetland habitat should not be overlooked by forest managers.

Vegetated buffers, where mature trees and other vegetation are retained around ephemeral wetlands during variable retention harvesting, would benefit local populations of wood frogs and other amphibians. Shade provided by trees and surrounding vegetation is likely to influence water evaporation and drying rates, as well as help moderate water temperatures. The basin and riparian areas of ephemeral wetlands should be avoided during harvest operations, and at a minimum, riparian vegetation and woody shrubs, such as alder and willow species, should be retained, as these will provide shade and cover around wetland basins. Retention of trees and other vegetation around ephemeral wetlands and associated wet areas, combined with connections to upland forest habitat, will benefit local populations by maintaining suitable conditions in the aquatic environment for larval growth and development, providing cover and refuge for adult and young-of-the-year amphibians, and providing travel corridors to facilitate movements between habitat types and nearby populations.

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