Spatio-temporal patterns in beaver pond complexes as habitat for Eastern spotted newts (*Notophthalmus viridescens*) in a hemlock-northern-hardwood zone in Western New York State.

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Spatio-temporal Patterns in Beaver Pond Complexes as Habitat for Eastern Spotted Newts (*Notophthalmus viridescens*) in a Hemlock-northern-hardwood Zone in Western New York State

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ABSTRACT

Amphibians are among the most threatened of animal groups, so understanding the nature and dynamics of their habitats is essential to their conservation. The Eastern Spotted Newt (*Notophthalmus viridescens*) prefers shallow quiescent soft-bottomed habitat, generally in small streams and pools. An increasingly important source of such habitat in the Northeast has been beaver ponds, which are abundant within the 27K ha Allegany State Park, NY, studied during this thesis. The main objective was to determine the influence of landscape-scale (size, age, and stability of ponds) and local habitat conditions (flow regime, sedimentary environment, submerged/emergent vegetation) on the use of beaver ponds as spotted newt habitat. Georeferenced satellite imagery between 1995 and present-day of five multi-pond complexes and one artificial impoundment were used to assess spatio-temporal stability of ponds and pond complexes, while proximate habitat characteristics were catalogued at individual survey points. Newts were visually surveyed in shallow water within 1 m of shoreline on multiple dates during April – June 2015. Both a factorial ANOVA (pond complex X habitat type) and multivariate Principle Components Analysis (PCA) ordination of landscape and habitat variables were used to assess patterns in habitat use by spotted newts. Newts were consistently abundant at pond complexes that were the most stable and predictable over time, which was a reflection of smaller watershed areas and lower potential for flood damage and breaching of dams. In contrast, less stable ponds yielded lower newt abundances. Some evidence suggested mud-bottomed pond margins, back-flooded connecting channels, and former pond remnants might be preferred habitat within ponds, but the overarching pattern was driven by landscape-scale variables.

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INTRODUCTION

Spatio-temporally dynamic ecosystems (e.g. riparian zones, tidal zones, estuaries) can provide a diverse mosaic of habitats for a variety of living things. Beaver-dominated landscapes potentially provide a geographically widespread example of such a spatio-temporal dynamic. Once hunted to the brink of extinction, North American beavers (*Castor canadensis*) have made remarkable population comebacks, with present population estimates of about 6-12 million in their formal ranges (Naiman et al. 1988, Butler 1995, Butler and Malanson 2005, Butler 2012). Beavers, with their ability to manipulate their environment, are considered a major keystone species and "ecological engineer", second only to humans in their capability to geomorphically alter the terrestrial landscape (Johnston and Naiman 1987, Meentemeyer and Butler 1999, Cunningham et al. 2007, Hossack et al. et al. 2015).

Low-order (1^{st} - 4^{th}) streams are dammed and impounded by beavers to create suitable habitat conditions with adequate food sources (Naiman 1988, Butler 1995, Meentemeyer and Butler 1999, Fuller and Peckarsky 2011, Butler 2012). Impounded streams lead to the development of beaver ponds and pond complexes, which may have lifespans ranging from one year to many centuries, and with physical and chemical conditions often varying, sometimes predictably, as they age (Naiman et al. 1988, Butler 1995). A widely documented process of dam and pond/or pond abandonment, recolonization, and abandonment again is referred to as the "beaver cycle" (Martell et al. 2006). Beaver "meadows" are usually the result of abandoned complexes, when ponds become infilled with sediment, creating meadows that are rich in organic material (Butler 1995, Snodgrass 1997). Rates of beaver-induced ecosystem changes are not temporally and/or spatially constant – beaver ponds even closely adjacent along streams do not necessarily have identical habitats or ecosystem parameters. Temporal shifts can also occur from fluctuations in beaver populations resulting from food supply, predation, and disease (Naiman et al. 1988).

Predictable successional patterns of various wetland and vegetation types may be a reflection of the beaver cycle process, and are important for biodiversity of organisms such as invertebrates, fishes, birds, and ungulates (Neff 1957, Snodgrass 1997, Cunningham 2003, Cunningham et al. 2007, Martell et al. 2006). For example, small fish use beaver ponds as rearing units and for feeding on plankton and other microorganisms found in ponds (Hardisky 2011) as well as for protection in the deep water during winter months (Hardisky 2011, Johnston 2011). Various stages of beaver ponds are beneficial to avian species as well. For example, waterfowl utilize active beaver ponds for feeding, nesting, and migratory stopovers (Hardisky 2011), and have higher species richness at these active sites (Johnston 2012). Birds as well as bats utilize dead tree stands in ponds as roosting habitat (Johnston 2012).

Amphibians are a diverse but severely threatened group of organisms that may benefit from beaver ponds, often occurring there at increased abundance and diversity, especially true for anurans (Stevens 2006a, Johnston 2012, Hossack et al. 2015). Because the majority of amphibians that inhabit aquatic environments are at risk of declines because of habitat degradation alone (Alford and Richards 1999, Gallant et al. 2007, Stevens 2006a, Karraker and Gibbs 2009), beaver-dominated landscapes that offer habitat heterogeneity could be imperative for the conservation of amphibians (Stevens 2006a, Karraker and Gibbs 2009). Hydroperiods, or the time span of wetland floodings, strongly regulate amphibian community structure, and because beavers are able to manipulate hydrology and increase the extent of long hydroperiod wetlands, beaver impoundments may be able to provide higher diversity and species richness among amphibians (Cunningham 2003, Cunningham et al. 2007, Karraker and Gibbs 2009). Beavers are also able to enhance connectivity of stream corridors by reducing the distance between suitable habitat sites, (Cunningham 2003, Joly et al. 2001, Hossack et al. 2015) and distance between wetlands and adjoining terrestrial environments that may attract amphibians (Marcin and Metrack 2014). Therefore, in order to conserve amphibian species richness, connectivity and diversity of wetlands with regard to hydroperiod must be maintained (Cunningham 2003, Marcin and Metrack 2014). As beaver populations become greater, the number of available wetlands increases while inter-wetland distances decrease, potentially benefitting amphibian species because of the expansion of preferred habitat and decreased mortality rates in areas considered unsuitable (Joly et al. 2001, Cunningham 2003). Beaver complexes also contain shallow pond margins and have high insolation: conditions that are highly preferred by pond-breeding amphibians, for which warmer waters are essential for rapid growth and development of larvae (Dalbeck et al. 2007, Hossack et al. 2015, Stevens et al. 2006a).

The Eastern spotted red newt (*Notophthalmus viridescens*) is a pond-breeding salamander that serves as a proxy for studying a beaver-generated habitat matrix. Newts are adapted to ponds that can spatially and temporally shift rapidly, and beaver ponds, given their small size and dynamic morphology, may provide particularly suitable habitats (Gill 1978, Metts et al. 2001). Adult spotted newts may also have the ability to colonize new ponds quickly (Gill 1978), and the temporal shifts of beaver ponds to suddenly emerge in a season may be alluring to adult spotted newts. At the 27,000 hectare Allegany State Park (ASP, FIGURE 1), scores of active and inactive beaver complexes are widespread throughout the area (NY State Office of Parks, Recreation, and Historic Preservation 2010). Historical anthropogenic activities such a logging and farming were abundant amid the property, and although not practiced today, areas that were logged were often replaced with timber plantations, or were recolonized by early successional hardwoods (NY State Office of Parks, Recreation, and Historic Preservation 2010). Historical distributions of beavers within the park are not fully known (but see Shadle and Austin 1939, Shadle et al. 1943), but, at present, pond complexes are clearly concentrated within these areas of anthropogenic impact. Personal observations indicated spotted newts were abundant in and around beaver pond complexes within Allegany State Park. However, 1^{st} - 4^{th} order streams not modified by beavers usually do not contain any newts, which instead prefer shallow wetlands with abundant vegetation and still bodies of water that are no deeper than 1 meter (Sousa 1985, Pfinsten and Downs 1989, Marion and Hay 2011).

It is important to understand amphibian responses to changes at both local (pond) and landscape scale in order to properly manage their conservation (Cunningham 2003, Stevens et al. 2006a), so investigating spatio-temporal patterns of selected ASP beaver complexes and how they provide varying degrees of preferred habitat may contribute to amphibian conservation.

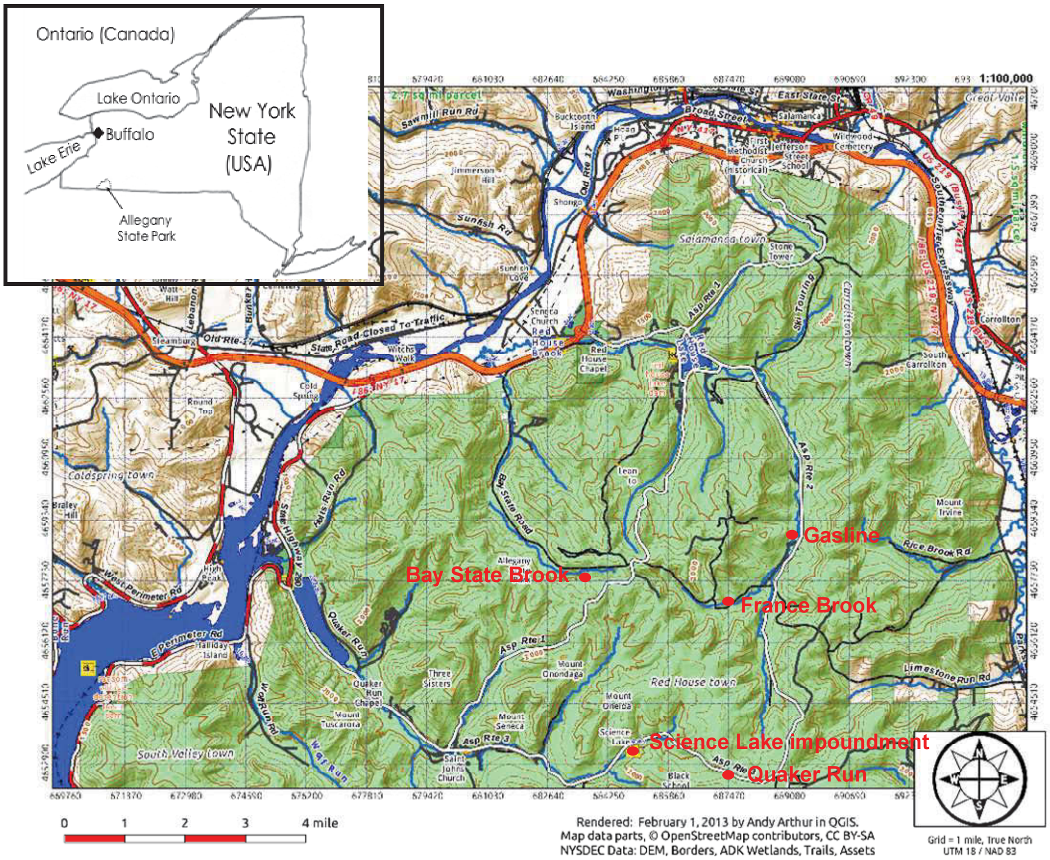

FIGURE 1. Regional site location and Allegany State Park detail showing locations of beaver pond complexes and Science Lake impoundment.

The main objective of this study is to determine the influence of size, age, and stability of beaver ponds on their occupancy by Eastern spotted red newts, and also how basic spatio-temporal (seasonal to decadal) dynamics of beaver ponds and their specific environmental characteristics influence their role as suitable habitat for Eastern spotted red newts. More specifically, patterns of stability and predictability of whole beaver complexes and individual ponds were assessed at a landscape scale (10's-100's hectares), whereas local characteristics such as water depth, current flow, and substrate type were cataloged to evaluate, at a finer scale (meters to tens of meters), habitat suitability at individual newt survey locations. Thus, this study's major objective can be envisioned as two broadly testable hypotheses: 1) that landscape-scale pond dynamics significantly influence newt abundance, and 2) that local-scale habitat characteristics do so. Of course, these two factors may interact to varying degrees.

LITERATURE REVIEW

Eastern spotted red newts (*Notophthalmus viridescens*)

Life History

Notophthalmus viridescens (Eastern spotted red newt) has one of the most complex life histories in regards to salamanders (Pfingsten and Downs 1989, Roe and Grayson 2008, Pfingsten et al. 2013), and is also one of the most widely distributed salamanders in North America (Marion and Hay 2011). The spotted red newt has four metamorphic life stages. The egg and larval stages are entirely aquatic, but after metamophosis from the larvae to the juvenile stage, newts will emigrate out of their natal ponds and become entirely terrestrial for about 3-7 years, after which they metamorphose into an aquatic adult (Pfingsten and Downs 1989, Roe and Grayson 2008, Pfingsten et al. 2013). Courtship occurs in March through June and eggs are laid in temporary or permanent ponds or shallow lakes in which females will usually deposit 50-300 eggs several days after mating (Pfingsten and Downs 1989, Mitchell and Gibbons 2010). Larvae will start to appear 3-5 weeks after deposition, usually appearing in June and continuing to appear throughout the summer and early fall (Pfingsten and Downs 1989, Pfingsten et al. 2013).

At the end of July to November, the larvae will metamorphose into the post larval or terrestrial "red eft" stage, having a snout-vent length of 27-71 mm. The eft skin is dry, granular, and has a reddish-orange dorsal coloration with yellow spots (Pfingsten and Downs 1989, Mitchell and Gibbons 2010). The skin of all the life stages contains a powerful neurotoxin, tetrodotoxin (TTX) that makes them able to escape predation. The red eft stage is the most toxic (ten times more than adults), followed by adults, eggs, and the larval stage (Pfingsten and Downs 1989, Marion and Hay 2011). While not a focus of thesis, it is interesting to suggest that such predator resistance may play a role in the newts' tendency to often occupy very exposed positions in both aquatic and terrestrial habitats. Efts will migrate away from their natal ponds, sometimes exceeding several kilometers, and are able to travel across open and forested areas where they take cover under logs, boards, and brush (Pfingsten and Downs 1989, Roe and Grayson 2008, Rinehart et al. 2009). Being active both day and night, efts can survive in drier conditions where they forage the forest floor for worms, grubs, and small insects (Pfingsten and Downs 1989, Mitchell and Gibbons 2010). Optimal temperatures for abundant eft activity are usually above 14°C (53°F), and growth and development are determined by the amount of rainy days, with wetter years leading to more foraging and faster growth (Pfingsten and Downs1989).

Transformation to the final adult stage (snout-vent length of 30-54 mm) happens in August and September when efts migrate back to the home ponds, becoming completely aquatic in early autumn (Pfingsten and Downs 1989, Mitchell and Gibbons 2010). The dry, orange skin will turn olive green with the same yellow spots and become smooth and moist (Pfingsten and Downs 1989, Roe and Grayson 2008). Males develop particularly large tail fins (Roe and Grayson 2008). The newly transformed adults start to breed the following spring. Their diet changes as well, now preying on zooplankton, mayfly nymphs, caddisfly larvae, mosquito larvae and pupae, and the eggs and larvae of other species of amphibians (Pfingsten and Downs 1989).

The adults can either remain entirely aquatic or can migrate to a terrestrial habitat during the non-breeding season, whereupon the tail fin will reduce in size, and a light to dark brown skin coloration will develop (Pfingsten and Downs 1989, Mitchell and Gibbons 2010). Adults have shown various behaviors in migration, depending on sex and size (Roe and Grayson 2008). Males may have more of an advantage by staying close to home ponds in order to gain an early breeding start, whereas females have been shown to migrate far from home ponds, possibly skipping a breeding season, and remaining in the terrestrial habitat (Roe and Grayson 2008). Size of the body may also play a role in migration, and reproductive success can be related to body size. Smaller adults may migrate far from home ponds in order to skip a breeding year to forage, whereas larger adults will remain close to the home ponds to mate each year (Roe and Grayson 2008).

Habitat

Notophthalmus viridescens is distributed in the Eastern United States and Southeastern Canada, and found occupying lentic bodies of water that can be permanent or temporary, including small shallow ponds, roadside ditches, vernal pools, and beaver impoundments (Pfingsten and Downs 1989, Marion and Hay 2011, Pfingsten et al. 2013). Newts, however, are also capable of inhabiting lakes and slow-moving streams (Pfingsten and Downs 1989, Mitchell and Gibbons 2010). Hardwood forests are the primary habitat for red efts and terrestrial adults, but terrestrial newts can also occur in pine forests and in nearby fields (Sousa 1985, Mitchell and Gibbons 2010), usually persisting in drier conditions underneath boards, logs, or brush (Pfingsten and Downs 1989, Pfingsten et al. 2013). Preferred habitats for aquatic life stages are shallow wetlands with abundant vegetation and still bodies of water that are no deeper than 1 meter (Pfingsten and Downs 1989, Marion and Hay 2011). It is thought that adult newts will stay and breed in their home pond year-round (even throughout the winter) as long as the pond is deep enough not to freeze (Pfingsten and Downs 1989, Pfingsten et al. 2013). If the ponds do freeze solid, or if they dry up, adults will either migrate to a different pond or find protection in moist semi-aquatic environments until the pond fills up again or until the following breeding season (Pfingsten and Downs 1989, Mitchell and Hay 2011).

Threats

Amphibians face major population declines world-wide, from major threats such as exposure to UV radiation, pollutants, climate change, diseases, land use practices, exotic pet trade, and invasive species (Alford and Richards 1999, Gallant et al. 2007, Karraker and Gibbs 2009, Rinehart et al. 2009). Emerging diseases that amphibians have been facing recently include the chyrid fungus *Batrachochytrium dendrobatidis*, the *Saprolegnia* fungi, ranoviruses, and *Ribeiroia* trematodes (Raffel et al. 2008, Piovia-Scott et al. 2011, Eskew and Todd 2013). The disease Chytridiomycosis is caused by the fungal pathogen *Batrachochytrium dendrobtidis* (Bd), and is the leading and most common disease causing amphibian population declines, especially those amphibians residing in montane or higher elevation habitats (Raffel et al. 2008, Piovia-Scottet al. 2011). Because *Bd* is an aquatic fungus, it can survive in aqueous environments for several weeks, causing mortality by infecting the keratinized skin of adult amphibians, blocking oxygen exchange and causing electrolyte imbalance that will ultimately result in suffocation and cardiac arrest (Piovia-Scott et al. 2011, Eskew and Todd 2013). Even though the origin of the disease is relatively unknown, its pathogenicity may have increased as a result of climate change or land degradation (Eskew and Todd 2013). The international pet trade may be a major factor in spreading *Bd* infection; amphibians residing in pet stores, zoos, food markets, and museums are known to carry the disease (Eskew and Todd 2013).

Chemical pollutants that may turn aquatic ecosystems acidic may limit the abundance and distribution of amphibians (Alford and Richards 1999, Sherman and Van Munster 2012). Because of their permeable skin and aquatic breeding activities, amphibians are especially vulnerable to acidic environments, causing health problems such as immune functions, embryonic development and hatching, larval growth and development, and ion regulation (Alford and Richards 1999, Sherman and Van Munster 2012). Nitrogenous compounds from fertilizers and cattle pastures are increased in aquatic habitats, and could negatively impact amphibians (Secondi et al. 2013). Oxygen transfer is disrupted by nitrate and resistance to physical effort is reduced (Secondi et al. 2013). Larval amphibians exposed to nitrate can suffer reduced growth and survival, and oxygen fixation can be disrupted in adults. This could increase the number of times they surface, exposing them to predation risks, and suspending courtship behaviors for aquatic breeders (Secondi et al. 2013).

Drier conditions associated with global climate change may cause amphibian declines, being a threat the life history and physiology of amphibians (Alford and Richards 1999, Rohr and Madison 2003). Accelerated drying in ponds and the lakes can dehydrate eggs and larvae warming trends and prolonged hydrologic variability (Rohr and Madison 2003), yet land use practices are probably the most severe threats to amphibians, in which habitat loss and fragmentation can alter availability and spatial arrangements of habitats as well as alter the natural disturbance regime (Alford and

Richards 1999, Gallant et al. 2007, Rinehart et al. 2009). Terrestrial amphibian distribution is negatively related to urban land cover, while positively related to percentage of forest cover (Rinehart et al. 2009). As new housing developments are built, road densities are increased and natural cover is reduced. Roads may directly contribute to amphibian mortality, if their location requires amphibians to cross them when migrating between habitats (Rinehart et al. 2009). Ecosystems that are close to roadsides can also be affected by chemical run-off from road deicing salts, primarily NaCl and MgCl2, with roadside habitats having higher Cl- concentrations than non-roadside habitats (Hopkins et al. 2013). Amphibians residing along roads are especially vulnerable to deicing salts their permeable skin and eggs (which can hatch earlier and underdeveloped), and they may also suffer possible spinal and gill deformities and growth of cysts (Hopkins et al. 2013).

North American Beaver (*Castor canadensis*)

Life History

Castor canadensis is the largest rodent in North America, with adults having an average weight of 14-29 kg and a body length of 89-135 cm and a tail length of 24-45 cm (Hardisky 2011). They have powerful muscles and incisor teeth used for cutting trees and peeling bark, and these semi-aquatic animals are well-adapted to watery environments and to dark and humid enclosures such as burrows and lodges. The hind feet are webbed to propel themselves through water, whereas the front paws are not webbed but heavily clawed for digging, and the scaly, flat tail is used to maneuver while swimming, signaling danger, balancing themselves on land, heat exchange, and storing fat during winter (Butler 1995, Hardisky 2011).

Food and construction preferences are dependent on the region and availability of resources. Preferred species are typically aspens, cottonwoods, willows, birch, and poplars, but beavers will use softwoods such as pines if necessary (Butler 1995). The beaver's digestive system can utilize cellulose, and they can maximize nutritional value even when consuming only bark (Hardisky 2011). Wild beavers do not live for more than 10 years, but can live to 21 years in captivity. Human beings are currently the beaver's major predator. The only other predator to make significant impacts on adult beaver populations is the timber wolf, but others such as coyotes, river otters, bobcats, minks, and bears will prey on juveniles (Hardisky 2011).

Habitat

The North American beaver is extremely widespread in North America, with the exceptions of peninsular Florida, the Arctic north of the tree line, and arid environments of the southwest (Butler 1995). The extensive range of the *Castor canadensis* can include a variety of geologic settings such as mountain streams, blackwater streams in the southeastern U.S., river deltas and floodplains, karst terrain, and peatlands (Johnston 2012). Beavers are major zoogeomorphological agents in low-order, 1^{st}-4^{th} order streams as they dam and impound running water in order to create suitable habitat conditions with adequate food sources (Butler 1995, Meentemeyer and Butler 1999, Fuller and Peckarsky 2011, Butler 2012). Beaver colonies occupy ponds or stretch of a stream and use common food supplies and maintain a common dam or dams (Gurnell 1998). As beaver populations increase, they can rapidly spread into suitable neighboring habitats, making it possible for the beaver to colonize as far as 736 km from the original site over a 46-year period (Gurnell 1998).

If the population density is too high, or surface streams are too large, or if there is not enough woody vegetation to build a dam, beavers will dig bank burrows and dens (Butler 1995). Colony density will vary depending on habitat quality and on the degree of geomorphic stability of the immediate environment, and this is an important factor in the number of dams that may be built (Gurnell 1998). Beavers are also able to inhabit areas that are too large to dam, such as along the margins of lakes and rivers inside burrows or lodges (Johnston 2012). Beaver lodges are built mainly out of wood and mud, and usually located at the center of the pond (Butler and Malanson 2005). Pond complexes can function for decades, and act as sediment sinks, efficiently trapping sediments, reducing stream velocity, and altering the landscape (Meentemeyer and Butler 1999, Butler and Malanson 2005).

Beaver Conservation and History

Before the colonization of Europeans to North America, the American beaver (*Castor canadensis*) occupied every state in the U.S. except Hawaii, and every Canadian province (Butler and Malanson 2005). Beavers were driven to near extinction across North America during the 1700's and 1800's for their highly valued fur, with an estimated 500,000 beavers taken in North America in the mid 1700's (Hardisky 2011). Beavers had been eliminated in most of North America by the end of the 1800's (Hardisky 2011), but by the turn of the 20th century, strong conservation laws came into practice (Butler 1995), with successful restoration practices during the 1920's and 1930's bringing substantial population growth (Hardisky 2011).

Today, population estimates of about 6-12 million beavers reside in almost all of their formal ranges. However, this is still only about 10% of their pre-European population of 60-400 million (Butler 1995, Butler and Malanson 2005, Butler 2012). However, beaver recovery has been successful, with dam building and development of ponds expanding. Despite beaver activities having some negative impacts on anthropogenic land uses, such as plugging culverts, damaging roads flooding, downing valuable timber, and killing desirable wetland plant species, beaver ponds are generally regarded as beneficial because they create wetland ecosystems (Butler 1995, Johnston 2012).

<u>Beaver Dams</u>

Beavers are opportunists when it comes to construction material used for dam building. Even though harvested wood and brush (and mud) are the primary materials, they may also use logs that were brought down from natural disasters, along with human trash (Butler 1995). Mud is used for sealing the dam, with most mud condensed along the upstream slope of the dam (Butler 1995). Dam sizes can range from 15-70 meters long and 1-2 meters wide, usually arched and concave upstream (Butler 1995). This may be dependent on the nature of the materials being used. For example, willows are not as sturdy as aspen trees, and their use would result in smaller dams and more ephemeral ponds, but they could still be used if they were more abundant in an area than other sturdier species (Butler 1995).

Beaver dam site suitability is heavily influenced by stream gradient, with stream gradients of 6% or less considered optimal, and gradients greater than 15% considered unsuitable for beaver, according to the U.S. Fish and Wildlife Service habitat suitability index (HSI) (Johnston 2012). Force of the stream increases from steeper slopes, increasing the likelihood that high stream flows will burst through dams (Johnston 2012).

In cooler climates, dams are active in the spring and summer, while in more humid conditions they are maintained year-round, and can last for decades or centuries (Butler 1995).

Types of Dams

There have been four morpho-hydrological types of beaver dams recognized (Waddington and Woo 1990):

1. Dams with stream-flow overtopping, or "overflow" dams
2. Dams with water funneling through gaps in the dam crest, or "gap-flow" dams
3. Dams with water moving through the weakened bottom structure, or "underflow" dams
4. Dams with water seeping through the entire dam structure, or "through-flow" dams

Effects of Beaver Dams

Beaver dams have various hydrological effects, including alterations of the drainage pattern of areas, developments of diversion channels, multiple-surface flow paths, downstream discharge reduction during dry spells below overflow and gap-flow dams, discharge alterations during high flow, and alterations to the overall water balance (Butler 1995). Damming can also elevate the water table, recharge groundwater and impact groundwater flow patterns, and expand riparian ecosystems and flooded soils (Butler 1995, Fuller and Peckarsky 2011). Elevated water tables from beaver damming can sometimes have negative impacts on surrounding forested ecosystems, causing tree death from saturated root zones. An estimated 50-60% of wood material collected for construction of their ponds may result from this source of mortality (Butler 1995). It has been found that when beaver dams are removed, water tables will drop, diversity and productivity of riparian vegetation may decline, and downstream water quality may be impacted by the release of stored sediment and nutrients (Butler 2005). Severe entrenchment (i.e. the new stream carving a very direct and narrow path) can also occur from dam removal, which will increase stream power after and erosive effects (Butler and Malanson 2005).

<u>Catastrophic Dam Failure</u>

Beaver dams may fail suddenly from natural causes, an event known as catastrophic dam failure (Butler and Malanson 2005). This could result from many different processes, including rapid snowmelt, intense precipitation in a short amount of time, animals burrowing through the dam (such as otters), collapse of upstream dams causing a "domino effect" to dams located downstream, and human interference (Butler 1995, Butler and Malanson 2005). Beavers will also breach their own dams from time to time to drain water from the ponds. Although this reason for this is unknown, it has been speculated that this is done for sanitary purposes (Butler 1995). The minimum precipitation that is necessary to cause a dam to collapse may depend on topography and vegetation, with reported measurements of 75-80 mm of precipitation exceeded in a 24-hour period causing a dam to collapse (Butler 1995). Stream morphology and biota may be severely impacted by beaver flooding from dam bursts (Butler 1995). Base levels of the stream beds have been found to be lowered, gravels that were deposited against the upstream part of the beaver dam were flushed away, and silt deposited in the channels below the dam may cover and suffocate benthic organisms and fish eggs (Butler 1995). Catastrophic dam collapse could be considered an unpredictable disturbance event when looking at landscape ecology and geomorphology (Butler 1995).

Beaver Ponds

Ponds provide many benefits to resident beavers, including protection from predators, easy access to food and construction material, and a defense perimeter around the beaver lodges (Butler 1995). Lodges will have an underwater outlet that leads from the pond to inside the lodge, and the construction material provides sturdy structure and longevity to the lodges (Butler 1995). Beaver canals can range in size from less than 1 meter to well over 100 meters in length, and can be 35 cm to 1.0 meter or greater in width (Butler 1995). Canals are usually used to transport logs to the lodges and also to divert water for pond depth maintenance and to access bank burrows (Butler 1995). Several bank burrows can be built around the pond, having particular importance in environments where the conditions for dam and pond development are not fit (Butler 1995). The creation of bank burrows may be dependent on the type of substrate. For example, fine-grained alluvium would be easy to burrow in, as opposed to gravely or rocky alluvium, where burrows would most likely be absent (Butler 1995).

Beaver Pond Succession

The sequence of stages that beaver ponds go through during their lifespans is known as succession, and although a dynamic process, few investigations have been made on classifying pond stages. Four stages of pond succession were identified from a study in Pennsylvania that was based on initial conditions and beaver activity: 1) new-forested, 2) new-open, 3) old-active, and 4) abandoned (Brown 1999, Hardisky 2011).

The first two stages happen when a dam is built and a pond is created, with forested cover and surface water present (Brown 1999). The old-active stage has a wider dam and larger pond with little forested cover, and finally the abandoned stage has water level decreases from breaks in the unmaintained dam, and shrubs and herbaceous plants eventually become the dominant vegetation (Brown 1999).

The reduced ability of beaver dams to transport sediment via a lowering of the slope of the stream channel will ultimately lead to ponds becoming infilled with sediment (Butler 1995). Beaver dams and ponds will act as settling pools that will step down flow velocity and then reduce erosion potential. Beaver meadows are thus created from these events, or those meadows that are rich in organic material following the events (Butler 1995). There have been few studies on the rate of sedimentation in beaver ponds, with reports claiming that beaver ponds may form meadows in 12 years, with infilling rates of about one cm per year (Butler 1995). Small channels openings at the crest of the dams are created in order to relieve pressure from high waters, and overflow and through-flow can serve to relieve high pressure and to defend against high water events (Butler 1995).

Ecological Influences of Beavers and their Activity

Beavers are considered a major keystone species and "ecological engineers" and are second only to humans to geomorphically alter the terrestrial landscape (Meentemeyer and Butler 1999). Accumulations of water and sediment in stream channels from beaver dams are known as patch bodies, and are important for ecosystem stability because they provide large reserves of carbon and nutrients (Naiman et al. 1988). The beaver pond, aerobic soil beneath the pond, and the underlying anaerobic soil make up a patch body which has different processes and importance than the original stream channel patch bodies (Naiman et al. 1988). For instance, invertebrate taxa that inhabit running water are replaced by invertebrate taxa that inhabit ponds finer sediments and a decrease in current speed (Naiman et al. 1988). Biomass and total density are greater in ponds that at riffle sites, being 2-5 times greater in ponds (Naiman et al. 1988).

Beavers can drastically change the diversity and composition of vegetation. Until adequate food sources are reestablished, vegetation such as rushes, woolgrass, tussock sedge, and other grasses are usually found in beaver meadows, and can promote growth of other plant species, increasing herbaceous plant diversity (Bonner et al. 2009, Johnston 2012). Following beaver dam development, plant species richness increases and species will change in composition, and seed banks along flooded ponds will establish new vegetation when there are changes in water levels (Bonner et al. 2009). Even though beaver activity can increase plant species richness, little is known about the impacts to rare vegetation and community composition (Bonner et al. 2009).

Forest succession is altered from flooding caused by dam construction, leading to changes in stream morphology, sediment retention, vegetative composition, and invertebrate communities (Bonner et al. 2009). Beavers cut down about a metric ton of wood within 100 m of their ponds annually in northern regions (Naiman et al. 1988). Deciduous trees in riparian zones that are preferred by beavers may be completely clear-cut, and non-browsed species such as black spruce and balsam fir may eventually become the primary streamside vegetation (Naiman et al. 1988). In forested areas, construction of beaver dams can cause predictable patterns of vegetation changes:

1. flooded forest
2. tree death and toppling

3. ponds containing submergent, floating-leaved, and emergent wetland plants
4. drained ponds with exposed sediments
5. drained pond revegetated to grasses and sedges

In previously abandoned areas that were converted into meadows, beavers will often re-flood those areas and turn them back into beaver ponds (Johnston 2012).

Ecological Benefits of Beaver Activity to Fish and Wildlife

Beaver ponds and meadows can provide important habitats to fish and wildlife as well, including river otters, small mammals, waterfowl, fish, aquatic invertebrates, reptiles and amphibians. Increased willow growth from beaver flooding also provides browse for elk and other ungulates (Johnston 2012). Small fish use ponds as rearing units from plankton and other microorganisms found in the ponds, as well as protection in the deep water during the winter months (Hardisky 2011). Avian, waterfowl, and aquatic mammals benefit as well from the plant diversity and standing water that beaver impoundments provide (Hardisky 2011). Stages of beaver ponds are beneficial to avian species, for example, waterfowl utilize active beaver ponds for feeding, nesting, and migratory habitat (Hardisky 2011). Songbirds that are dependent on wetlands benefit from different successional stages for nesting and foraging requirements (Hardisky 2011). Beaver ponds have been found to increase abundance and diversity of amphibians, especially anurans, and beaver lodges can also promote amphibian diversity (Johnston 2012). However, little is known about how beaver impoundments affect herpetofauna as compared to other wildlife (Metts et al. 2001).

Beaver Ponds as Habitat for *Notophthalmus viridescens*

Although relatively few studies specifically address how amphibian populations are influenced in beaver modified landscapes (e.g. Metts et al. 2001, Cunningham 2003, Stevens et al. 2006a, 2006b), these have revealed the influence that impoundments have on amphibian species. In amphibian communities, hydroperiods strongly regulate community structure, and because beavers are able to manipulate hydrology and increase longer hydroperiod wetlands, beaver impoundments may be able to provide higher diversity and species richness among amphibians (Cunningham 2003). A study by Metts et al. (2001) found that herpetofauna communities and diversity were significantly influenced by beaver impoundments in western South Carolina (Metts et al. 2001). Although beaver ponds supported richness and diversity of turtles, lizards, and anurans, unimpounded streams contained more salamander species than did beaver impoundments (Metts 2001). Predatory fish species inhabiting the ponds may have been responsible for the lower salamander abundance, along with species-specific life history traits and habitat conditions that account for the variation of abundance between beaver impoundments (Metts et al. 2001). For example, salamander species (such as *Desmognathus* spp.) that inhabit fast-flowing streams will usually not be present in lentic ponds and slow-flowing streams. However, other salamander species that are pond-breeders, such as *Notophthalmus viridescens*, have been found to be more abundant near beaver impoundments than in unimpounded streams (Metts et al. 2001).

METHODS

Study Area

Allegany State Park (42° 0'N/78° 45'W) is a 27K ha state park located in Cattaraugus County in southwestern New York that is adjoined to the Allegheny National Forest in Northern Pennsylvania (Mason 1936, NY State Office of Parks, Recreation, and Historic Preservation 2010). The park has a maximum relief of 305 meters and most of its hills range from 152 to 213 m high, rising much steeper in the narrow valleys (Mason 1936) and being dissected by abundant streams (NY State Office of Parks, Recreation, and Historic Preservation 2010). Because the main drainage divide extends from north to south, the western and eastern portions of the park differ greatly in their valleys. The valleys on the west side are longer with a gentle slope, whereas those valleys on the east side are steeper and shorter. The underlying Paleozoic rock is horizontal and sedimentary, and the park on whole was affected little by the folding disturbance at the end of the Paleozoic era that occurred in the western regions of the Allegheny Plateau (Mason 1936, NY State Office of Parks, Recreation, and Historic Preservation 2010).

The park was never entirely affected by glaciation. Areas north and outside of ASP that were beneath ice have glacial-drift-filled valleys and lowered hills, whereas areas that were not under ice have deeper valleys and steep slopes (Mason 1936, NY State Office of Parks, Recreation, and Historic Preservation 2010). Surface streams in Allegany State Park are abundant the amount of annual rainfall. However, because the runoff is partitioned by the large number of valleys, the streams in the park are small (Mason 1936). The climate at Allegany State Park is overall cool and humid with variations in temperatures and rainfall, which is caused by the area's mountainous topography (Mason 1936, NY State Office of Parks, Recreation, and Historic Preservation 2010). The winters tend to be long and snowy and the summers short and somewhat rainy, with evenly distributed precipitation occurring throughout the year (Mason 1936, NY State Office of Parks, Recreation, and Historic Preservation 2010).

Allegany State Park sits on the Allegheny Plateau and is part of the Allegheny Highlands, an ecoregion with temperate broad-leafed mixed forest type that lies in eastern portions of Ohio, northern Pennsylvania, and northwestern New York (NY State Department of Parks, Recreation, and Historic Preservation 2010, World Wildlife Fund 2015). The highlands were primarily dominated by beech (*Fagus grandifolia*), and hemlock (*Tsuga canadensis*), during presettlement days, but heavy logging on the Allegheny Plateau between 1890 and 1920 cleared most of the hardwoods and coniferous species, leading to widespread fires that promoted species such as pin cherry (*Prunus pensylvanica*), aspen (*Populus tremuloides*), honeysuckle (*Lonicera* spp.), grasses, and sedges (NY State Office of Parks, Recreation, and Historic Preservation 2010, World Wildlife Fund 2015). Allegany State Park, at present, contains 283 ha of old growth forest (World Wildlife Fund 2015). The 728 ha Big Basin contains 162 ha of old growth, with a possibility of 202-243 ha of old growth and trees as old as 250-350 years old (Davis 2003). Trees such as hemlock (*Tsuga canadensis*), sugar maple *(Acer* saccharum), black cherry (*Prunus serotina*), and yellow birch (*Betula alleghaniensis*), are the dominant tree species (Davis 2003). Various tree stands occur depending on the geography of the park. Oak-chestnut stands are dominant on the southwestern steeper slopes where the ridges are dry and exposed, the red oak (*Quercus rubra*), being the primary species and the formally abundant chestnut (*Castanea dentata*), being replaced with red maple (*Acer rubrum*), hickory (*Carya* spp), and black oaks (*Quercus velutina*), (Mason 1936). The oak-chestnut understory is dominated by dogwood (*Cornus* spp.), blueberry (*Vaccinium* spp), and sassafras (*Sassafras albidum*). Beech-maple-hemlock stands dominate the slopes below moist ridge tops with an understory consisting of red elderberry (*Sambucus racemosa*), and hobblebush (*Viburnum lantanoides*) (Mason 1936).

The park was a good resource for the manufacturing of black salts by early settlers in Cattaraugus county, a process in which birch, beech, oak, elm, or maple were burned and then used water to leak through the ashes, which was boiled to crystallize the salts (Mason 1936). Other primary tree species were used for other purposes, such as hemlock in the tanning industry, white pine for lumber, and other hardwoods such as maple, beech, and oak for the chemical wood industry, in which acetate lime and wood alcohol were distilled from the wood (Mason 1936). It wasn't until 1921 that Allegany State Park became an official state park by the State Legislature in partnership with the Buffalo Society of Natural Resources and the Erie County Society for the Protection of Birds, Fish and Game (Mason 1936, NY State Office of Parks, Recreation, and Historic Preservation 2010). The creation of the park met the need for western New York to have recreational land which would be "forever reserved and maintained for the use of all the people" (NY State Office of Parks, Recreation, and Historic Preservation 2010).

Beaver Conservation in New York State

Beaver populations made remarkable comebacks in New York state during the 1900's after being nearly eradicated in the 1800's, with much of the recovery the state's beaver management plans (NYS Dept. of Environmental Conservation 2015). Beaver populations had re-inhabited New York by the early 1940's aided by management practices such as habitat restoration, harvest restrictions, and trap and transfers (NYS Dept. of Environmental Conservation 2015). From the 1940's through the 1970's, an increase in human/beaver conflicts from recovering populations, beaver populations were controlled at lower levels by longer fur-trapping seasons. However, this ended in the 1980's when wildlife biologists discovered the benefits of beaver impoundments to wetlands and wildlife (NYS Dept. of Environmental Conservation 2015).

Trapping seasons were regulated to conserve beavers at sustainable levels and the goal was to have New Yorkers benefit from having more wetlands and wildlife provided from beaver impoundments (NYS Dept. of Environmental Conservation 2015). Today, beaver populations in the wildlife management units in New York are at or even above management objectives, with a 19% increase in population statewide since 1990 (NYS Dept. of Environmental Conservation 2015). For example, there were an estimated 17,500 active beaver colonies within New York State in 1993, which was 3,500 more than the 14,000 state-wide goal (NYS Dept. of Environmental Conservation 2015). Beaver populations in New York State are managed by the Bureau of Wildlife by allowing open season for licensed trappers (NYS Dept. of Environmental Conservation 2015). Beaver management objectives are set in the state's divided Wildlife Management Units (WMU's) that intend on maintaining beaver populations in 10-30% of beaver-suitable habitats (NY State Dept. of Environmental Conservation 2015).

Environmental, Habitat, and Geographic Characterization

Five beaver complexes (Bay State Brook, Gasline, upstream and downstream Quaker Run, France Brook [see FIGURE 1, APPENDIX]) were selected for this study in Allegany State Park, along with one artificial impoundment, Science Lake. Allegany

State Park has three man-made lakes (Quaker, Red House, and Science Lakes), but Science Lake, being shallow and eutrophic, is the only human impoundment with a quasi-natural shoreline (NY State Office of Parks, Recreation, and Historic Preservation 2010), so it was chosen as an artificial habitat example. Beaver pond complexes were selected based on accessibility, presence of beaver ponds (i.e., complexes with only beaver meadows were not included because this is not suitable newt habitat), and to represent multiple successional stages and independent stream catchments. The pond complexes varied in successional stage and stability. Within each pond complex, newt survey points were selected to represent varying sub-habitats, which were classified as follows: Pond Margin, Back of Dam, Connecting Channel, Small Dam/Pond, Pond Remnant, Re-established Stream (these are briefly described in TABLE 1, with photos of each found in FIGURE 2).

Proximate environmental variables were measured within each beaver complex at each newt survey point. These variables included water depth, current velocity, substrate type, and presence/absence of vegetation and/or organic material. Water depth was visually estimated, with the greatest depth within 1 m of shoreline reported (i.e. the distance within which newts were surveyed at each location). Current velocity was qualitatively described as quiescent, slow, medium, or fast. Use of a current meter for more quantitative flow data would have been unnecessary and possibly counterproductive for several reasons, particularly that many survey points were entirely quiescent, and others were quite shallow, with current velocity varying markedly over a fine spatial scale. A current meter would likely have been useful only under “fast” current conditions, which were the least common situation during this study. Substrate type was

Table 1. Sub-habitat types and numbers of newt survey points represented at pond complexes and Science Lake. The asterisk indicates inclusion of summer 2015 post-dam breach pond remnants at Gasline pond complex.

Sub-habitat	Bay State	Gas Line	France Brook	QR Upstream	QR Downstream	Science Lake
1. Pond margin. Area alongside ponds, tends to be shallow and mud-bottomed.	13	0	14	1	6	5
2. Back of Dam. Area behind dam, usually deep with muddy or organic bottom.	6	5	2	1	3	0
3. Connecting or side channel. Small channels or streams connecting from pond to pond, medium depth with slow current and wide range of substrate type (cobble, mud).	5	5	3	3	2	2
4. Satellite ponds. Smaller ponds and dams within complex, not as deep as main ponds.	3	0	3	1	0	0
5. Pond remnant. Leftover ponds post-breach, very shallow and mud-bottomed.	0	6*	0	1	0	0
6. Reestablished stream. Typical ASP stream with fast current and cobble bottom.	0	1	1	4	0	0

FIGURE 2. Images of beaver ponds, study subject animals, and examples of sub-habitat types (described in Table 2). Phots courtesy of author except where noted.

a) Active pond with intact, well maintained dam and lodge.

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b) American beaver (*Castor canadensis*)

c) Eastern spotted newt (*Notophthalmus viridescens*) adult.

d) Eastern spotted newt (*Notophthalmus viridescens*) terrestrial juvenile, known as a red eft.

e) Habitat – Pond Margin (habitat type 1 [from TABLE 3])

f) Habitat – Back of Dam (Habitat type 2)

g) Habitat – Connecting or Side Channel (habitat type 3)

h) Habitat – Pond Remnant, post-breach (habitat type 5)

i) Habitat – Re-established Stream (habitat type 6)

j) Habitat – Unmodified Allegany State Park Stream (habitat type 7) assigned visually as “fines” (mud/silt/clay), gravel, and cobble/boulder. Presence/absence of vegetation (i.e. emergent/floating vegetation such as algae, aquatic plants, and/or submerged shoreline plants) and organic material (i.e. leaf litter, twigs, woody debris) was recorded at each newt survey point.

Pond complex age and stability were assessed for Bay State Brook, Gas Line, the upper portion of France Brook, and Quaker Run Upstream (i.e. the four pond complexes with the best quality aerial images) by obtaining Google Earth images from between 1995 and 2015. Aerial images with finer spatial data could not be obtained because of corrupted files; therefore Google Earth was the second-best option. Ponds and streams at these four pond complexes were delineated and digitized using ArcMap version 10.2, and images from selected dates were georeferenced to quantify changes in pond shapes and areas. Because of poor image quality and possible confusion between open water and tree shadows, the Quaker Run Downstream pond complex was not georeferenced and delineated. The Science Lake site was not included in these GIS analyses because it is an artificial impoundment. Therefore any temporal changes in shoreline and/or surface area were not related to the integrity of the dam (which is permanent), unlike the case for beaver ponds. Watershed areas upstream of these four pond complexes were measured in ArcMap from a topographic basemap of Allegany State Park using the measure tool. Given the heavily and generally uniformly dissected nature of ASP's topography, drainage basin area is likely an excellent surrogate for stream size and potential for flood influence on pond complexes. These analyses were not pursued for the Science Lake artificial impoundment, because changes in its outline over the years have been due only to sedimentation and expansion of wetland vegetation, and not to any changes in its dam itself, which is of course permanent.

"Instability" (i.e. an assessment of the changeability in pond sizes, locations, and extent over time) values were then calculated for whole pond complexes and for selected individual major ponds within each site. Instability was calculated by first summing up the total changes in surface area of the selected ponds, i.e., a sum of both the increases in pond area between consecutive images and any decreases in pond area. Next, this summed change in area was divided by the maximum surface area observed in Google Earth for each pond, i.e., representing total change in area as a proportion of pond size. Finally, this proportion was divided by the total time interval of the examined aerial images to yield a yearly "instability" value, reported as a running average of percent change in pond size per year. This quantity was calculated for each selected pond and for each whole pond complex (the reader can follow these calculations as presented in Results, TABLE 10).

Eastern Spotted Newt Surveys

Spotted newt surveys were taken in the Spring and Summer of 2015 for each sub-habitat within each complex where represented, for a total of 80 survey points (TABLE 2). The six study locations (five beaver pond complexes and the Science Lake impoundment) were each surveyed for spotted newts at least three times during April thru June of 2015. Newts were also surveyed during exploratory work in 2014, but only the more systematically collected data from 2015 were analyzed statistically during this study. At each point, surveys were conducted along 3 m of shoreline and extending 1 m outward. The newts were surveyed visually, which was facilitated by the clear shallow water, and by the habit of the newts to typically rest quietly on the bottom or float near

Table 2. Newt surveying schedule and associated weather conditions. An "X" indicates newts surveyed at site on date.

	04/15/15	04/24/15	04/29/15	05/13/15	05/20/15
Weather °C	11°C Partly Cloudy	23°C Sunny	17°C Sunny	15°C Sunny	13°C Partly Cloudy
Bay State			X		
Gas Line				X	
France Brook					
QR Upstream	X				X
QR Downstream	X				X
Science Lake	X	X			

	05/24/15	06/10/15	06/17/15	07/18/15	07/23/15
Weather °C	24°C Sunny	27°C Sunny	21°C Cloudy	31°C Partly Cloudy	25°C Partly Cloudy
Bay State	X		X		
Gas Line	X			X	
France Brook		X		X	X
QR Upstream		X			
QR Downstream			X		
Science Lake			X		

the surface. Hence, surveys were not conducted after hard rains, or when water was otherwise turbid (e.g. from nearby beaver activity or from algal growth as the summer progressed). Spotted newts that were readily visible at the survey points were counted, and then gentle agitation with a 2-m hiking stick was used along the shoreline and bottom to uncover newts hiding under rocks, grasses, and bottom debris. These newts were then counted as they swam out.

Funnel traps were not recommended for use in beaver ponds, because they might have been vulnerable to chewing or gnawing by beavers as foreign objects in their ponds (D. Butler, *pers. comm*.). Funnel traps also are intended primarily to sample migrating salamanders, which was not the objective of this study. Dip nets were unnecessary here, given the excellent underwater visibility and relatively stationary behavior of the newts, and would have needlessly stirred up the water.

Analysis and Statistics

In preparation for statistical analysis, survey-point-specific substrate type and current velocity data were converted to ranks, vegetation and organic material were left as presence/absence, and water depth was left as a ratio scale estimated measure. Geographic Information System-derived instability calculations and upstream watershed areas were also left as ratio scale measurements. Newt abundances are reported and analyzed as means of multiple survey dates.

Most statistical procedures were conducted in SPSS Statistics Package for the Social Sciences, version 20) under two scenarios: once while including newt survey data from Pond Remnants left after a major breach at the Gas Line pond complex in June 2015, and again while *not* including these post-breach Pond Remnants. This was because it was uncertain whether high newt abundances here represented actual habitat preference, or simply resulted from newt aggregation in a shrinking aquatic environment.

Newt abundances at survey points were subject to 6x6 two-factorial ANOVA (Pond Complex x Habitat Type). Also, a one-factor non-parametric Kruskall-Wallis test was run because newt abundance was highly non-normal, as is often seen with biological distributions (Hampton and Havel 2006). However the ANOVA was likely robust, and is preferred because it treated Pond Complex and Habitat Type independently (Hampton and Havel 2006).

The factorial analysis was informative in terms of the influence of Pond Complex and Habitat Type on newt distributions, but they did not address specific habitat and/or landscape variables (e.g. current velocity, beaver pond stability). Therefore, the suite of independent environmental and landscape variables was subjected to multivariate ordination. For studies involving multiple species distributions (i.e. dependent variables) distance-based non-metric multidimensional scaling (NMDS) is often the preferred approach. However, this study involves only a single dependent variable (newt abundance) but numerous independent variables, so eigenvector-based Principle Components Analysis (PCA), often preferred for environmental data, was chosen instead. Two separate PCAs were explored, reflecting the relative availability of proximate habitat data and GIS-generated landscape data. The first represented an analysis of *only* the proximate environmental variables estimated at newt survey points, but it included all pond complexes and Science Lake. The second included both the environmental/habitat variables and the GIS-generated landscape data but included *only* the subset of pond complexes for which reliably high-quality imagery was available. Temporal sequences of selected aerial images of these four georeferenced pond complexes, and for Science Lake, are presented in FIGURES 3 – 7.

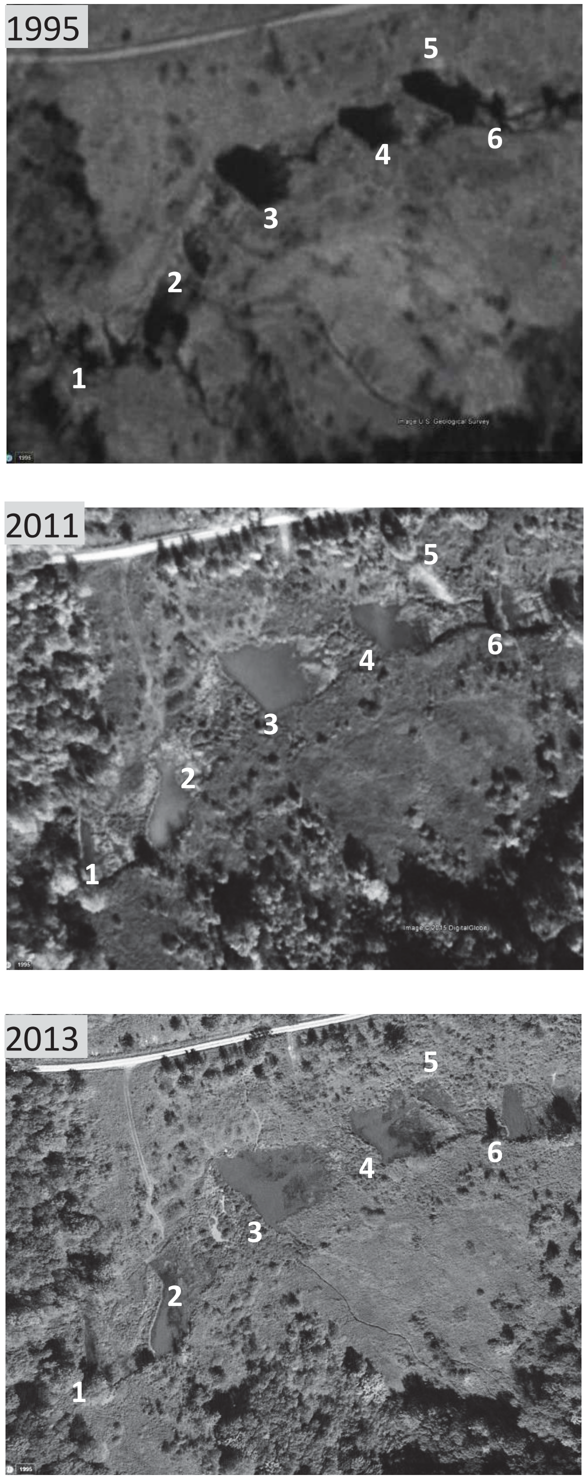


FIGURE 3. Aerial image time series of Bay State Brook beaver pond complex (location in FIGURE 1). Numerals denote digitized and georeferenced ponds.

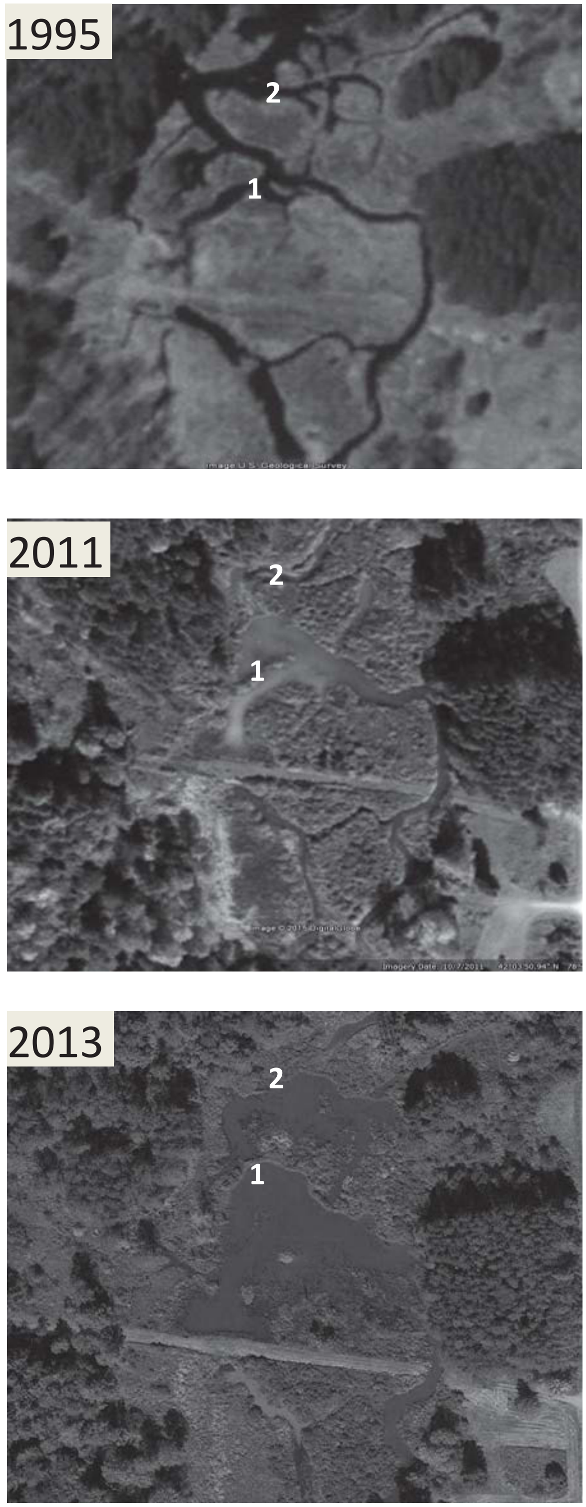


FIGURE 4. Aerial image time series of Gasline beaver pond complex (location in FIGURE 1). Numerals denote digitized and georeferenced ponds.

FIGURE 5. Aerial image time series of Upstream Quaker Run beaver pond complex (location in FIGURE 1). Numerals denote digitized and georeferenced ponds.

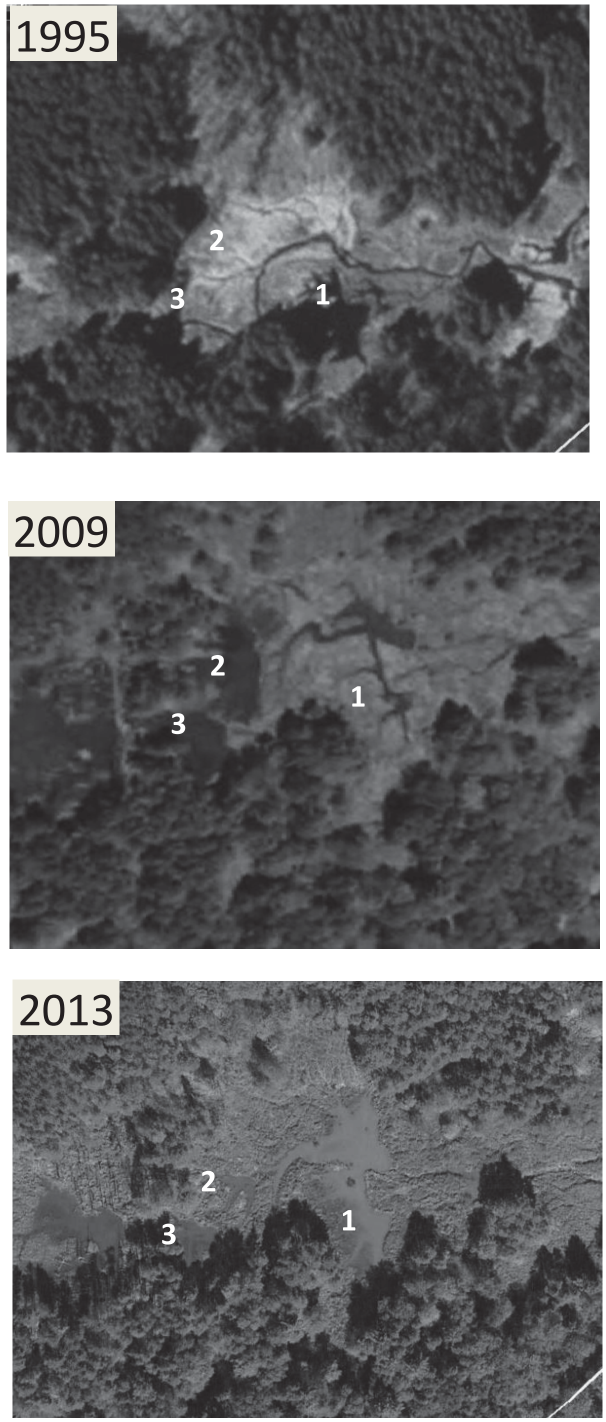


FIGURE 6. Aerial image time series of France Brook beaver pond complex (location in FIGURE 1). Numerals denote digitized and georeferenced ponds.

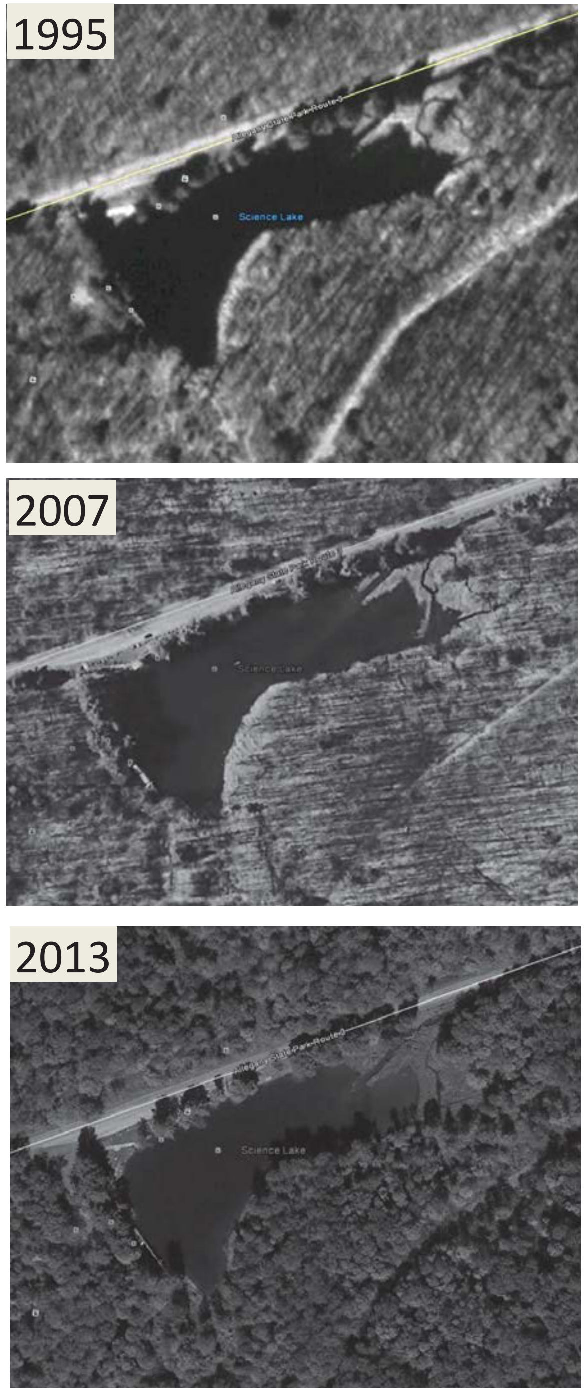


FIGURE 7. Aerial image time series of Science Lake impoundment (location in FIGURE 1).

RESULTS

Newt Abundances

The overall newt abundance was highest at the Bay State Brook pond complex, at a mean of 8.0 per individual survey, with Connecting Channels and Pond Margins holding the most newts here (TABLES 3, 4, and 5). The Gas Line pond complex also had very high newt abundances after the June 2015 dam breach event (mean of 6.7 per survey), but due entirely to the very high counts at the newly stranded pond remnants (TABLES 4 and 5). The Quaker Run Downstream pond complex, in contrast, had the lowest newt abundance (0.2 newts per survey) with Pond Margins being the only habitat type occupied by newts here. The artificial impoundment Science Lake had respectable newt abundances (mean of 1.8 per survey), with the shallow lakeshore that resembles the beaver Pond Margin habitat type being the most favorable. Across all the pond complexes, newt abundance was highest at Pond Margins (except for post-breach Pond Remnants at the Gas Line pond complex) and lowest along Back of Dams.

Factorial Results

The two-factorial ANOVA run for Beaver Complex x Habitat Type when including post-breach Gas Line data was significant for both factors, but showed no interaction (TABLE 6). When conducted without post-breach data, only pond complex was a significant factor, and again there was no interaction (TABLE 7). Without post-breach data, the only significant difference was that newts were more abundant at Bay State Brook than at all other complexes (Post-hoc Tukey's test). With post-breach data, both Bay State Brook and Gas Line had higher newt abundances than at other complexes, and Pond Remnants had higher newt abundances than other habitat types as well (Post-

Table 3. Individual date newt survey counts and means at pond complexes by habitat type.

Habitat type		
	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM
	7	UNMODIFIED STREAM

Complex	**Survey point**	**Habitat**	**# of newts** 4/29/2015	5/25/2015	6/17/2015	**Mean**
Bay State Brook	A	1	3	3	0	2.0
	B	2	1	4	0	1.7
	C	1	1	6	0	2.3
	D	3	3	1	0	1.3
	E	2	2	0	2	1.3
	F	1	7	6	6	6.3
	G	1	6	8	1	5.0
	H	3	17	4	0	7.0
	I	4	4	5	1	3.3
	J	4	1	1	0	0.7
	K	1	5	45	0	16.7
	L	2	1	5	1	2.3
	M	1	7	31	15	17.7
	N	1	20	5	0	8.3
	O	3	10	33	0	14.3
	P	1	5	3	1	3.0
	Q	2	5	10	3	6.0
	R	1	10	20	5	11.7
	S	3	16	20	19	18.3
	T	3	6	20	2	9.3
	U	2	2	3	0	1.7
	V	1	17	1	1	6.3
	W	1	12	12	0	8.0
	X	4	32	4	3	13.0
	Y	1	27	10	4	13.7
	Z	1	45	21	18	28.0
	AA	2	3	6	9	6.0

Habitat type		
	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM
	7	UNMODIFIED STREAM

			# of newts		
Complex	**Survey point**	**Habitat**	**5/13/2015**	**5/24/2015**	**Mean**
Gasline	A	2	0	0	0.0
	B	2	0	0	0.0
	C	2	0	0	0.0
	D	3	0	0	0.0
	E	3	0	0	0.0
	F	5	2	0	1.0
	G	6	3	3	3.0
	H	3	0	0	0.0
	I	2	0	0	0.0
	J	3	0	0	0.0
	K	3	1	1	1.0
	L	2	0	0	0.0

		After breach		
		7/18/2015	**7/23/2015**	
1	5	60	25	42.5
2	5	35	60	47.5
3	5	8	13	10.5
4	5	1	1	1.0
5	5		8	8.0

Habitat type		
	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM
	7	UNMODIFIED STREAM

			# of newts			
Complex	**Survey point**	**Habitat**	**4/15/2015**	**5/20/2015**	**6/10/2015**	**Mean**
Quaker upstream	A	6	0	0	0	0.0
	B	6	0	0	0	0.0
	C	6	0	0	0	0.0
	D	7	0	0	0	0.0
	E	7	0	0		0.0
	F	7	0	0	0	0.0
	G	3	0	0	0	0.0
	H	2	0	0	0	0.0
	I	4	0	0	0	0.0
	J	6	0	0	0	0.0
	K	5	13	6	3	7.3
	L	1	2	1	3	2.0

			4/15/2015	**5/20/2015**	**6/17/2015**	
Quaker Downstream	A	7	0	0	0	0.0
	B	1	1	0	0	0.3
	C	1	0	0	0	0.0
	D	2	0	0	0	0.0
	E	7	0	0	0	0.0
	F	1	0	0	0	0.0
	G	1	2	1	0	1.0
	H	1	0	0	1	0.3
	I	3	0	0	0	0.0
	J	2	0	0	0	0.0
	K	2	0	0	0	0.0
	L	1	0	0	0	0.0
	M	3	0	0	0	0.0

Habitat type		
	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM
	7	UNMODIFIED STREAM

			# of newts			
Complex	**Survey point**	**Habitat**	**6/10/2015**	**7/18/2015**	**7/23/2015**	**Mean**
France Brook	A	1	0	0	0	0.0
	B	1	0	0	0	0.0
	C	1	3		0	1.5
	D	1	0	0	0	0.0
	E	7	0	0	0	0.0
	F	1	0	0	0	0.0
	G	1	0	1	0	0.3
	H	1	4	0	0	1.3
	I	3	1	0	0	0.3
	J	1	1	0	3	1.3
	K	1	1	0	0	0.3
	L	4	2	1	0	1.0
	M	4	0	3	8	3.7
	N	1	0	1	3	1.3
	O	4	0	0	0	0.0
	P	2	0	2	3	1.7
	Q	1	0			0.0
	R	1	2			2.0
	S	6	0	0	0	0.0
	T	3	0	0	1	0.3
	U	1	5	7	6	6.0
	V	1	5	0	0	1.7
	W	3	1	0	0	0.3
	X	2	0	1	0	0.3
	Y	7	0	0	0	0.0
			4/15/2015	**5/24/2015**	**6/17/2015**	
Science Lake	A	1	9	8	0	5.7
	B	1	0	0	0	0.0
	C	1	4	6	4	4.7
	D	7	0	0	0	0.0
	E	1	1	1	0	0.7
	F	3	0	2	0	0.7
	G	3	1	0	0	0.3
	H	1	1	0	0	0.3

Table 4. Newt count data matrix for pond complex X habitat type two-factor ANOVA. Data are means of all survey points for each cell. Blank cells indicate habitat type not represented at pond complex. Number of surveys (points x dates) given in parentheses for totals and for mean abundances greater than 10.0. Table includes newt surveys conducted at pond remnants left by summer 2015 dam breach at Gasline complex.

	Pond Margin	Behind dam	Channel	Small ancillary Pond	Pond remnant	Re-established Stream	**Totals**
Bay State Br.	10.0 (39)	3.2	10.1 (15)	5.7			**8.0 (81)**
Gas Line		0	0.2		19.4 (11)	3	**6.7 (33)**
Quaker Run UP	2	0	0	0	7.3	0	**1.0 (27)**
Quaker Run DOWN	0.3	0	0				**0.2 (33)**
Science Lake	2.3		0.5				**1.8 (21)**
France Br.	1.1	1	0.3	1.6		0	**1.0 (64)**
Totals	**4.2 (112)**	**1.4 (46)**	**3.2 (49)**	**3.1 (21)**	**16.8 (14)**	**0.4 (17)**	

Table 5. Newt count data matrix for pond complex X habitat type two-factor ANOVA. Data are means of all survey points for each cell. Blank cells indicate habitat type not represented at pond complex. Number of surveys (points x dates) given in parentheses for totals and for mean abundances greater than 10.0. Table does NOT include newt surveys conducted at pond remnants left by summer 2015 dam breach at Gasline complex.

	Pond Margin	Behind dam	Channel	Small ancillary Pond	Pond remnant	Re-established Stream	**Totals**
Bay State Br.	10.0 (39)	3.2	10.1 (15)	5.7			**8.0 (81)**
Gas Line		0	0.2		1	3	**0.4 (24)**
Quaker Run UP	2	0	0	0	7.3	0	**1.0 (27)**
Quaker Run DOWN	0.3	0	0				**0.2 (33)**
Science Lake	2.3		0.5				**1.8 (21)**
France Br.	1.1	1	0.3	1.6		0	**1.0 (64)**
Totals	**4.2 (112)**	**1.4 (46)**	**3.2 (49)**	**3.1 (21)**	**4.8 (5)**	**0.4 (17)**	

Table 6. ANOVA output table (SPSS version 20.0) for pond complex X habitat type two-factor ANOVA. Data presented in Table 4, including newt surveys conducted at pond remnants left by summer 2015 dam breach at Gasline complex.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	6425.931[a]	23	279.388	5.071	.000
Intercept	1496.036	1	1496.036	27.153	.000
Habitat2	1246.290	5	249.258	4.524	.001
Complex2	1732.807	5	346.561	6.290	.000
Habitat2 * Complex2	652.260	13	50.174	.911	.543
Error	12947.606	235	55.096		
Total	23250.000	259			
Corrected Total	19373.537	258			

a. R Squared = .332 (Adjusted R Squared = .266)

Table 7. ANOVA output table (SPSS version 20.0) for pond complex X habitat type two-factor ANOVA. Data presented in Table 6, NOT including newt surveys conducted at pond remnants left by summer 2015 dam breach at Gasline complex.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	3677.216[a]	23	159.879	4.680	.000
Intercept	455.525	1	455.525	13.333	.000
Habitat	149.358	5	29.872	.874	.499
Complex	1771.866	5	354.373	10.373	.000
Habitat * Complex	460.658	13	35.435	1.037	.416
Error	7721.060	226	34.164		
Total	13901.000	250			
Corrected Total	11398.276	249			

a. R Squared = .332 (Adjusted R Squared = .266) hoc Tukey's test). One-factor Kruskall-Wallis tests run for Beaver Complex x Habitat Type for both before and post-breach scenarios were highly significant and gave the same results as the two-factorial ANOVA.

<u>Habitat and Landscape Variables</u>

In terms of habitat characteristics, the large majority of survey points had quiescent flow and fine sediments (TABLE 8). However, some survey points, particularly associated with reestablished streams, had notable current velocity and coarse substrate. Vegetation was often present at Pond Margins and Connecting Channels. Organic debris was also found at many survey points but with no obvious pattern in terms of habitat type (TABLE 8).

Overall, the Bay State Brook pond complex was the most stable in terms of pond area change (whole complex “instability” = 2.9% per year), whereas Gas Line pond complex was the least stable (10% per year), and also had the largest major pond examined during this study (maximum area = 9126 m^2 in 2015 immediately before the major breach). The four most stable individual ponds were all at the Bay State Brook pond complex. (TABLES 9 and 10)

The Gas Line pond complex, located on a 4^{th} order reach of Red House Brook (FIGURE 1) has by far the largest watershed area upstream (3598 ha). Bay State Brook has the least upstream watershed area at only 185 ha.

Table 8. Values of local/proximate habitat characteristics at newt survey points. Habitat type also given.

Habitat type	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM

				Ranks			
			cm	**1 thru 4**	**1 thru 3**	**1 or 2**	**1 or 2**
	Survey point	**Habitat**	**depth**	**velocity**	**substrate**	**debris**	**vegetation**
Bay State Brook	A	1	20	1	1	2	1
	B	2	30	1	1	1	1
	C	1	20	1	1	1	2
	D	3	40	1	1	1	1
	E	2	40	1	1	2	2
	F	1	15	1	1	1	1
	G	1	10	1	1	1	2
	H	3	50	1	3	1	2
	I	4	20	1	1	1	2
	J	4	30	1	1	1	1
	K	1	30	1	3	1	1
	L	2	40	1	1	1	1
	M	1	50	1	1	1	2
	N	1	20	1	1	1	2
	O	3	20	1	1	1	1
	P	1	30	1	3	1	1
	Q	2	10	1	1	1	1
	R	1	10	1	1	2	1
	S	3	10	2	1	1	1
	T	3	30	2	1	2	1
	U	2	30	1	1	2	1
	V	1	10	1	1	2	1
	W	1	20	1	1	2	1
	X	4	30	1	1	1	1
	Y	1	30	1	1	1	1
	Z	1	10	1	1	1	1
	AA	2	15	1	1	1	1

Table 8 cont.

Habitat type	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM

				Ranks			
			cm	**1 thru 4**	**1 thru 3**	**1 or 2**	**1 or 2**
	Survey point	**Habitat**	**depth**	**velocity**	**substrate**	**debris**	**vegetation**
Gas line	A	2	20	1	1	2	1
	B	2	40	1	1	2	1
	C	2	40	1	1	2	1
	D	3	15	2	1	2	1
	E	3	20	3	2	1	1
	F	5	15	1	1	1	2
	G	6	30	1	1	2	1
	H	3	15	4	3	1	1
	I	2	30	1	1	2	1
	J	3	15	2	2	1	1
	K	3	15	2	1	2	1
	L	2	20	1	1	1	2
after breach	1	5	20	1	1	1	1
	2	5	30	1	1	1	1
	3	5	40	1	1	1	1
	4	5	30	1	1	1	1
	5	5	30	1	1	1	1

Table 8 cont.

Habitat type	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM

				Ranks			
			cm	**1 thru 4**	**1 thru 3**	**1 or 2**	**1 or 2**
	Survey point	**Habitat**	**depth**	**velocity**	**substrate**	**debris**	**vegetation**
Quaker Run upstream	A	6	20	4	3	1	1
	B	6	20	4	3	1	1
	C	6	20	4	3	1	1
	G	3	10	2	1	2	1
	H	2	20	1	1	2	2
	I	4	20	1	1	1	1
	J	6	10	4	3	1	1
	K	5	10	1	1	1	2
	L	1	20	1	1	1	2
Quaker Run downstream	B	1	20	1	1	1	2
	C	1	15	1	1	2	1
	D	2	20	1	1	2	1
	F	1	5	1	1	1	2
	G	1	10	1	1	1	2
	H	1	10	1	1	2	2
	I	3	20	2	1	2	1
	J	2	20	1	1	2	1
	K	2	20	1	1	2	1
	L	1	20	1	1	1	2
	M	3	10	2	1	1	2

Table 8 cont.

Habitat type	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM

				Ranks			
			cm	**1 thru 4**	**1 thru 3**	**1 or 2**	**1 or 2**
	Survey point	**Habitat**	**depth**	**velocity**	**substrate**	**debris**	**vegetation**
France Brook	A	1	20	1	1	2	1
	B	1	15	1	1	1	2
	C	1	10	1	1	1	2
	D	1	10	2	3	1	1
	F	1	15	1	1	1	1
	G	1	30	1	1	2	1
	H	1	30	1	1	1	2
	I	3	15	1	1	1	2
	J	1	30	1	1	1	2
	K	1	30	1	1	2	1
	L	4	40	1	1	1	2
	M	4	40	2	1	1	2
	N	1	10	1	1	1	1
	O	4	15	1	1	1	2
	P	2	40	1	1	1	1
	Q	1	15	1	1	1	1
	R	1	15	1	1	2	1
	S	6	40	4	1	2	1
	T	3	10	2	1	1	1
	U	1	15	1	1	2	1
	V	1	15	1	1	1	1
	W	3	30	1	1	1	1
	X	2	20	2	1	1	1

Table 8 cont.

Habitat type	1	POND MARIGIN - NOT DAM
	2	BACK OF MAJOR DAM
	3	CONNECTING CHANNELS
	4	SMALL DAM/POND
	5	FORMER POND REMNANT
	6	RE-ESTABLISHED STREAM

				Ranks			
			cm	**1 thru 4**	**1 thru 3**	**1 or 2**	**1 or 2**
	Survey point	**Habitat**	**depth**	**velocity**	**substrate**	**debris**	**vegetation**
Science Lake	A	1	15	1	1	2	1
	B	1	10	1	2	1	1
	C	1	5	1	1	1	2
	E	1	15	1	1	2	2
	F	3	30	1	1	1	2
	G	3	15	1	1	1	2
	H	1	15	1	1	2	1

Table 9. Surface areas (m^2) of major ponds in years with good satellite imagery (Google Earth), georeferenced and delineated in ArcMAP (ArcGIS version 10.2). Total change over time interval equals total growth in area plus total decline in area. Shaded cells indicate largest area observed for each pond.

Bay State Brook	Area in m^2					
	Pond					
Year	**1**	**2**	**3**	**4**	**5**	**6**
1995	927	1601	1744	919	1264	306
2011	479	1336	2538	1275	0	343
2013	570	1442	3037	1413	452	806
Total growth	**91**	**106**	**1293**	**494**	**1264**	**500**
Total loss	**448**	**265**	**0**	**0**	**452**	**0**
Total Change	**539**	**371**	**1293**	**494**	**1716**	**500**

Gasline	Area in m^2	
	Pond	
Year	**1**	**2**
1995	0	0
2007	2251	0
2011	4140	0
2013	7638	3254
2015	9126	0
post-breach 2015	0	0
Total growth	**9126**	**3254**
Total loss	**9126**	**3254**
Total Change	**18252**	**6508**

Table 9 cont.

Quaker Run upstream	Area in m^2		
	Pond		
Year	**1**	**2**	**3**
1995	0	1458	4399
2007	2406	0	6002
2013	0	0	0
2015	0	1617	0
Total growth	**2406**	**1617**	**1603**
Total loss	**2406**	**1458**	**6002**
Total Change	**4812**	**3075**	**7605**

France Brook	Area in m^2		
	Pond		
Year	**1**	**2**	**3**
1995	2745	0	0
2009	1913	2040	1380
2013	4247	426	508
2015	6532	670	1659
Total growth	**4619**	**2284**	**2531**
Total loss	**832**	**1614**	**872**
Total Change	**5451**	**3898**	**3403**

Table 10. Instability (i.e., % change per year averaged over whole imagery time interval) for individual ponds and for whole complexes. Data from Table 9. Also given is drainage area upstream from lower boundary of each pond complex (ArcGIS 10.2), which thus includes the area of the complex itself.

Complex	Major pond	Instability (whole)	Instability (pond)	Drainage (ha)
Bay State Brook	1	2.9	3.2	185.0
	2	2.9	1.3	185.0
	3	2.9	2.4	185.0
	4	2.9	1.9	185.0
	5	2.9	5.6	185.0
	6	2.9	3.4	185.0

Gas line	1	10.0	10.0	3598.0
	2	10.0	10.0	3598.0

Quaker Run upstream	1	7.7	10.0	487.0
	2	7.7	9.5	487.0
	3	7.7	6.3	487.0

France Brook	1	6.6	4.7	753.0
	2	6.6	9.6	753.0
	3	6.6	10.3	753.0

Multivariate Analysis

The Principal Components Analysis run for local/proximate environmental/habitat variables only, and for all beaver complexes, yielded three PCA axes explaining 82.4% of total data variance (TABLE 11). However, for simplicity of presentation (i.e. presenting a single ordination plot rather than three), only the first two, explaining 62.3% of variance, were plotted and considered further. Also, the third axis had an eigenvalue of only 1.001 (i.e. no better than an average variable in terms of variance explained), and it was entirely associated with water depth (TABLE 11), which may be of only modest ecological influence. Current velocity and substrate coarseness loaded strongly positively on PCA1, while presence of debris and presence of vegetation loaded on PCA2 (positively and negatively, respectively).

Although there were no instances of newts found at survey points to the far right of the PCA1 x PCA2 ordination plot (FIGURE 8), all possible survey results can be seen to the left of the y-axis, ranging from zero newts per survey to the highest abundances recorded. This suggested that the current velocity and substrate coarseness contributing to PCA1 had little influence on newt abundance. Also, there was no apparent pattern in newt abundance related to PCA2, suggesting that presence or absence of organic debris and/or vegetation did not influence newt abundance either (FIGURE 8).

The PCA run for local/proximate habitat variables *and* landscape-scale GIS-derived variables (for the sub-set of four pond complexes with reliable aerial imagery) yielded three PCA axes explaining 74.0% of total data variance when post-breach Gasline

Table 11. Principle Components Analysis (PCA) output table (SPSS version 20.0) for proximate habitat variables only (data presented in Table 8) at newt survey points, NOT including Pond Remnants left after major dam breach at Gasline pond complex.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	1.776	35.523	35.523	1.776	35.523	35.523
2	1.341	26.818	62.341	1.341	26.818	62.341
3	1.001	20.024	82.365	1.001	20.024	82.365
4	.541	10.812	93.177			
5	.341	6.823	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
depth	-.076	.140	.985
current	.872	.057	-.044
substrate	.883	-.145	.138
debris	-.259	.846	-.075
vegetation	-.404	-.762	.069

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

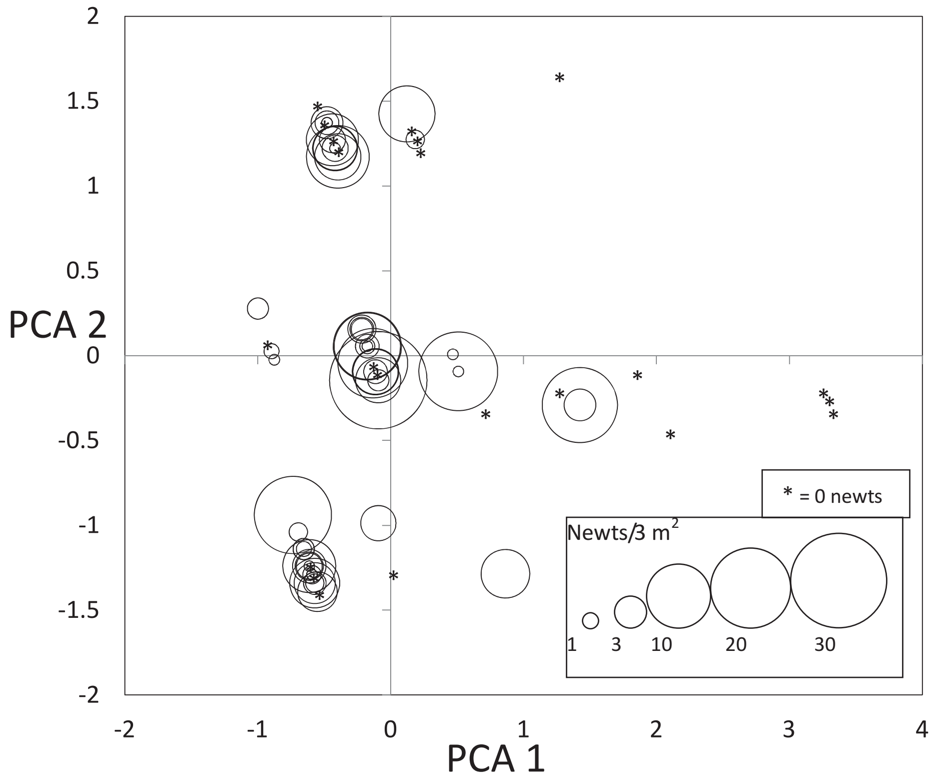


FIGURE 8. Principle Components Analysis ordination of local/proximate habitat variables, plotted by newt survey point. Data from Table 8. Plot circle diameters scaled to mean newt abundance. An asterisk indicates no newts found at survey spot. Data and plot do not include post-breach pond remnants at Gasline complex.

pond complex data were included (TABLE 12). When NOT including post-breach data the PCA also yielded three axes, now explaining 75.1% of variance (TABLE 13). In both cases, pond and complex instability, and upstream watershed area loaded strongly positively on PCA1, whereas current velocity and substrate coarseness loaded positively on PCA2 (TABLES 12 and 13). Again, for simplicity of presentation, only the first two axes have been plotted. The third axis in both cases was only modestly informative (eigenvalues ~1.2), and was dominated by presence of debris and presence of vegetation.

In contrast to the habitat-only PCA ordination (FIGURE 8), convincing trends emerged from ordination of PCA axes that included GIS-derived landscape scale data (FIGURES 9 and 10). Both with and without post-breach Pond Remnant newt surveys from the Gasline pond complex, there was a clear distinction in newt abundances along PCA1, i.e., the x-axis. Newts were generally abundant at survey points located to the left of the y-axis, representing stable pond complexes, and rarely found at points to the right, where ponds and pond complexes were unstable. The only exception to this was in terms of the post-breach Pond Remnants shown in FIGURE 9, which displayed high newt abundances despite being located at a pond complex that otherwise appeared to be less than ideal as habitat

Table 12. Principle Components Analysis (PCA) output table (SPSS version 20.0) for proximate habitat variables at newt survey points (data presented in Table 8) and GIS-derived landscape-scale variables (Table 10), *including* Pond Remnants left after major dam breach at Gasline pond complex.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.810	35.126	35.126	2.810	35.126	35.126
2	1.892	23.654	58.780	1.892	23.654	58.780
3	1.218	15.220	74.000	1.218	15.220	74.000
4	.967	12.086	86.086			
5	.604	7.544	93.630			
6	.265	3.312	96.942			
7	.193	2.411	99.352			
8	.052	.648	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
stablewhole	.961	-.082	.182
stablepond	.908	-.172	.150
watershed	.880	-.246	.070
depth	-.068	-.343	.196
current	.388	.825	-.051
substrate	.148	.870	.071
debris	.205	-.423	-.710
vegetation	-.262	-.251	.779

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

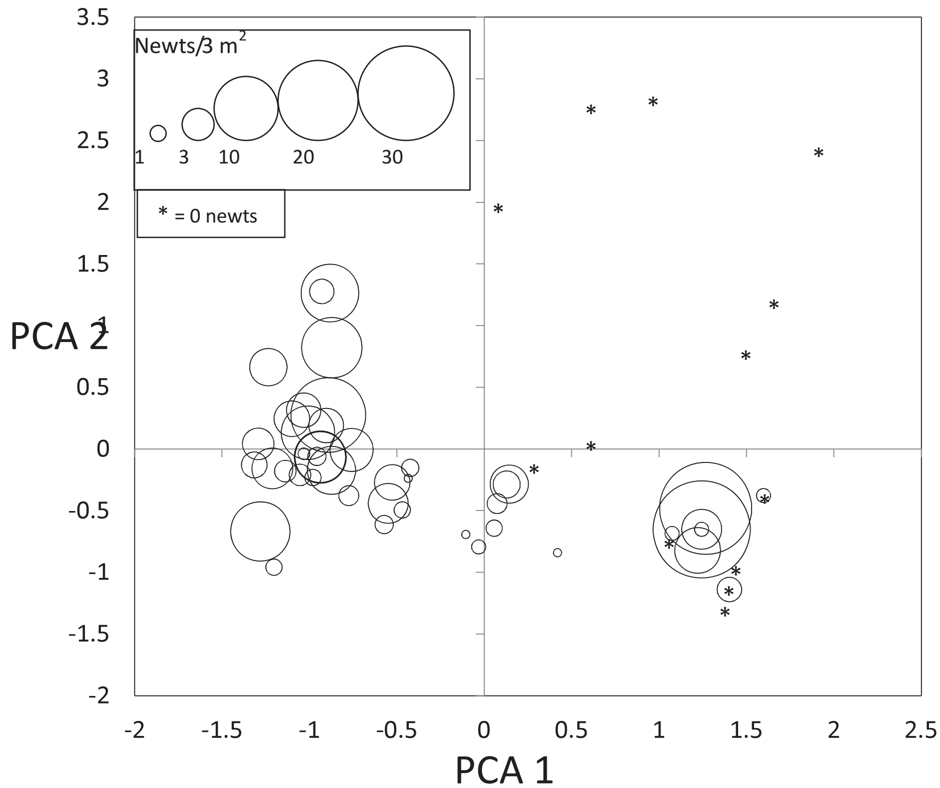


FIGURE 9. Principle Components Analysis ordination of local/proximate habitat variables (subset of Table 8), and of pond and pond complex instability and watershed areas (Table 10), plotted by newt survey point. Plot circle diameters scaled to mean newt abundance. An asterisk indicates no newts found at survey spot. availability and quality of satellite imagery this analysis includes only Bay State Brook, Gasline, upstream Quaker Run, and the upstream survey points at France Brook. Data and plot include post-breach pond remnants at Gasline complex.

Table 13. Principle Components Analysis (PCA) output table (SPSS version 20.0) for proximate habitat variables at newt survey points (data presented in Table 8) and GIS-derived landscape-scale variables (Table 10), NOT including Pond Remnants left after major dam breach at Gasline pond complex.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.888	36.094	36.094	2.888	36.094	36.094
2	1.880	23.505	59.599	1.880	23.505	59.599
3	1.246	15.572	75.171	1.246	15.572	75.171
4	.976	12.200	87.371			
5	.449	5.614	92.985			
6	.291	3.636	96.621			
7	.210	2.623	99.244			
8	.060	.756	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
stablewhole	.949	.121	.209
stablepond	.883	.222	.185
watershed	.849	.277	.055
depth	-.184	.280	.116
current	.511	-.758	-.049
substrate	.248	-.846	.030
debris	.288	.552	-.634
vegetation	-.217	.259	.863

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

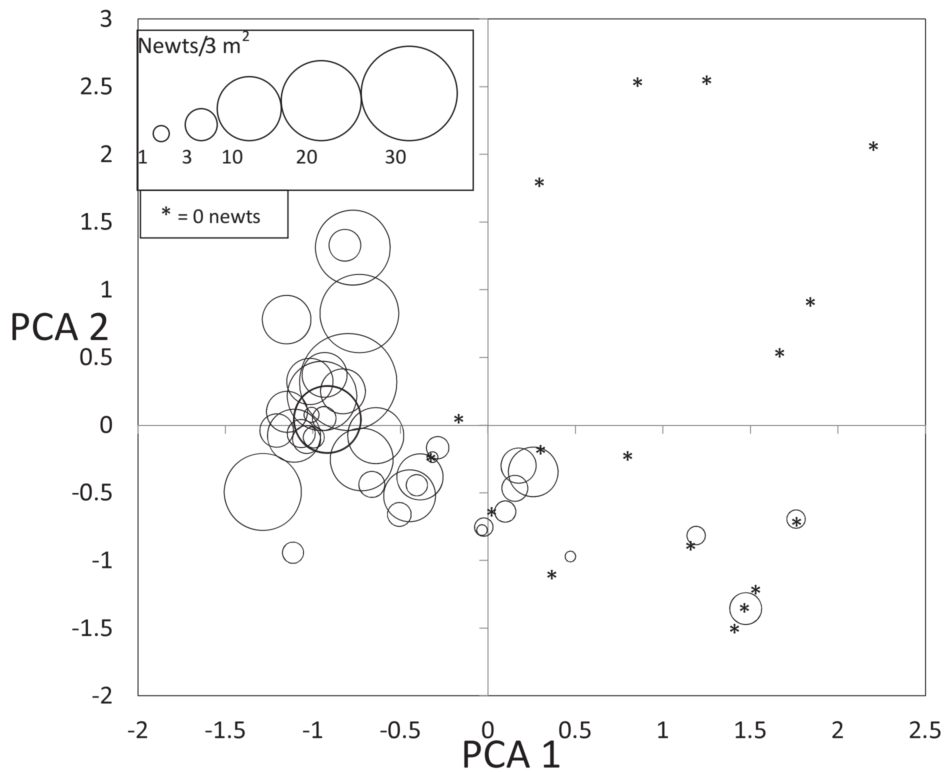


FIGURE 10. Principle Components Analysis ordination of local/proximate habitat variables (subset of Table 8), and of pond and pond complex instability and watershed areas (Table 10), plotted by newt survey point. Plot circle diameters scaled to mean newt abundance. An asterisk indicates no newts found at survey spot. availability and quality of satellite imagery this analysis includes only Bay State Brook, Gasline, upstream Quaker Run, and the upstream survey points at France Brook. Data and plot do NOT include post-breach pond remnants at Gasline complex.

DISCUSSION

Eastern spotted red newts were consistently most abundant at Bay State Brook, especially in areas that may be considered preferred habitat (i.e. Pond Margins and Connecting Channels with either quiescent or low flow waters), based on knowledge of the species' preferences. Bay State Brook was also very accessible to visitation, and had a wide diversity of potential newt habitat to be surveyed. In contrast, Quaker Run Downstream had the lowest newt abundances, with newts found along Pond Margins, and in very low numbers. Interestingly, this pond complex was surveyed in Summer 2014 and newts were found in moderate numbers, so it was surprising to discover low newt abundances at this location during the systematic 2015 surveying. Prior to the June 2015 breach, Gas Line pond complex also had very low newt abundances, although there were no Pond Margin habitats surveyed at this location (poor access by foot). After the major dam breach, however, astounding numbers of newts were found in Pond Remnants. This habitat type is usually shallow and quiescent and would be considered suitable habitat for spotted red newts (Pfingsten and Downs 1989, Pfinsten et al. 2013). Interestingly, Science Lake impoundment had overall higher newt abundances than most beaver complexes, especially in habitat types that are similar to preferred types found in beaver complexes (such as warm, shallow, and productive Pond Margins, [e.g. see Hossack et al. 2015]). This suggests that artificial impoundments, if their upstream margins are not further modified (as is the case at Red House and Quaker Lakes – two recreational lakes in ASP that have completely modified shorelines), could perhaps serve as surrogates for beaver ponds as habitat for spotted newts.

The surrounding forest type could have some influence on newt abundances at the six locations. It was observed at Bay State Brook that the primary tree species were hardwoods, whereas at France Brook and Gas Line were primarily softwoods. However, it was observed that hardwoods are also re-colonizing the conifer plantations. Not only do beavers prefer hardwoods for food and building material, but red efts and terrestrial adult newts are also inclined to inhabit hardwood forests because of high moisture content (Sousa 1985). A tree species analysis would have to be conducted in future studies and used as a possible factor in explaining newt abundances across all locations.

It was somewhat unexpected that the Bay State Brook pond complex dominated in newt abundance over all the others. When reconnaissance work was being done in Summer 2014, a broad range of successional stages and sub-habitat types was chosen for study in different locations throughout the park, so it was curious that only this pond complex consistently contained large numbers of spotted newts. It was anticipated instead to perhaps encounter more similar numbers of newts among pond complexes, especially along the Pond Margins and in the Connecting Channels that qualitatively suggested the best habitat (i.e. shallow, quiescent, and soft-bottomed). This suggests that local proximate habitat type may not influence newt abundances as much as was initially suspected. The quiescent soft-bottomed Back of Dams habitat type was also *a priori* expected to have high newt abundances, but this was not the case. This could possibly be explained by the deeper and more exposed waters commonly found behind the dams, or perhaps this area experiences high beaver activity that may disturb newts.

Pond remnants always had higher newt abundances where present, especially after the June 2015 breach at the Gas Line pond complex where very large numbers of newts were surveyed. This habitat type was basically unavailable at Bay State Brook, so it is not known if it would have been a highly occupied type here. These remnants, although most likely not permanent, may act as preferred habitat for pond-breeding amphibians (Petranka et al. 2004) and especially for adult spotted newts (Gill 1978). Three possible hypotheses could explain why large numbers of newts occupy former pond remnants:

1. Following a dam breach when ponds start to shrink, newts might not have neighboring ponds to migrate to, and could remain until the pond remnant dries up.
2. Newts following a breach will stay in the pond remnants because of site fidelity (i.e. the tendency to remain in or return to a specific locale), or they may even return there after metamorphosis from eft stage into the adult stage.
3. Pond remnants, being shallow, warm, and quiescent, may actually be a preferred habitat type in beaver complexes.

Further field investigations will need to be performed in order to analyze these three hypotheses.

The Bay State Brook pond complex was the most stable out of four effectively georeferenced pond complexes, experiencing relatively modest and incremental change over a 20-year period (only one of six major ponds underwent a cycle of complete decline and redevelopment). Bay State Brook also has the smallest upstream watershed area compared to the other georeferenced locations. In contrast, the Gas Line pond complex was the most unstable area with the largest upstream watershed by far. Unlike Bay State Brook which had perennial beaver ponds going back to 1995 (GoogleEarth satellite imagery), Gas Line may have had a faster and more dramatic beaver cycle, with longer and more frequent periods of breached dams and drained ponds.

Quaker Run Upstream had high instability values as well (as thus a smaller stream) than at the Gas Line pond complex. This area had active beaver ponds from 1995 to 2007, but after this date the complex's largest major pond started to infill. Presently, this pond is a complete beaver meadow and its large dam is covered in *Salix* (willow) spp. thickets. However, new beaver activity (as observed in Spring 2015) is occurring downstream from the old dam, complete with a new main dam, pond, lodge, and several smaller ponds. This is the only site where the full beaver cycle took place during the study's time frame.

France Brook pond complex is only moderately unstable for its upper portion (less than Quaker Run but more than Bay State Brook), but the watershed area is much larger than at Quaker Run Upstream. Beaver activity had been present going back to 1995, although the main ponds encountered major growth and declines over the years. It is evident that watershed size is related to pond complex stability, although not necessarily in a linear fashion.

Conversely, pond complexes within large watersheds (such as Gas Line) may develop large ponds over a shorter period of time because of larger stream size and greater discharge. However, these ponds may become less stable because of the constant necessity of maintaining a dam and pond on a larger stream with greater hydraulic power and flood potential. This may give the surrounding resources (hardwoods) less time to grow back because beavers would require more resources to make constant repairs on their dams, thus depleting resources at a faster rate. If a major breach occurs, even more resources still would have to be used, further depleting these resources. However, this idea may not hold true for the Quaker Run Upstream pond complex, which resides on a smaller stream but had high instability values. It is possible that the beavers here simply used up all of the resources for food and building materials, possibly trying to provide for a large beaver colony. This is speculative, but this pond complex has a long history of beaver occupation (since at least the 1930s [Shadle et al. 1943]), and there are many ponds and former ponds in this complex.

It was originally expected that proximate habitat type might be the primary influence on newt abundance, but as it turned out, pond complex instability and watershed area had a greater influence on newt abundance. Stable pond complexes may have longer successional stages which could affect newt density. If a complex is more stable, it may be favorable to species with marked site fidelity (Gill 1978, Metts et al. 2001, Stevens et al. 2006a). If a pond complex eventually becomes a series of meadows, newts would likely abandon the area and migrate elsewhere, or simply would fail to reproduce and persist.

Newt abundances in other areas of the park would have to be measured to further support this study. For instance, pond complexes near Bay State Brook that reside on the same watershed may be expected to have higher newt abundances, whereas pond complexes on larger watersheds with dams built on fast streams may be expected to have lower newt abundances. This is a possible study that may be conducted in the future.

CONCLUSIONS and RECOMMENDATIONS

Pond complex stability and watershed sizes seem to play a major role in affecting spotted newt abundances, whereas specific habitat types and characteristics within pond complexes may only have a minor affect. The shifting mosaics of habitats that beavers create are highly variable from complex to complex—instability values, pond sizes, environmental parameters, and newt densities all varied drastically, and no one location and habitat was exactly the same as any other. As long as suitable habitat types are within relatively stable pond complexes, they will most likely yield high newt abundances. Artificial impoundments may also provide surrogate habitats for spotted red newts, given that these impoundments can contain similar environments to those of a stable beaver complex. Allegany State Park, having evidence of active beaver complexes going back to the 1920's, may provide essential and suitable habitat that spotted newts, and perhaps other pond-breeding amphibians, need to survive and reproduce. Bringing back the North American beaver to its former population size may be the key idea for conserving a shrinking and delicate group of organisms that are dependent on specific habitats. Many future studies would have to be conducted in order to strengthen this idea. Possible studies include:

1. A vegetation/tree species analysis of the studied beaver complexes.
2. Revisit the Gas Line pond complex to observe any repairs made on the

breach and relate it to surrounding vegetation and tree cover.

3. More studies on pond remnants and how/why they strongly affect newt abundances.
4. Possible studies on other pond-breeding amphibians in beaver ponds.
5. Comparing vernal pools to beaver ponds, in terms of spotted newts and other pond-breeding amphibians.
6. Performing similar studies to other pond complexes near the original five.
7. Studies on stream salamanders near beaver complexes: if the stream habitat was modified, how would this affect stream salamanders? How would this affect fish and macro populations?
8. Life history studies on adult newts and migratory studies on red efts near "natal" beaver ponds—a site fidelity study (where do they go if complexes become a meadow?)
9. Possible study of the benefits amphibians provide for beaver ponds, perhaps via trophic cascades.
10. Biogeographical study of beaver history at ASP, especially as related as land use changes.

REFERENCES

Alford RA, Richards SJ. 1999. Global Amphibian Declines: A Problem in Applied Ecology. Ann. Rev. Ecol. Syst. 30: 133-165.

Bonner JL, Anderson JT, et al. 2009. Vegetative composition and community structure associated with beaver ponds in Canaan Valley, West Virginia, USA. Wetlands Ecology Management 17:543-554.

Brown NM. 1999. "The Life of a Pond." Penn State News. Retrieved Sep 3 2015. http://news.psu.edu/story/141558/1999/05/01/research/life-pond.

Butler DR. 1995. *Zoogeomorphology: Animals as Geomorphic Agents*. Cambridge University Press. pp. 148-183.

Butler DR. 2012. Characteristics of beaver ponds on deltas in a mountain environment. Earth Surface Processes and Landforms 37, 876-882.

Butler DR, Malanson GP. 2005. The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71, 48-60.

Cunningham J. 2003. Pond-Breeding Amphibian Species Distributions in a Beaver-Modified Landscape, Acadia National Park, Mount Desert Island, Maine. University of Maine, 73 pp.

Cunningham JE, Calhoun AJK, Glanz WE. 2007. Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. Journal of Wildlife Management 71(8): 2517-2526.

Dalbeck L, Luscher B, Ohlhoff D. 2007. Beaver ponds as habitat of amphibian communities in a central European highland. Amphibia-Reptilia. 28: 493-501.

Davis MB. 2003. *Old Growth in the East: A Survey.* Revised Edition. Appalachia-Science in the Public Interest, pp. 38-39.

Eskew EA, Todd BD. 2013. Parallels in amphibian and bat declines from pathogenic fungi. Emerging Infectious Diseases. Vol. 19, No. 3.

Fuller MR, Peckarsky BL. 2011. Does the morphology of beaver ponds alter downstream ecosystems? Hydrobiologia 668: 35-48.

Gallant AL, Klaver RW, et al. 2007. Global rates of habitat loss and implications for amphibian conservation. Copeia(4), pp. 967-979.

Gill DE. 1978. The Metapopulation Ecology of the eastern spotted red newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48:145-166.

Gurnell AM. 1998. The hydrogeomorphological effects of beaver-dam building activity. Progress in Physical Geography 22, 2 pp. 167-189.

Hampton RE, Havel JE. 2006. *Introductory Biological Statistics*, Second Edition. Waveland Press, Inc., pp. 95-96, 104-107.

Hardisky T. 2011. Beaver Management in Pennsylvania. Pennsylvania Game Commission, 106 pp.

Hopkins GR, French SS, et al. 2013. Increased frequency and severity of developmental deformities in rough-skinned newt (Taricha granulosa) embryos exposed to road deicing salts (NaCl &MgCl2). Environmental Pollution 173: 264-269.

Hossack BR, Gould WR, et al. 2015. Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. Biological Conservation 187: 260-269.

Johnston CA. 2012. Beaver Wetlands. In DE Batzer and A Baldwin *Wetland Habitats of North America: Ecology and Conservation Concerns*. University of California Press, Berkley.

Johnston CA, Naiman RJ. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology Vol. 1 No. 1 pp. 47-57.

Joly P, Mraud C, et all. 2001. Habitat matrix effects on pond occupancy in newts. Conservation Biology Vol. 15 No. 1 pp. 239-248.

Karraker NE, Gibbs JP. 2009. Amphibian production in forested landscapes in relation to wetland hydroperiod: A case study of vernal pools and beaver ponds. Biological Conservation 142, 2293-2302.

Marcin B, Metrack M. 2014. Spring migration rates and community structure of amphibians breeding in an old and newly established midfield pond. Folia Zool. 63(3): 161-170.

Marion ZH, Hay ME. 2011. Chemical defense of the eastern newt (*Notophthalmus viridescens*): Variation in efficiency against different consumers and in different habitats. PloS ONE 6(12): e27581.

Martell KA, Foote AL, Cummings SG. 2006. Riparian disturbance beavers (*Castor canadensis*) in Alberta's boreal mixedwood forests: Implications for forest management. Ecoscience 13(2): 164-171.

Mason CY 1936. The Geography of Allegany State Park. NYS Museum Circular 16. Albany NY. 67 p.

Mathewson BG. 2014. The relative abundance of the juvenile phase of the eastern red-spotted newt at Harvard Forest prior to the arrival of the hemlock woolly adelgid. Southeastern Naturalist, 13(Special Issue 6): 117-129.

Meentemeyer RK, Butler DR. 1999. Hydrogeomorphic effects of beaver dams in Glacier National Park, Montana. Physical Geography 20, pp. 436-446.

Metts BS, Lanham JD, Russell KR. 2001. Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the Upper Piedmont of South Carolina. Am. Midl. Nat. 145: 54-65.

Mitchell J, Gibbons W. 2010. *Salamanders of the Southeast*. University of Georgia Press.

Naiman RJ, Johnston CA, Kelley JC. 1988. Alteration of North American streams by beaver. Bioscience, Vol. 38 No. 11 pp. 753-762.

Neff DJ. 1957. Ecological effects of beaver habitat abandonment in the Colorado Rockies. Journal of Wildlife Management Vol. 21, No. 1.

New York Department of Environmental Conservation. 2015. Controlling Beaver Damage: Solving Beaver Problems. Retrieved Nov 15 2015. http://www.dec.ny.gov/animals/9982.html.

New York Department of Environmental Conservation. 2015. Nuisance Beaver:

Techniques for Controlling Nuisance Beaver. Retrieved Sep 2 2015. http://www.dec.ny.gov/animals/6992.html.

The New York State Office of Parks, Recreation, and Historic Preservation. 2010. Allegany State Park Final Master Plan/FEIS, 163 pp.

The New York State Office of Parks, Recreation, and Historic Preservation 2010. Allegany State Park Final Master Plan/FEIS, Appendix C- History and Timeline of Allegany State Park, 3 pp.

Nummi P, Kvuluuainen T. 2013. Forest disturbance by and ecosystem engineer: beaver in boreal forest landscapes. Boreal Environment Research 18 (suppl. A): 13-24.

Petranka JW, Smith CK, Scott AF. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. Ecological Applications. 14(4), pp. 1065-1078.

Pfingsten RA, Downs FL. 1989. *Salamanders of Ohio.* Bulletin of the Ohio Biological Survey. Volume 7 Number 2 (79-87).

Pfingsten RA, Davis JG, et al. 2013. *Amphibians of Ohio.* Ohio Biological Survey. Volume 17 Number 1 (425-435).

Piovia-Scott J, Pope KL, et al. 2011. Factors related to the distribution of prevalence of the fungal pathogen *Batrachochytrium dendrobatidis* in *Rana cascadae* and other amphibians in the Klamath Mountains. Biological Conservation 144 2913-2921.

Pollock MM, Heim M, Werner D. 2003. Hydrolic and geomorphic effects of beaver dams and their influence on fishes. American Fisheries Society Symposium 37, 22 pp.

Raffel TR, Bommarito T, et al. 2008. Widespread infection of the eastern red-spotted newt (*Notphthalmus viridescens*) by a new species of *Amphibiocystidium*, a genus of fungus-like mesomycetozoan parasites not previously reported in North America. Parasitology 135, 203-215.

Rinehart KA, Donovan TM, et al. 2009. Factors influencing occupancy patterns of eastern newts across Vermont. Journal of Herpetology, Vol. 43, No. 3, pp. 521-531.

Roe AW, Grayson KL. 2008. Terrestrial movements and habitat use of juvenile and emigrating adult eastern red-spotted newts, *Notophthalmus viridescens*. Journal of Herpetology, Vol. 42 No. 1 pp. 22-30.

Rohr JR, Madison DM. 2003. Dryness increases predation risk in efts: support for an amphibian decline hypothesis. Oecologia 135: 657-664.

Secondi J, Lepetz V, et al. 2013. Nitrate affects courting and breathing but not escape performance in adult newts. Behavioral Ecology Sociobiology 67: 1757-1765.

Sherman E, Van Munster K. 2012. Pond pH, acid tolerance, and water preference in newts of Vermont. Northeastern Naturalist. 19(1): 111-122.

Shadle AR, and Austin TS. 1939. Fifteen months of beaver work at Allegany State Park, NY. J. Mammalogy. 20: 299-303.

Shadle AR, Nauth AM, et al. 1943. Comparison of tree cuttings of six beaver colonies in Alegany State Park, New York. J. Mammalogy 24: 32-39.

Smith KG. 2006. Keystone predators (eastern newts, *Notophthalmus viridescens*) reduce the impacts of an aquatic invasive species. Oecologia 148: 342-349.

Snodgrass JW. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American Landscape. Journal of Applied Ecology 34, 1043-1056.

Snodgrass JW, Meffe GK. 1998. Influence of beavers on steam fish assemblages: effects of pond age and watershed position. Ecology, 79(3), pp. 928-942.

Sousa PJ. 1985. Habitat Suitability Index Model: Red Spotted Newt. U.S. Fish and Wildlife Service Biological Report 82 (10.111).

Stevens CE, Paszkowski CA, Foote AL. 2006a. Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. Biological Conservation 134: 1-13.

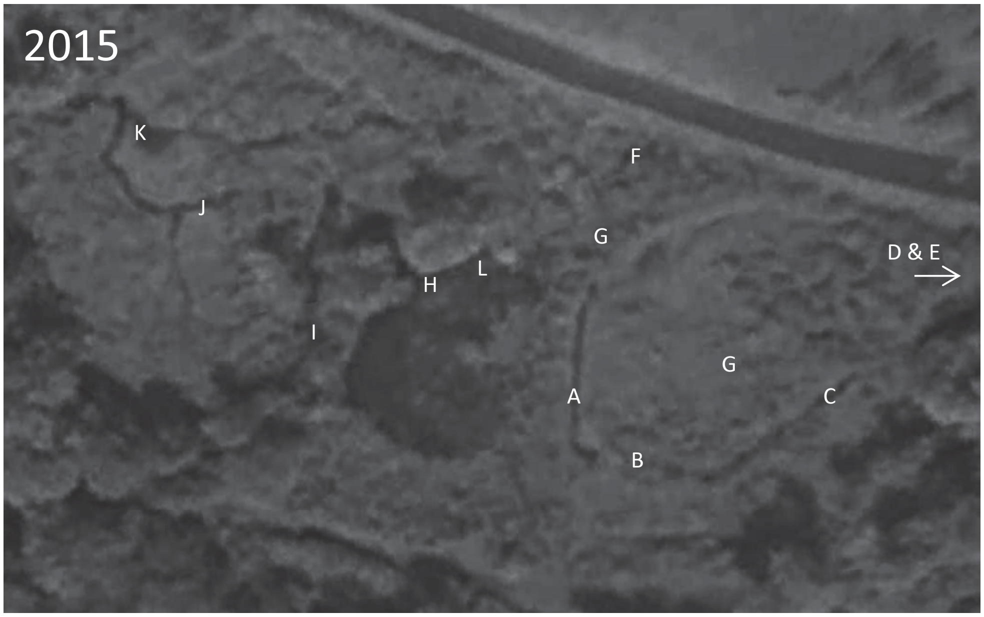
Stevens CE, Paszkowski CA, Serimgzour GJ. 2006b. Older is better: Beaver ponds on boreal streams as breeding habitat for the wood frog. Journal of Wildlife Management 70(5): 1360-1371.

World Wildlife Fund. 2015. Allegheny Highlands forests. Retrieved Sep 20 2015. http://www.worldwildlife.org/ecoregions/na0401.

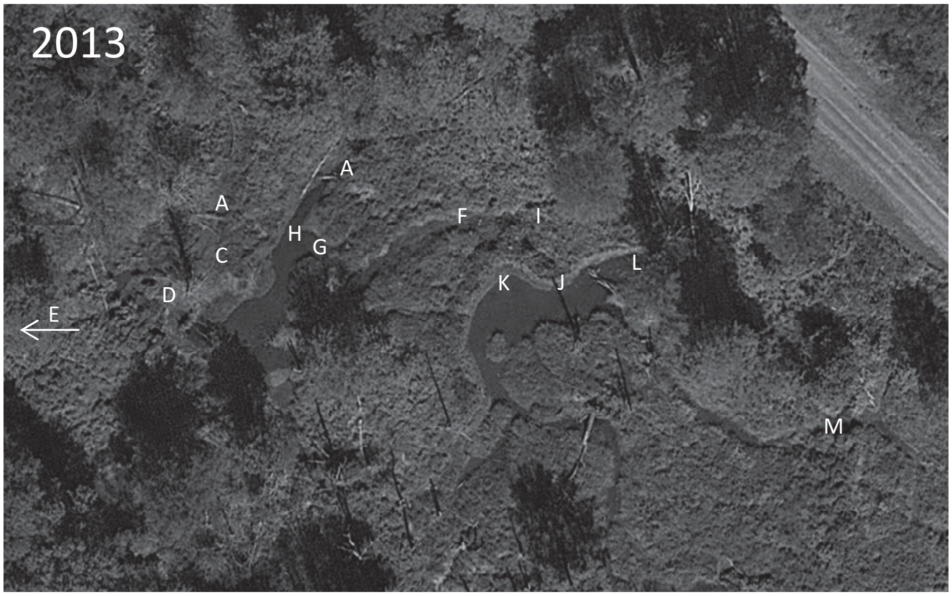
APPENDIX – Pond complex aerial images with newt survey point designations

Bay State Brook

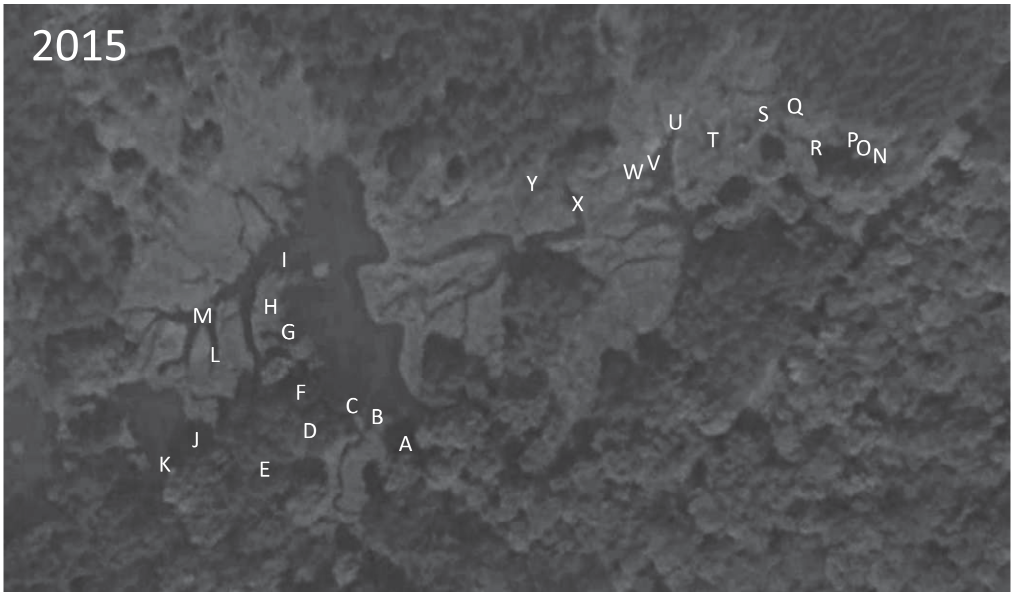
Gas line



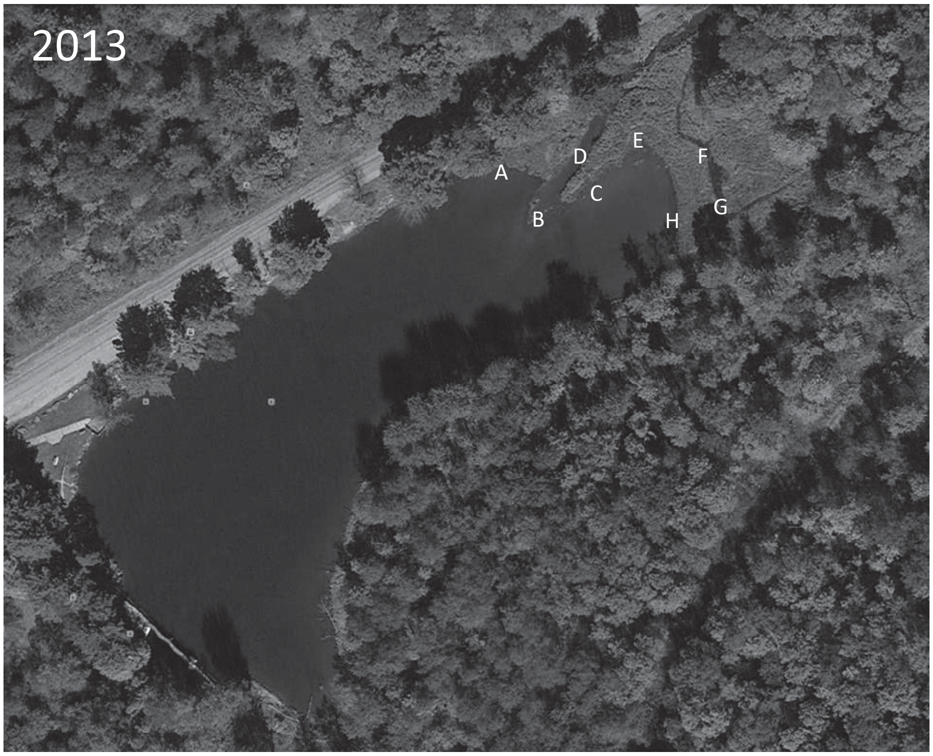
Upstream Quaker Run



Downstream Quaker Run



France Brook



Science Lake impoundment