The Influence of Local and Landscape Scale Factors on the Presence, Relative Abundance and Characteristics of Brook Trout (*Salvelinus fontinalis*) in Beaver Ponds

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Abstract

Beaver ponds are a characteristic component of northern Ontario stream ecosystems and display a great deal of variation through their natural cycle of establishment and abandonment. Ponds also provide habitat for brook trout (*Salvelinus fontinalis*) within small-stream systems. However, the habitat characteristics of ponds used by brook trout, and the characteristics of brook trout in the ponds is poorly understood. I evaluated the local and landscape scale habitat characteristics of beaver ponds that are associated with the presence, relative abundance and physical characteristics of brook trout. Brook trout were captured in 40% of 50 beaver ponds sampled. Angling proved to be the most reliable method to sample brook trout in ponds, however, catchability appeared to be strongly influenced by temperature. Catch per unit effort (CUE) was significantly higher in ponds with water temperatures within the approximate preferred thermal range of brook trout (11 °C to 18 °C) (ANOVA, $F_{2,48} = 5.259$, $p = 0.026$). Peak CUE occurred between approximately 14 °C to 18 °C. Beaver ponds with brook trout present were generally characterized by greater upstream catchment area (UCA), lower water temperature, higher dissolved oxygen, higher conductivity, higher alkalinity, and greater depth. Brook trout were never captured in ponds with an upstream catchment area (UCA) less than 2.9 sq. km. In a logistic regression model, UCA correctly predicted brook trout presence and absence in beaver ponds (82.4%). In beaver ponds with a mean water temperature greater than 11 °C, predicted group membership using UCA was greater (92.9%). Model parsimony and predictive ability increased when beaver ponds with an overall mean water temperature greater than 11 °C were used in the analysis. Brook trout captured in beaver ponds were, on average, 105 mm and 72 g larger than those in adjacent streams ($F_{1,1321} = 1658.2$, $P < .001$). Brook trout average size in ponds was larger in smaller UCAs, whereas, brook trout in streams were larger in larger UCAs. My research illustrates that beaver ponds provide complimentary and/or supplementary habitat for brook trout living in stream systems. It is clear that pond characteristics at both a landscape and local scale are associated with brook trout presence or absence, likely through the ability of brook trout to colonize the pond and the suitability and stability of habitat within the pond. Further research is required to better understand the linkage between local and landscape scale characteristics influencing brook trout habitat and abundance in small headwater streams and insure the protection of these linkages from disturbance.

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"One is inclined to use the past tense in writing of the wild brook trout. Constitutionally incompatible with the advance of civilization, this exquisite fish is dying. Where man has dried up his springs by deforestation, polluted his waterways, straightened streams into ditches and denuded them of their natural cover, the wild brook trout has vanished."

Henry David Thoreau

1.0 Introduction

Stream dwelling brook trout (*Salvelinus fontinalis*) populations are common throughout boreal forest stream networks in northwestern Ontario and are often the only fish species present in small headwater streams. The brook trout is an endemic and widely distributed species (Scott and Crossman 1973, Power 1980, Hartviksen and Momot 1989) exhibiting a variety of life history strategies, as well as considerable variation in reproduction, age of maturity, life span, and habitat preferences (Carlson and Hale 1973, Scott and Crossman 1973, Power 1980, Hutchings 1993, Hutchings 1996). They occupy habitats ranging from small intermittent streams and temporally variable ponds to large rivers and deep cold lakes (Scott and Crossman 1973, Benke 2002). Brook trout along the Atlantic coast and Hudson Bay exhibit migratory behavior, moving between fresh and salt water (Power 1980, Benke 2002). Typically, these anadromous brook trout, often referred to as 'Salters', are mature adults that migrate into coastal streams to spawn and then return to saltwater. Juvenile brook trout emerge and rear in streams for a period of time dependent on river specific conditions (approximately 1 to 3 years) before eventually returning to the ocean following smolting (Scott and Crossman 1973, Power 1980, Benke 2002). Temporary movements into or out of these streams by both juveniles and adults presumably occur while foraging or in search of refugia in response to changing environmental conditions (Curry *et al.* 2002). In both lakes Nipigon and Superior, brook trout migrate to and from tributary streams to spawn and possibly forage, although little is known about the mechanisms that drive these movements (Mucha 2003).

Brook trout are a member of the Charr (*Salvelinus*) Genus. The endemic distribution of brook trout overlaps both Lake trout (*Salvelinus namaycush*) and Arctic charr (*Salvelinus alpinus*). However, brook trout are smaller and shorter lived than both these charr species and exploit a more diverse range of habitats (Scott and Crossman 1973, Power 1980, Benke 2002). Although considered a generalist among the charrs, brook trout distribution, habitat utilization, and movements are constrained by specific bio-physiological and environmental requirements (Power 1980).

Brook trout exhibit considerable variation in body shape, size, and coloration depending on habitat, season, and state of maturity (Scott and Crossman 1973, Power 1980). In general, brook trout can be distinguished by their elongate and trout-like body, relatively large head with terminal mouth, square or flat edged tail, and unique coloration and markings (Power 1980, Benke 2002). Brook trout exhibit some degree of variation in colouration; though generally they have a dark, olive-green, brown, to almost black back with lighter, iridescent silvery sides fading into a whitish belly. The back is covered with distinct vermiculations fading into spots in addition to the characteristic red spots surrounded by blue halos (Power 1980). The anal, pelvic, and pectoral fins are generally an orange to red colour that has a distinct white leading edge bordered by a black line. Like many salmonids, brook trout colouration intensifies prior to spawning, especially in males (Wilder 1952, Scott and Crossman 1973). Brook trout consume a wide variety of organisms. Brook trout size and habitat determines diet (Power 1980). Scott and Crossman (1973) state that brook trout will eat "anything their mouth can accommodate" which commonly consists of invertebrates, crustaceans, small reptiles and mammals, baitfish and even other brook trout. Generally, brook trout life spans rarely exceed 5 to 8 years with age of maturity at 2 or 3 years of age (Carlson and Hale 1973, Scott and Crossman 1973). However, brook trout in the Mackenzie River watershed study area are small bodied, can mature at 1 to 2 years of age, and rarely if ever survive beyond 3 years of age (Armstrong 2005, pers. comm.).

The natural range of the brook trout occurs entirely within eastern North America (MacCrimmon and Campbell 1969, Scott and Crossman 1973, Power 1980). The distribution of brook trout is delimited by, and contiguous with, the Atlantic seaboard to the east and the Mississippi and Great lakes drainage to the west. The northern range of brook trout is contiguous with Hudson's and James Bay along Ontario and Manitoba as well as northern Quebec and Ungava Bay. The range extends into the higher elevations of the Appalachian Mountains as far south as the headwaters of the Chattahoochee River in Georgia (Ryder *et al.* 1964, MacCrimmon and Campbell 1969, Scott and Crossman 1973, Power 1980).

The Laurentian great lakes basin has been colonized by fish species over the past 14 000 years (Bailey and Smith 1981). Extensive fluctuations in glacial advances and retreats allowed fish populations to persist in slowly shifting environments and glacial refugia (Bailey and Smith 1981, Holt 1997, Power 2002, Wilson and Mandrak 2004). Brook trout likely persisted in both the Atlantic and Mississippian periglacial refugia and re-colonized what is now their endemic range following the most recent Wisconsinan glacial retreat (Bailey and Smith 1981). In temporally variable proglacial lakes, extensive stochastic extinction and re-colonization events were likely common as dispersal corridors and drainage connections shifted with the ebb and flow of glacial expansion and retreat (Bailey and Smith 1981, Rempel and Smith 1998, Wilson and Mandrak 2004). The temporal nature, scope, and environmental conditions of proglacial lakes and glacial refugial connections were likely significant in shaping modern distributions of freshwater fish fauna (Bailey and Smith 1981, Wilson and Hebert 1996, Rempel and Smith 1998, Wilson and Mandrak 2004). Brook trout likely colonized the Mackenzie River watershed approximately 11 200 – 11 600 years ago from Lake Duluth. Lake Duluth, which filled what is currently the western portion of the Lake Superior basin, had an elevation higher than has existed in the Superior basin subsequently (currently up to approximately 331 m above sea level). It was during this relatively brief time period that fish were able to colonize Lake Superior tributaries above their current dispersal barrier falls (Bailey and Smith 1981).

Historical circumstances and ecological characteristics are critical components determining the contemporary distribution of brook trout (Bailey and Smith 1981, Power 2002). Generally, where brook trout are present their distribution is continuous within a stream catchment. Although, at certain times of the year their distribution may become discontinuous or patchy as they may be restricted physically and spatially by unstable stream habitat conditions. Brook trout have specific habitat requirements that ultimately influence distribution, abundance, and fitness (Power 1980). Local scale environmental habitat variables as well as landscape scale characteristics of stream ecosystems and in particular, beaver ponds, may be associated with brook trout presence and relative abundance and may be useful for predicting brook trout distribution patterns.

Temperature has been identified as an important determinant of brook trout distribution and may be useful for discriminating between potential brook trout streams and non-brook trout streams (Picard *et al.* 2003). A broad range of both preferred and lethal temperatures has been reported for brook trout. These values were dependent on both environmental and experimental laboratory conditions, as well as the age and physical condition of the trout. Brook trout distribution is constrained by maximum water temperature tolerances that are between approximately 19 °C (Creaser 1930) and 24 °C (Ricker 1934). The preferred temperature range for brook trout is between 14 °C and 19 °C (Fry *et al.* 1946). However, reported brook trout preferred thermal optimum also varies from 14 – 16 °C (Cherry *et al.* 1975), to 15.5 – 16.8 °C (Cherry *et al.* 1977), and 16.0 °C (Peterson 1973). Brook trout are also expected to be absent from waters where their maximum lethal temperature is reached or surpassed. Published lethal maxima for brook trout are 23.4 – 25.3 °C (Fry *et al.* 1946), 24.0 °C (Cherry *et al.* 1975), 26.2 – 27.8 °C (Grande and Andersen 1991) and 27.7 – 29.8 °C +/- 0.1 °C (Benfey *et al.* 1997). McRae and Edwards (1994) defined brook trout habitat suitability by four thermal ranges after Raleigh (1982): lower range (< 11 °C), an optimal range (11 - 16 °C), an upper range (17 – 23 °C), and a lethal range (greater than 24 °C). Salmonids will occupy areas within their preferred thermal range or move to habitat where waters in that temperature range exist (Reynolds and Casterlin 1979, Garret and Bennett 1995, Biro 1998). Temperature also influences timing of brook trout spawning, which occurs from early September to early December. However, Witzel and MacCrimmon (1983) indicate that peak spawning occurs at water temperatures between 6 – 8 °C. Hokanson *et al.* (1973) reported ovulation and spawning occurred in temperatures as high as 16° C. However, the upper median limit for egg viability was 11° C and the upper median tolerance limit for a normal hatch was 12.7° C with the optimum temperature at approximately 6° C. Temperature has also been demonstrated to influence foraging and feeding rates in brook trout (Baldwin 1956, Hokanson *et al.* 1973, Cunjak *et al.* 1987, Drake and Taylor 1996).

Many characteristics of stream ecosystems, which may influence brook trout distribution and abundance, are a function of the landscapes or watersheds the stream drains. For example, groundwater is an important characteristic in stream ecosystems and brook trout habitat (Freeze and Cherry 1979, Curry and Noakes 1995, Curry *et al.* 1995, Curry *et al.* 1997, Baxter and Hauer 2000). Groundwater discharge sites have been related to landscape scale hydrogeological characteristics in a watershed (Curry and Devito 1996) such as surficial geology and catchment topography (Quinn *et al.* 1991, Buttle *et al.* 2000, Buttle *et al.* 2001). Groundwater discharge may significantly influence the physiochemical characteristics of stream ecosystems and beaver ponds and thus influence the abundance and distribution of fish (Curry and Noakes 1995, Curry *et al.* 1995, Curry *et al.* 1997, Baxter and Hauer 2000).

Groundwater is thought to be an important factor limiting salmonid spawning areas and survival (Curry and Noakes 1995, Blanchfield and Ridgway 1997, Curry *et al.* 1997, Biro 1998, Power *et al.* 1999, Baxter and Hauer 2000). The presence of groundwater inputs, along with the ability of brook trout to exploit them, may enable populations to persist in otherwise marginal habitats (Gibson 1966, Bowlby and Roff 1986, Biro 1998). Upwelling groundwater often differs physio-chemically from surface water (White 1990); however, the most important difference may be temperature regime (Baxter and Hauer 2000). For instance, where stream temperatures exceed thermal tolerances of brook trout, discrete areas of localized groundwater may act as thermal refugia (Gibson 1966, Bowlby and Roff 1986). Spawning sites of brook trout in lakes are generally influenced by upwelling interstitial pore water and groundwater (Witzel and MacCrimmon 1983, Curry and Noakes 1995, Blanchfield and Ridgway 1997). Brook trout redds are generally constructed on clean gravel, however, spawning areas appear to be less influenced by substrate than the presence of upwelling groundwater (Fraser 1982, Witzel and MacCrimmon 1983, Curry and Noakes 1995, Blanchfield and Ridgway 1997). Groundwater likely improves the survival and development of eggs by creating a stable environment through regulation of instream temperature and limiting ice formation (Cunjak and Power 1986, Cunjak 1988, Cunjak 1996, Curry *et al.* 1997, Lindstrom and Hubert 2004).

In northern boreal forest stream systems brook trout physiology and life history strategies are adapted to maximize survival in harsh, highly variable environments. Brook trout are very efficient at assimilating nutrients and have one of the lowest energy requirements of any fish (Tucker and Rasmussen 1999). This may enable brook trout to persist in a wide variety of habitats such as low productivity headwater streams. Brook trout evolved in cold, nutrient poor, periglacial refugia which have allowed them to thrive in environments that experience extreme variation in temperature and seasonal ice conditions (Bailey and Smith 1981, Power 2002). Historically, brook trout were thought to be relatively sedentary (Gerking 1959, Power 1980, Gowan *et al.* 1994, Gowan and Fausch 1996a), however, recent studies suggest they can be extremely motile (Gowan *et al.* 1994, Gowan and Fausch 1996a, Curry *et al.* 2002, Gowan and Fausch 2002). The benefit of the evolution of migratory behavior in brook trout, particularly anadromous and potadromous movements may be that it facilitated temporary range extensions during glacial expansion and retreat ultimately enabling brook trout to colonize its current range following the last glaciation (Power 2002). However, the contemporary benefit of migration may be the ability to move between variable or intermittent habitats and exploit and persist in marginal environmental conditions.

The association between habitat characteristics and brook trout presence and abundance is complicated by the natural fragmentation of stream ecosystems by beaver ponds. Beaver dams are potential barriers to fish movement within a stream and may disrupt fish dispersal and distribution depending on the dams' physical characteristics and season (Rupp 1955, Gard 1961, Naiman *et al.* 1986, Naiman *et al.* 1988, Schlosser 1995b, Snodgrass and Meffe 1998, Collen and Gibson 2001). If movement is a critical characteristic of brook trout life history, the potential isolation from necessary habitat by beaver dams may prove disastrous for stream populations (Dunning *et al.* 1992, Gowan and Fausch 1996a, Gowan and Fausch 1996b, Warren and Pardew 1998, Labbe and Fausch 2000, Fausch *et al.* 2002). Beaver ponds may reduce the connectivity between spatially sub-divided populations within a watershed and may also restrict access to complementary and supplementary upstream and downstream habitats (Dunning *et al.* 1992, Schlosser and Kallemeyn 2000). However, fish exploit beaver ponds amidst the extensive stream environment in which they are embedded (Schlosser 1995b, Schlosser and Kallemeyn 2000). The unique environmental characteristics created by beaver ponds, relative to the adjacent stream, may influence the distribution and relative abundance of various fish species (Naiman *et al.* 1986, Winkle *et al.* 1990, Johnson *et al.* 1992, McRae and Edwards 1994, Schlosser 1995a, Schlosser 1995b, Schlosser 1998, Snodgrass and Meffe 1998, Snodgrass and Meffe 1999, Schlosser and Kallemeyn 2000, Collen and Gibson 2001). Despite disrupting the stream channel, beaver ponds may provide additional foraging opportunities, pool habitat, and over-wintering areas (Naiman *et al.* 1986, Naiman *et al.* 1988, Naiman *et al.* 1994, Chisholm *et al.* 1987, Schlosser 1995a, Schlosser 1995b, Cunjak 1996, Snodgrass 1997, Schlosser and Kallemeyn 2000). Beaver ponds may also provide temporary thermal, spatial, and predatory refugia during adverse conditions (Hanson and Campbell 1963, Chisholm *et al.* 1987, Winkle *et al.* 1990, Johnson *et al.* 1992, Cunjak 1996, Hagglund and Sjoberg 1999).

The beaver (*Castor canadensis*) is a large, ubiquitous rodent that is endemic Northwestern Ontario and can be found in most stream drainages in the region (Barn 1997). Beaver affect stream and riparian ecosystem composition and dynamics and have the ability to severely alter stream habitat and the surrounding riparian area (Naiman *et al.* 1986, Naiman *et al.* 1988, Naiman *et al.* 1994, Johnston and Naiman 1990, Schlosser 1995b, Barnes 1997, Barnes and Dibble 1998, Hagglund and Sjoberg 1999, Schlosser and Kallemeyn 2000, Collen and Gibson 2001). Beaver ponds are often restricted to small headwater streams due to seasonal variations in discharge that would be potentially destructive on larger streams (Naiman *et al.* 1986, Naiman *et al.* 1988). Beaver dam construction and the impoundment of water creates extensive pond habitat in small stream drainages (Barnes and Mallik 1996, Barnes 1997). Small headwater streams are typically narrow and heavily shaded; however, when beaver ponds are present, the drainage is characterized by areas of open canopy, increased wetland areas, and increased bio-geochemical interactions with riparian areas (Naiman *et al.* 1986). Beaver ponds are generally characterized by large edge-to-surface-area ratios incorporating extensive near-shore habitat not found in un-impounded streams (Pollock *et al.* 2004). The successional nature of beaver ponds has the potential to alter bio-geochemical cycles at large spatial and temporal landscape scales (Johnston and Naiman 1990, Naiman *et al.* 1994, Schlosser and Kallemeyn 2000).

Naiman *et al.* (1986, 1988) suggest that beaver ponds confer stability within stream drainage networks improving the overall ecological value of the system. Beaver ponds within stream drainage networks may stabilize stream flows buffering both flood and base flow conditions (Baxter 1977, Naiman *et al.* 1986, Naiman *et al.* 1988, Woo and Waddington 1990, Collen and Gibson 2001). For example, streams with beaver dams in series may exhibit a decrease in flood potential by retaining water leading to increased duration of flow above base flow, and produce sustainable flows in otherwise intermittent streams (Rutherford 1955, Naiman *et al.* 1986, Snodgrass 1997, Collen and Gibson 2001). Beaver impoundments in stream drainages may also influence habitat heterogeneity by creating patches of temporally variable lentic habitat within the extensive lotic drainage network (Naiman *et al.* 1986, Naiman *et al.* 1988, Naiman *et al.* 1994, Schlosser 1995a, Schlosser 1995b, Snodgrass 1997, Schlosser and Kallemeyn 2000, Pollock *et al.* 2004).

Beaver activity alters nutrient availability and movement, carbon cycles, sediment transport (Baxter 1977, Naiman *et al.* 1986, Naiman *et al.* 1988, Smith *et al.* 1991), riparian vegetation (Barnes and Dibble 1988, Johnston and Naiman 1990), and water quality characteristics (Devito and Dillon 1993, Klotz 1998, Margolis *et al.* 2001) in stream drainage networks. The beaver pond may act as a reservoir trapping nutrients that would otherwise be distributed downstream (Naiman *et al.* 1986, Naiman *et al.* 1988). This may produce patches of nutrient-rich habitat nested within nutrient-poor stream drainages. Water quality parameters such as pH, dissolved oxygen, conductivity, total dissolved solids and temperature can be affected by riparian disturbance and alteration to lotic habitat by beaver dam construction (Johnston and Naiman 1990, Woo and Waddington 1990, Devito and Dillon 1993, Naiman *et al.* 1994). Beaver ponds may alter water chemistry downstream of the impoundments through physical, chemical, and biological processes within the ponds (Johnston and Naiman 1990, Margolis *et al.* 2001). The contribution of organic material by beaver, in addition to the initial input of inundated forest vegetation, timber, and soil, represents the long term source of nutrients and ions in both the pond and stream outflow (Francis *et al.* 1985, Johnston and Naiman 1990, Devito and Dillon 1993).

Beaver ponds decrease peak discharge during runoff events similarly decreasing the potential for the transport of sediment and nutrients downstream (Naiman *et al.* 1986, Naiman *et al.* 1988, Johnston and Naiman 1987). A reduction in stream velocity results in a corresponding decrease in the carrying capacity of suspended solids and an increase in deposition (Baxter 1977, Naiman *et al.* 1986, Naiman *et al.* 1988, Naiman *et al.* 1994, Johnston and Naiman 1990). The quantity and quality of organic material contributed to the pond by beaver activity has important implications for decomposition dynamics and nutrient chemistry in the impoundment and the area downstream (Hodkinson 1975a, Naiman *et al.* 1986, Naiman *et al.* 1994). The impoundment of stream water by beavers generally increases the input and storage of organic material and sediment (Baxter 1977, Francis *et al.* 1985, Naiman *et al.* 1986) influencing the composition of the invertebrate community (Sprules 1940, Baxter 1977, Francis *et al.* 1985, McDowell and Naiman 1986, Smith *et al.* 1991, Clifford *et al.* 1993). Small headwater streams that are derived primarily from groundwater are naturally low in productivity, which is reflected by low species diversity and richness in the macroinvertebrate community (Pinder and Farr 1977, Plafkin *et al.* 1989, Challen 2001). When a stream is dammed and a beaver pond is formed, lotic benthos will eventually be replaced by lentic organisms (Hodkinson 1975b, Baxter 1977, McDowell and Naiman 1986, Naiman *et al.* 1988, Clifford *et al.* 1993). Also, the impoundment will generally produce an increase in species richness and abundance as well as the size distribution of aquatic invertebrates relative to the stream (Hodkinson 1975b, Baxter 1977, McDowell and Naiman 1986, Smock *et al.* 1989). Vegetation and timber that is contributed directly or indirectly to ponds by beaver activity has important implications for the colonization and composition of macroinvertebrate communities (Smock *et al.* 1989, Clifford *et al.* 1993) and may potentially influence the overall invertebrate biomass available to brook trout.

Beaver ponds will influence water temperature within stream drainages depending on the region and specific site characteristics (Rupp 1955, Gard 1961, Naiman *et al.* 1988, Naiman *et al.* 1994, McRae and Edwards 1994, Collen and Gibson 2001). Water temperature may be the single most important environmental characteristic limiting the distribution of salmonids (MacCrimmon and Campbell 1969, McRae and Edwards 1994, Picard *et al.* 2003). Salmonid species, such as brook trout, are often restricted to headwater streams where cool groundwater maintains suitable summer water temperatures (McRae and Edwards 1994, Power *et al.* 1999). Elevated summer water temperatures can detrimentally affect fish condition by reducing their aerobic capacity and increasing their metabolic oxygen demand (Benfey *et al.* 1997). In addition to their potential to restrict movement within a stream, beaver ponds may also be detrimental to salmonids due to the potential increase in summer water temperature in downstream reaches (Knudsen 1962, Avery 1992, McRae and Edwards 1994). Beaver ponds expose a greater surface area to sunlight, increasing thermal radiation and pond surface temperatures, relative to non-beaver impacted streams (McRae and Edwards 1994). This may be of particular concern at the southern periphery of the brook trout's endemic range where even a small increase in water temperature may restrict or extirpate brook trout from marginal thermal habitat (Meisner 1990, McRae and Edwards 1994). However, the increased volume, depth, temperature stratification, and interaction with groundwater may not only stabilize pond temperatures, but also create areas of cooler water within, and immediately, downstream of the pond relative to the stream during summer months. For instance, Leidholt-Brunner *et al.* (1992) found that Oregon streams with beaver ponds had lower peak water temperatures than streams without beaver ponds. Similarly, discrete localized areas influenced by groundwater discharge are often used as thermal refugia when in-stream temperatures are inadequate (Gibson 1966, Bowlby and Roff 1986, McRae and Edwards 1994). Anecdotal evidence suggests that beaver construct their lodge, food cache, and pond in areas of groundwater upwelling, however, there has been little research done to quantify beaver pond-groundwater association. Thus, beaver ponds may create patches of temperature refugia that allow brook trout to colonize marginal habitat within stream drainages.

Northern Ontario winters include extended periods of extreme cold resulting in thick ice accumulations on streams and beaver ponds often persisting for five or six months. Extended periods of ice cover may increase the potential for winter fish mortality. As winter progresses, dissolved oxygen levels in ponds can be depleted to lethal levels culminating in extensive fish kills (Tonn and Magnuson 1982, Hall and Ehlinger 1989, Fox and Keast 1990). Thick ice on ponds eliminates the absorption of atmospheric oxygen (Klotz 1998) and greatly reduces the available space in pond habitats. The anaerobic condition in beaver ponds is exacerbated by the decomposition of accumulated organic matter and sediment (Baxter 1977, Naiman 1983, Naiman *et al.* 1986, Naiman *et al.* 1988). The same discrete localized areas influenced by groundwater discharge during summer may also serve as thermal or spatial refugia where temperatures and space are inadequate or limited by ice conditions during winter (Cunjak 1996).

The creation of beaver ponds produces a mosaic of temporally variable habitat patches within stream drainage networks (Naiman *et al.* 1994, Snodgrass 1997, Schlosser and Kallemeyn 2000). The limited availability of an accessible food supply as well as construction material to maintain the dam and lodge restricts beaver residency time at individual pond sites. Beaver ponds are abandoned when resources within the ponds influence have been exhausted (Lawrence 1952, Barnes 1997, Snodgrass 1997, Snodgrass and Meffe 1998). However, the successional nature of the pond environment enables future re-colonization of the site, once the necessary resources have regenerated (Lawrence 1952, Snodgrass 1997, Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). The successional nature of beaver ponds may also influence the abundance and distribution of brook trout within both beaver pond and stream habitats by acting as a semi-permeable barrier to fish movement temporally sub-dividing fish populations and necessary habitats (Schlosser and Kallemeyn 2000).

Streams are influenced by the landscape they flow through (Vannotte *et al.* 1980, Hynes 1983, Fausch *et al.* 2002) and characteristics at the landscape scale may have a significant effect on stream ecosystems, influencing brook trout presence and abundance. This includes not only the physiochemical characteristics of the immediate stream and surrounding riparian area, but also catchment topography, geomorphology, surficial geology, as well as perturbations within the catchment (Baxter *et al.* 1999, Baxter and Hauer 2000, Buttle and Metcalfe 2000, Fausch *et al.* 2002, Borwick *et al.* 2006). The alteration of headwater streams by beaver will ultimately influence the ecological processes downstream (Vannotte *et al.* 1980, Naiman *et al.* 1986, Naiman *et al.* 1988). Local and landscape scale characteristics influencing stream ecosystems are hydrologically interconnected both temporally and spatially within the watershed (Vannotte *et al.* 1980, Sedell *et al.* 1990, Fausch *et al.* 2002, Borwick *et al.* 2006). For instance, the increased area associated with beaver ponds may encompass a greater number of groundwater sites, thus intensifying its effect relative to the adjacent stream. If groundwater is an important factor influencing brook trout distribution (Curry and Noakes 1995, Curry *et al.* 1997, Biro 1998, Power *et al.* 1999) then beaver ponds may provide critical habitat within a stream drainage with highly variable environmental conditions.

Variation in landform and surface topography may have a strong influence on stream ecosystems and pond morphology. In the Precambrian shield, sandy till commonly forms local aquifers (Freeze and Cherry 1979), which influences groundwater retention and discharge. The impoundment of water behind beaver dams alters the hydrologic patterns within streams (Baxter 1977, Naiman *et al.* 1986, White 1990). Beaver ponds, especially deep ponds in narrow constrained valley segments, have the potential to recharge and store groundwater by elevating the water table (Naiman *et al.* 1986, Johnston and Naiman 1987, White1990, Baxter *et al.* 1999). The elevated water table and cool groundwater output may influence the thermal and physiochemical characteristics of both the immediate pond and the downstream environment (Baxter 1977, Hynes 1983, White1990, Brunke and Gosner 1997, Baxter *et al.* 1999, Baxter and Hauer 2000, Fausch *et al.* 2002).

The hyporheic zone is functionally linked to groundwater and surface water processes in streams (Grimm and Fisher 1984, Brunke and Gosner 1997, Vallett *et al.* 1997, Baxter and Hauer 2000, Franken *et al.* 2001) and is similarly influenced by landscape scale geomorphic characteristics. Hyporheic exchange is known to vary with discharge, stream gradient, surficial geology and streambed permeability (Thibodeux and Boyle 1987, White 1990, Hendricks and White 1991, Baxter and Hauer 2000). Hyporheic exchange influences stream physical properties and the ecology of fish and invertebrates over various spatial and temporal scales (Brunke and Gosner 1997, Vallett *et al.* 1997, Baxter and Hauer 2000, Franken *et al.* 2001). White (1990) found that the pressure of impounded water behind beaver dams displaced substrate pore-water, while underflow transported convected streamwater beneath the dam. The decrease in pressure downstream of the beaver dam resulted in sudden upwelling of under-flowing stream-water and cooler pore-water from deeper in the substrate. The potential benefits of this process may be magnified in streams with multiple beaver ponds in succession.

Land-use practices, particularly forestry activities, may influence or alter localized groundwater exfiltration into potential brook trout habitat. Locations of brook trout spawning areas, rearing habitat, and thermal refugia are potentially linked to hydrological processes within the landscape (Curry and Devito 1996). Linkages between aquatic and terrestrial processes may operate at landscape spatial scales and determine brook trout distribution and abundance (Borwick *et al.* 2006). Management and protection of brook trout is dependent upon identifying and protecting critical habitat. Recognizing broad-scale habitat requirements and developing an understanding of ecological processes and environmental linkages form the necessary foundation for forest management recommendations to protect these values. The protection of brook trout habitat from deleterious forestry practices and land use disturbance necessitates an understanding of the processes that link aquatic and terrestrial environments and potentially govern dispersal and distribution of the species.

The overall goal of my research was to examine brook trout inhabiting beaver ponds and evaluate their physical characteristics and habitat associations. The first objective was to evaluate the association between the presence and relative abundance of brook trout and the characteristics of beaver ponds measured at both a local and landscape scale. If beaver ponds vary in their ability to support brook trout then I expected that these ponds would also vary in their habitat characteristics. If so, then my second objective was to evaluate differences between brook trout inhabiting beaver ponds and those in adjacent streams. If brook trout are able to adapt to the conditions in beaver ponds then differences may exist between stream and beaver pond dwelling brook trout that are consistent with the variability between the two habitat types. The final objective was to determine which characteristics of beaver ponds were most important for predicting brook trout presence and absence. An evaluation of brook trout use of beaver ponds and the important characteristics of ponds that distinguish them as good brook trout habitat will improve our understanding of brook trout ecology in stream systems and our ability to protect and manage these habitat features.

2.0 Methods

2.1 Study Area

The study area was the Mackenzie River watershed, northeast of Thunder Bay, Ontario, Canada. The north-south extents (UTM zone 16, WGS84 datum) of the Mackenzie River watershed are 5,403,650 and 5,376,640, respectively and the east-west extents are 371,740 and 346,090, respectively and is approximately 369.6 sq. km in area (Figure 2.1.1). The Mackenzie River drains into Thunder Bay on Lake Superior; however, fish populations in the river are isolated from the lake by an impassable waterfall located approximately 3 km upstream from its mouth. The study area has relatively high summer temperatures as well as extremely low winter temperatures, when mean daily temperatures below freezing may persist for up to six months. The Mackenzie River is a cold-water drainage containing approximately 15 fish species (Ontario Ministry of Natural Resources (OMNR), Comparative Aquatic Effects Program (CAEP) data). Brook trout is a widely distributed fish in the drainage and may be the only fish species present in small headwater and tributary streams.

The watershed is predominated by northern boreal forest with forestry being the primary land-use impact. Forests in the watershed exhibit considerable variation in soil type and stand composition (Sims *et al.* 1997). In addition, wetlands make up a large portion of the study area (Harris *et al.* 1996). The landscape of the watershed exhibits a highly disrupted drainage pattern characterized by numerous small streams and wetlands but with few major rivers and relatively few lakes (Pye 1969, Mollard and Mollard 1981a, Mollard and Mollard 1981b, Harris *et al.* 1996). Meadow-marsh and pool-riffle complexes characterize streams in the watershed. Beaver ponds are present throughout the study area with some drainage systems highly impacted by beaver activity.

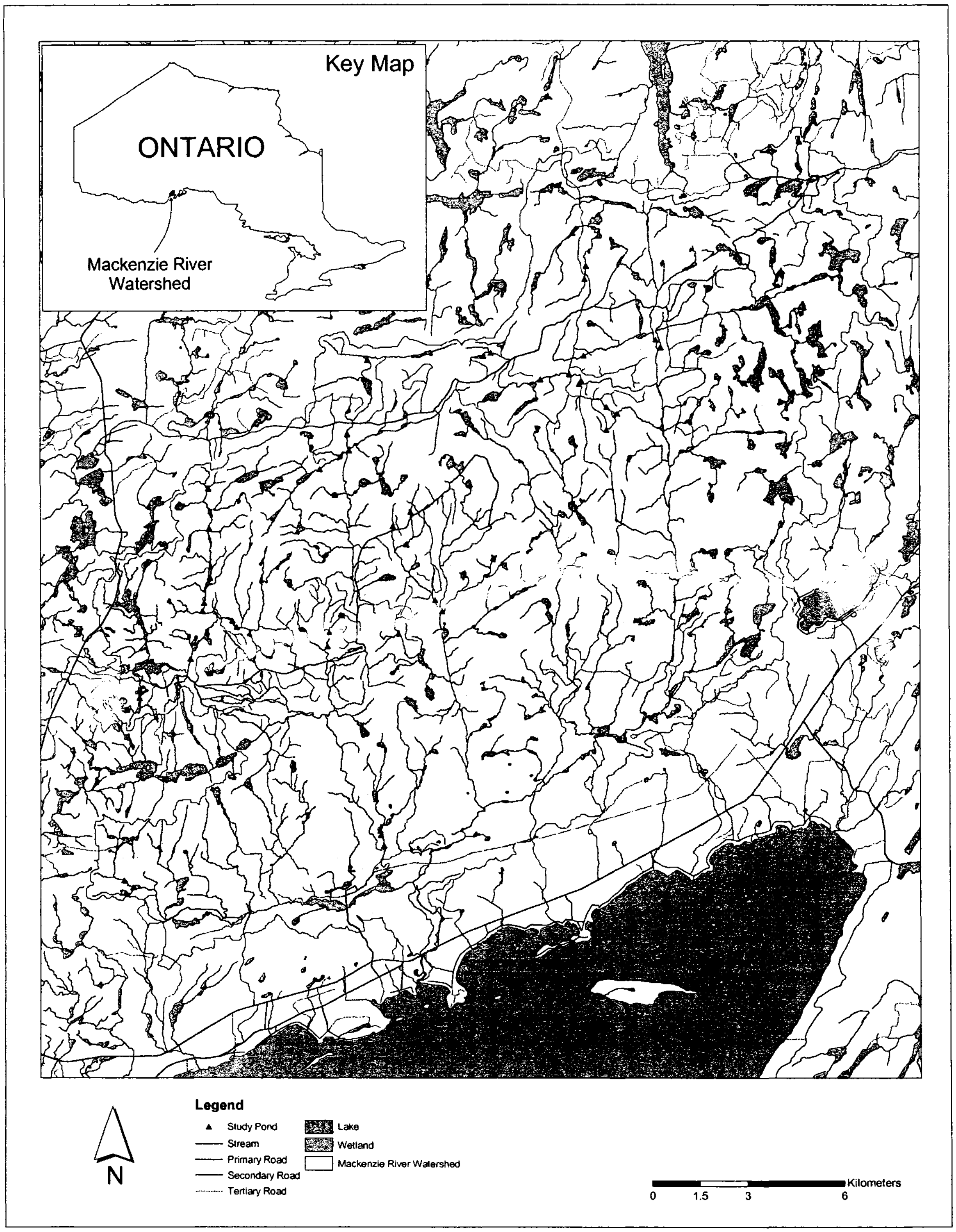


Figure 2.1.1 The Mackenzie River watershed, Northeast of Thunder Bay, Ontario, Canada.

The Mackenzie River watershed is within the Thunder Bay plains Eco-region (Wickware and Rubec 1989). The Thunder Bay plains Eco-region, situated along Lake Superior's north shore, is composed primarily of diabase, greywacke, and shale bedrock formations (Wickware and Rubec 1989). The study area is characterized by rolling, undulating terrain with frequent steep to vertical slopes and rocky outcroppings. Surficial geology, landform patterns and depositional material are distinct due to events, that occurred during glacial and early post-glacial periods (Zoltai 1961, Zoltai 1963, Zoltai 1965, Zoltai 1967, Wickware and Rubec 1989).

Generally, northern Ontario surficial geology exhibits poor water retention and soil drainage characteristics (Zoltai 1963, Zoltai 1965). Surficial deposits formed during the retreat of continental glaciers are of particular hydrogeologic importance (Freeze and Cherry 1979) in northwestern Ontario. Common surficial deposits include shallow undulating ablation and basal till of variable thickness, morainal features and large expanses of predominantly thin glacial sediments over rugged Precambrian bedrock formations (Zoltai 1963, Pye 1969, Wickware and Rubec 1989). Glacial till, glaciofluvial deposits and glaciolacustrine deposits are also very common but tend to be more localized in morainal or esker-like ridges, kames, valleys, and outwash plains of which glacial till is the most common material deposited (Zoltai 1963, Zoltai 1965, Sims *et al.* 1997). The Mackenzie interlobate moraine follows the valley of the Mackenzie River, paralleling the shore of Lake Superior. The moraine consists of various glaciofluvial deposits such as esker-like ridges and kames. The slopes of the ridges and the kames are usually steep, many exceeding 45 degrees. The material is stratified, unconsolidated sand and gravel with scattered large boulders, connected by outwash sand deposits (Zoltai 1965). Small outwash sandy plains are found in most valleys within this interlobate area (Zoltai 1963). Glacial and post-glacial events shaped not only the regional landscape and surficial geology but also the modern distribution of endemic fish fauna (Bailey and Smith 1981).

2.2 Sampling Methods

The sampling methods used during the 2002-2003 field seasons characterized beaver ponds based on fish community, landscape scale catchment characteristics, local scale physical characteristics of the pond, and associated wetland area. The selection of study sites (beaver ponds) was based on several criteria: first, only beaver ponds with an approximate upstream catchment area (UCA) of 30 sq. km or less were sampled. Second, beaver ponds had to have a maximum depth of at least 1 m. Generally, this required a beaver actively maintaining the pond; however, inactive ponds were not excluded. Also, the relative accessibility of each pond was assessed prior to sampling using provincial series topographic maps and maps of the Mackenzie watershed created in ArcView 3.2 as well as aerial photos and Ikonos satellite images. The accessibility of each pond was not measured or used in analyses; however, beaver ponds more than 1 to 2 km from a forestry access road or skidder trail were generally excluded due to the rugged terrain, amount of sampling equipment required, and time limitations of the study.

During the 2002 sampling period a variety of sample methods were employed to capture a representative sample of the fish assemblage from beaver ponds in the study area. Of particular interest was the capture of brook trout. The presence of brook trout in 7 of 20 beaver ponds surveyed was established using angling. Beaver ponds that contained brook trout were sampled multiple times. Sampling methods included small (30 mm opening) and large (50 mm opening) diameter standard size minnow traps, large minnow traps (100 mm diameter opening), fine mesh, short set gill net, beach seine net, and continuous set fyke net. Also, two-way weirs were installed at the inlet and outlet of two beaver ponds between September 10 and November 12, 2002, to capture brook trout moving into or out of ponds. Despite repeated sampling using a variety of gear, a total of only 4 brook trout were captured using passive traps in ponds and 8 in the two-way weirs during the year (Table 2.2.1). However, angling proved to be an effective method for sampling brook trout presence and relative size distribution in beaver ponds.

Table 2.2.1 Sampling methods used and species captured in beaver ponds during 2002.

* Sampling methods included passive sampling gear: standard minnow trap = MT, large opening standard minnow trap = LOMT, large opening-large diameter minnow trap = LMT, short set gill net = GN, beach seine net = SN, fyke net = FN, and angling = A. ** Fish captured (excluding brook trout): Phoxinus spp. = P, brook stickleback (*Culaea inconstans*) = BSB, pearl dace (*Margariscus margarita*)= PD, blacknose shiner (*Notropis heterolepis*) = BNS, blacknose dace (*Rhinichthys atratulus*) = BND, longnose dace (*Rhinichthys cataractae*) = LND, creek chub (*Semotilus atromaculatus*) – CC, mottled sculpin (*Cottus bairdii*) = SC.

Beaver Pond	Sampling Method*	Dates Sampled (2002)	Fish Captured** (excluding BT)	Brook Trout Captured in Passive Traps	Brook Trout Captured Angling
Walk 7	MT, LOMT, LMT, GN, A	Jun26/Jun27/Jun28/ Aug28	P, BSB, PD, LND, BNS, CC	0	7
Walk 7.1	MT, LOMT, LMT, A	Jun26/Jul12/Aug28/	P, BSB, PD, BD	0	4
Walk 7.2	MT, LOMT, LMT, A	Jun27/Jul16/Aug28	P, BSB, LND	0	0
Walk 7.3	MT, LOMT, LMT, A	Jul10/Jul11/Jul16	P, BSB, SC	0	0
Walk 7.4	MT, LOMT, LMT, GN, A	Jul10/Jul17/Jul18	P, BSB, PD	0	0
Walk 5.1	MT, LOMT, LMT, A	Jun03/Jun04/Aug09	P, BSB, PD, LND	0	4
Walk 5.15	MT, LOMT, LMT, GN, A	Jun03/Jun05/Aug08	P, BSB, PD, LND	1	6
Walk 5.2	MT, LOMT, A, LMT, GN, SN,	Jun05/Jun11/Jun14	P, BSB, PD	2	22
Walk 5.3	MT, LOMT, A	Aug07	P, BSB	0	0
Ecochallenge	MT, LOMT, LMT, A	Aug06	P, BSB	0	0
DSS	MT, LOMT, LMT, A	Jun20	P, BSB, PD, LND	0	0
Walk 6	MT, LOMT, LMT, A	Jun21	P, BSB	0	0
Mrackic-1	MT, LOMT, A, LMT, GN, FN,	Sep05/Sep06 Sep17 – Oct18	P, BSB	1	1
Mack2	MT, LOMT, LMT, GN, SN	Jun17/Jun18	P, BSB, LND	0	0
EWN-10K	MT, LOMT, A, LMT, GN, SN	Aug13/Aug20/Aug21/ Aug22/Aug23	P, BSB	0	9
Mack5	MT, LOMT, A	Jul05	P	0	0
Mack2-hl	MT, LOMT, A	Sep13	0	0	0
EWNW	MT, LOMT, LMT, A	Jul23/Jul24/Jul25/ Jul26	P, BSB	0	0
EW-1K	MT, LOMT, A	Aug15	0	0	0
MRP-1	MT, LOMT, LMT, A	Aug16	P, BSB	0	0
MRK-1	WEIRS	Sep 10 – Nov 12	P, BSB	5	n/a
MRK-2	WEIRS	Sep 10 – Nov 12	P, BSB	3	n/a

During the 2002 and 2003 field seasons electrofishing surveys, using a Smith-Root model 15-B backpack electrofisher, were conducted in streams adjacent to beaver pond sites to determine brook trout presence or absence, relative abundance, and size distribution. During electrofishing surveys, fish were shocked and then captured by one or two netters using long handled (1.5 m) soft-mesh dip nets. Captured fish were kept in a bucket containing stream water and an aerator, until sampled. Brook trout were separated and individually weighed to the nearest gram and total and fork lengths were measured, whereas, other fish species were counted and weighed in batches. Weight was measured using a Sartorius electronic balance and Pesola 100g, 500g, and 1kg, spring scales. Spring scales were calibrated using known masses at intervals during the sampling period. Stream reaches were approximately 50-100 m in length and generally required less than one hour to survey. Seines were placed at the beginning and end of stream reaches to isolate the sampling area. The seine at the end of each sampling reach was left in to form the beginning of the next sampling reach, with another seine placed upstream. In addition to the brook trout data collected during my study, I included brook trout data collected as part of the Ontario Ministry of Natural Resources Comparative Aquatic Effects Program. The Comparative Aquatic Effects Program (CAEP) utilized identical sampling methods in the study streams between 1995 and 2003. CAEP data was used only in analyses of brook trout size distribution in the study area.

Electrofishing was not possible in beaver ponds due to their depth and size. Angling was used exclusively in 2003. Beaver ponds were classified by the presence or absence of brook trout as determined by the 2003 angling survey. Catch per unit effort (CUE) was defined as the number of fish caught per angling hour in each beaver pond surveyed. Angling equipment consisted of a light-action spinning rod, spinning reel, four pound test line, size 12 wide-bend hooks, non-toxic split-shot, and worms as bait. Brook trout were netted using soft mesh polyester catch-and-release trout nets and kept in the water until sampled. The fork and total lengths and weight of each brook trout was measured using the same method and equipment as described above for stream surveys.

The 2002 sampling season began on June 06 and ended on November 12. The 2003 sampling season began on May 06 and ended on October 23. The 2003 sampling season was divided into categories of spring (May, June), summer (July, August), and fall (September, October).

Landscape scale variables were measured using a geographic information system (GIS), ArcView version 3.2 (a), and included surficial geology (material and landform), upstream catchment area (UCA), pond area, associated wetland area contiguous with each pond, pond position (channel length), and topographic index (TI) values. Despite a long history of forest harvesting in the Mackenzie River watershed, reliable quantitative information on past harvesting was not available for the majority of sites and thus, was not included as a variable. However, no sites occurred in recent (< 5 years) harvest areas.

Upstream catchment area is the land area contributing surface water runoff to each beaver pond as defined by the topography in a digital elevation model (DEM) (Figure 2.2.1). UCA for each site (beaver pond) was delineated using a 25 m raster-based DEM from the digital Ontario base map (OBM) series. In some analyses, the contributing UCA for each beaver pond was treated as a categorical variable. Beaver ponds were classified by upstream catchment area (UCA): 1 sq. km (0 – 2.9 sq. km), 5 sq. km (3.0 – 7.9 sq. km), 10 sq. km (8.0 – 19.9 sq. km), and 30 sq. km (20.0 – 38.0 sq. km). Beaver ponds were limited to 30 sq. km UCA or less because too few beaver ponds existed within the Mackenzie River watershed with UCAs greater than this size due to catchment shape and tributary length. Only four tributaries in the watershed were greater than 30 sq. km UCA and only one tributary, Walkinshaw Creek (only named tributary in watershed), was longer than approximately 50 sq. km UCA.

Pond position is a measure of the channel length between each beaver pond and a downstream channel position where the UCA equals 100 sq. km. I assumed that a stream position of 100 sq. km UCA or greater (Mackenzie River) was appropriate to support a source population of brook trout for the watershed. The surficial material and landform type comprising the greatest percentage area within the UCA for each beaver pond was delineated in ArcView by clipping the surficial geology layer from OBM with the contributing UCA. The surficial material and landform type was treated as a categorical variable in analyses. Pond size and wetland area were delineated and digitized using both geo-referenced IKONOS Satellite imagery and aerial photographs. The beaver pond was buffered by 25, 50, and 100 m areas beyond the perimeter of the wetland area to explore the relationship between greater contributing upslope area and TI value in the pond and associated wetland. Buffered areas were clipped to the delineated watershed area so that buffered areas did not fall outside of the pond catchment area.

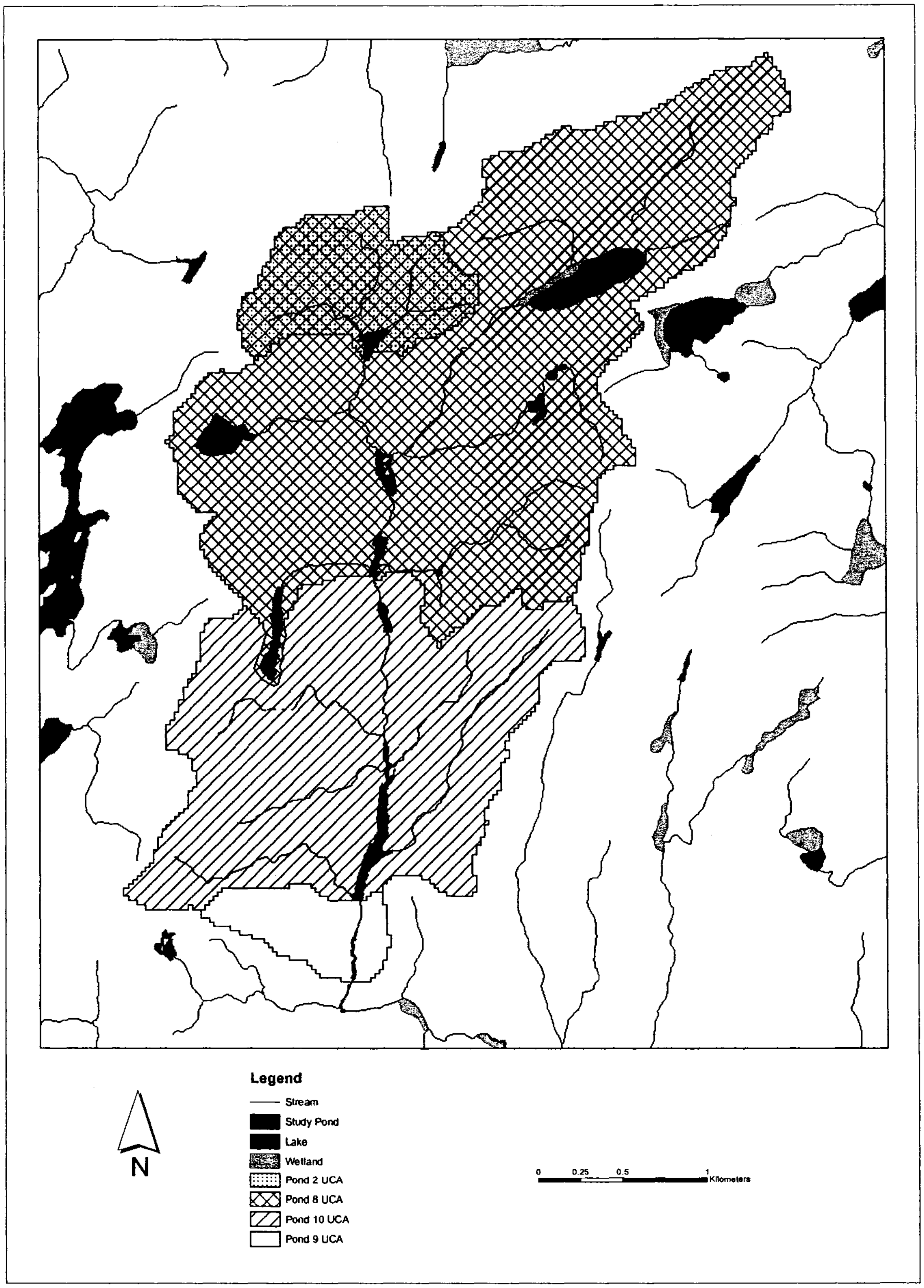


Figure 2.2.1 Upstream catchment area (UCA) for four beaver ponds in a sub-catchment of the Mackenzie River watershed.

The topographic index (TI) is a metric that is used to predict hydrological processes affecting the relative potential for groundwater discharge along the stream-terrestrial interface (Beven and Kirkby 1979, Buttle *et al.* 2001, Buttle 2002).

The topographic index (TI):

$$TI = \ln[a / \tan b]$$

where a = upslope area draining to a given location and tan b = the slope gradient at that point. The movement of subsurface flow in a catchment is a function of upslope recharge area (a) and the hydraulic gradient at that location (tan b). The TI value was used to represent the relative likelihood of overburden saturation at a discrete site by subsurface flow from contributing upslope area and the potential exfiltration of subsurface water at that discrete site (Buttle *et al.* 2001, Buttle 2002).

Local scale variables were sampled during field surveys conducted between May and October 2003. Variables included, mean pond depth, maximum pond depth, and beaver activity (the presence or absence of beaver actively maintaining the pond). To express the heterogeneity of individual beaver pond depths, measurements were taken at approximately 1 - 2 m intervals along multiple transects. Three transects were arranged with one along the longitudinal (longest) axis and two along the lateral (shorter) axis of each pond. Local scale physical variables sampled in the beaver ponds included water temperature, pH, conductivity, total dissolved solids (TDS), and dissolved oxygen. Water temperature, pH, conductivity, TDS, and dissolved oxygen were measured with a YSI 650 Multi-parameter Display System handheld meter interfaced to a 6-series sonde. To express the heterogeneity of individual beaver ponds, physical variable measurements were taken at multiple locations and depths. Measurements were taken at 0.5 m increments in the water column at each sampling location. A surface measurement was taken at approximately 10 cm below the surface and a measurement was taken approximately 10 cm above the pond bottom at each sampling location. One sampling location was situated approximately at the point of maximum pond depth. A minimum, maximum, and mean value for each variable was calculated for each sampling location within the pond. In addition, an overall average parameter value (i.e. mean temperature) was calculated for each sampling event. Lastly, the morpho-edaphic index (MEI) for each beaver pond was calculated using MEI = TDS/mean pond depth (Ryder 1965).

2.3 Analyses

Analyses were performed in SPSS version 9.0 or 11.5. Data were transformed where necessary to satisfy the assumption of normality.

Preliminary analyses suggested that seasonal water temperature differences might influence capture efficiency of brook trout in beaver ponds. I explored the association of water temperature in beaver ponds with variation in CUE. A broad range of preferred thermal ranges have been reported for brook trout as well as various upper tolerance limits below which they may be present (Ricker 1934, Fry *et al.* 1946, Cherry *et al.* 1975, Cherry *et al.* 1977, Grande and Andersen 1991, Benfey *et al.* 1997, and Picard *et al.* 2003). Beaver ponds were initially categorized as having a mean temperature above or below 11 °C because CUE decreased when mean water temperature in beaver ponds was below 11 °C. However, upon further analysis this simplistic classification was expanded to include the pond mean-minimum value that expressed the approximate preferred temperature range of brook trout within ponds across the sampling period. The mean-minimum value categorizes each beaver pond based on whether the minimum or mean pond temperature falls within the approximate 'preferred' thermal range of brook trout (11 °C to 18 °C). Raleigh (1982) and McRae and Edwards (1994) defined brook trout habitat suitability by thermal ranges and studies suggest brook trout will occupy areas within their preferred thermal range or move to habitat where waters in that temperature range exist (Reynolds and Casterlin 1979, Garret and Bennett 1995, Biro 1998).

To evaluate differences in local and landscape scale habitat variables among ponds I used MANOVA. Beaver ponds were grouped based on brook trout presence and absence. To identify habitat variables important for differentiating between groups that exhibited an overall significant effect in the MANOVA, I used Discriminant function analysis (DFA). The analyses were repeated for beaver ponds with a mean water temperature greater than 11 °C to evaluate differences among ponds within the preferred thermal range for brook trout.

To determine the relative effectiveness of local and landscape scale variables for predicting brook trout presence and absence I developed logistic regression models using both local scale physical variables and landscape scale variables. Of particular interest was the relative effectiveness of landscape scale variables for accurately predicting potential brook trout habitat, avoiding the need to collect local scale information. Predictive model development using stepwise logistic regression and automatic selection procedures was applied following variable reduction combined with averaging techniques and cross-validation (Menard 1995, Simonoff 2000, Wang 2000, Shtatland *et al.* 2001, 2003, 2004, Burnham and Anderson 2002).

A series of steps were performed to reduce the number of variables and remove multicollinearity among independent predictors. The number of variables used for model development was reduced using the variance inflation factor (VIF) in linear regression analysis, average linkage in a hierarchical cluster analysis, and condition number in principal components analysis (PCA). The VIF was obtained from a linear regression model developed using the same dependent and independent variables used in the development of the logistic regression models (Menard 1995, Allison 1999, Shtatland *et al.* 2001, 2003, 2004). The functional form of the model for the dependent variable, brook trout presence or absence, is unimportant as the VIF calculation is interested only in the relationship among independent variables (Menard 1995). The VIF is useful for detecting multicollinearity among predictor variables. Colinearity among variables generally inflates the variance of the coefficient, the standard error, and parameter estimates resulting in an injudicious model with mutually dependent and redundant predictors. The VIF expresses the amount that the variance of the coefficient estimate is being inflated through multicollinearity of independent variables (Menard 1995, Allison 1999).

Dendograms (Pearson correlations) in a hierarchal cluster analysis were used to compare the association of independent variables from the linear regression model. The linked variables, identified in the cluster analyses, were compared and the variable with the greater VIF was removed. Individual variables, with VIF's greater than 10, were removed from each subsequent linear regression model until no variables with VIF's greater than 10 remained in the model (Allison 1999, Menard 1995).

The condition number (k) was calculated using PCA to validate the non-multicollinearity assumption using the VIF approach. The condition number is a measurement of the magnitude of colinearity among variables represented by the degree of separation between the largest and smallest eigenvalue. When no colinearity exists among independent variables, both eigenvalues and condition number equal one. As colinearity among variables increases, eigenvalues begin to depart from one (values close to zero indicate multicollinearity) and the condition number will increase. The condition number is equal to the square root of the largest eigenvalue (λ_{max}) divided by the smallest eigenvalue (λ_{min}):

$$(\lambda_{\min})k = \sqrt{(\lambda_{\max} / \lambda_{\min})}$$

As a general rule, if the condition number is less than 15 then multicollinearity among variables is not a concern (Allison 1999). Thus, only subsets of variables with condition numbers less than 15 were used for the analyses.

Binary Logistic Regression was used to develop models to predict the presence or absence of brook trout in beaver ponds using both local and landscape scale characteristics (Menard 1995, Allison 1999, Hosmer and Lemeshow 2000, Burnham and Anderson 2002). The logistic equation:

$$P = {}^{1}\!\!\diagup_{1 + e^{-(\alpha+\beta_1 x_1+\beta_2 x_2+\ldots+\beta_i x_i)}}$$

where P is the probability of the event occurring, α is the constant of the equation and, β is the coefficient of the predictor variables.

The data set was randomly divided into a model construction subset and a model testing subset. I used the two subsets of independent cases and variables to construct and test individual logistic regression models (Menard 1995, Hosmer and Lemeshow 2000, Burnham and Anderson 2002, Shtatland *et al.* 2004). The first randomly selected subset included 34 of the initial 50 cases with the remaining 16 cases used to test the models validity. The models were developed utilizing a combination of variables identified using the procedure outlined previously (Moore 2000, Shtatland *et al.* 2001, 2003, 2004).

To further explore the hypothesis that seasonal differences in water temperature might influence capture efficiency (CUE) of brook trout and their presence in beaver ponds additional logistic regression models were constructed using only sites with a mean pond temperature greater than 11 °C. The set of models constructed and tested included all local and landscape scale variables from ponds with a mean temperature greater than 11 °C. These models were developed to evaluate variable selection and predictive capacity relative to the previously developed models.

Akaike's information criterion (AIC) is an automatic model selection procedure described by the equation:

$$AIC = -2\log L(m) + c \times K$$

where $\log L(m)$ is the maximum log-likelihood, K is the number of covariates and c is the penalty parameter (Shtatland *et al.* 2003, 2004, Mazerolle 2004). Model selection using AIC essentially penalizes the likelihood for model complexity (number of predictor variables). Hurvich and Tsai (1989), Burnham and Anderson (2002) and Shtatland *et al.* (2003) recommend using a corrected AIC (AIC_c) for small sample sizes when $N/K < 40$,

$$AIC_c = \frac{AIC + 2 \times K \times (K+1)}{(N - K - 1)}$$

where N is the sample size and K is the number of predictors in the model. Thus, I utilized Akaike's information criteria for small sample size (AIC_c) to select the best and most parsimonious model from a subset of models with different combinations of predictor variables (Anderson *et al.* 1994, Burnham and Anderson 2002). Forward stepwise selection produces a sequence of models beginning with the null model and culminating with a model that includes all predictor variables and maximizes the likelihood at each step (Shtatland *et al.* 2003, Mazerolle 2004). AIC_c produces an evidence ratio identifying the most parsimonious of the logistic models. Model parsimony improves as the AIC$_c$ evidence ratio number approaches 1. However, models with AIC$_c$ evidence ratio numbers < 10 cannot be discounted as being potentially effective (Burnham and Anderson 2002, Wang 2000, Shtatland *et al.* 2001, 2003, 2004, Mazerolle 2004). In the results section, only models with AIC$_c$ evidence ratio numbers $<$ 10 are presented for interpretation.

I used receiver operating characteristic (ROC) curves as a graphical approach to evaluate the discriminatory ability of predicted probabilities produced in each logistic regression model. ROC curves are useful for evaluating the discriminatory power of habitat models as they are independent of a P_{crit} threshold value and present a single parameter, the area under the curve or AUC value; whereas predictive accuracy of models based on cross-tabulation matrices depend on a chosen P_{crit} (Fielding and Bell 1997, Bonn and Schroder 2001). Before calculating the ROC curve, the discriminatory ability of each model was evaluated graphically by comparing the distributions of predicted probabilities of occupied to unoccupied sites (Swets 1986, 1988, Murtaugh 1996, Pearce and Ferrier 2000). A model with no discriminatory ability will produce a curve that follows a 45 ° line whereas perfect discrimination is indicated by curve that follows the left hand (y axis) and top axes (Swets 1986, 1988, Pearce and Ferrier 2000, Bonn and Schroder 2001). A smooth curve is drawn through the true positive proportion of probabilities (sensitivity) plotted against the false positive proportion (specificity) for a range of threshold probabilities to derive the ROC curve (Pearce and Ferrier 2000, Bonn and Schroder 2001). The 45 ° line represents the sensitivity and false positive values expected by chance for each decision threshold (Pearce and Ferrier 2000). The ROC curve analysis is independent of species occurrence and decision threshold effects [illegible] expressed as a proportion of all beaver ponds (sites) with a given observed state (Swets 1988, Pearce and Ferrier 2000). The area under the ROC curve expressed as a [illegible] of the total area is regarded as the most appropriate discrimination index that ranges from 0.5 (no discrimination ability) to 1 (perfect discrimination)(Bonn and Schroder 2001). Areas under the curve with index values between 0.5 and 0.7 indicate poor discrimination ability. Index values between 0.7 and 0.9 indicate relatively acceptable discrimination ability and values greater than 0.9 indicate good discrimination ability (Swets 1986, 1988, Hosmer and Lemeshow 2000, Pearce and Ferrier 2000). The ROC curve and associated discrimination index value are presented with the results of the logistic regression model.

Physical characteristics and size distribution of brook trout captured from streams and beaver ponds were compared to evaluate differences between the two habitats. Brook trout size distribution in both streams and beaver ponds were also expected to differ among UCA category due to differences in fish density and environmental physical characteristics. Analysis of variance (ANOVA) was used to evaluate differences in brook trout size between beaver ponds and adjacent streams. ANOVA was also used to evaluate differences in brook trout size among beaver ponds of differing UCA classes. If differences existed among UCA classes, Tukey's Honestly Significant Difference (HSD) test was performed to test where group differences occurred. Multiple aging structures (otoliths, scales, and left pectoral fin rays) were collected from nine brook trout following incidental hooking mortality. Scales and left pectoral fin rays were collected from six brook trout due to their large size on two sampling occasions and were released. These structures were aged by Northshore Environmental Services Limited.

3.0 Results

Brook trout were captured in 20 of the 50 beaver ponds sampled in 2003 (Table 3.0.1). The total number of brook trout captured from all beaver pond sites was 369 (including 2002 data). Brook trout relative abundance (CUE) was highly variable within and among beaver ponds where brook trout were known to be present. The number of brook trout captured in individual beaver ponds ranged from 0 to 60 and CUE ranged from 0 to 7.3 fish/hour. Brook trout were never captured in beaver ponds with an UCA less than 2.9 sq. km. Brook trout relative abundance (CUE) was lower in ponds with smaller UCA (Figure 3.0.1). Mean relative CUE of brook trout was 2.75, 0.88, and 0.21 fish per hour in 30, 10 and 5 sq. km UCA categories respectively. Brook trout were often not captured in beaver ponds where they had been previously caught. Relatively low or 0 catch rates in these ponds often corresponded to low water temperatures. Brook trout abundance was relatively consistent among beaver ponds of 5 and 10 sq. km UCA and variable in 30 sq. km UCA relative to variation in temperature and seasons (Figure 3.0.2).

Brook trout captured in beaver ponds had a mean total length of 196 mm (range: 110 to 354 mm) (Figure 3.0.3 a) and had a mean weight of 85 g (range: 5 to 412 g) (Figure 3.0.3 b). The attributes of brook trout captured for each beaver pond sampled during 2003 are summarized in Table 3.0.1. Brook trout captured in streams adjacent beaver ponds had a mean length of 91 mm and ranged in length from 6 mm to 245 mm (Figure 3.0.4 a). Brook trout in streams had a mean weight of 13 g and ranged in weight from 1 g to 141 g in beaver ponds (Figure 3.0.4 b). Length and weight relationships of brook trout caught in ponds and streams respectively are presented in Figures 3.0.5 a, b and 3.0.6 a, b.

Table 3.0.1 Sampling locations and features of brook trout captured in beaver ponds.

Beaver Pond	Dates Sampled (2003)	Brook Trout Captured	Brook Trout CUE (low-mean-high)	Brook Trout Mean Length (mm)	Brook Trout Total Biomass (g)	Brook Trout Mean Biomass (g)
Mackh-1K	21-Jun	0	0	0	0	0
Mack3	19-Sep	0	0	0	0	0
Ewmid	18-Jun	0	0	0	0	0
Mooseland	03-Jun	0	0	0	0	0
Mack2h1	15-Jul	0	0	0	0	0
Mack3.1	20-Sep	0	0	0	0	0
Mack2h2	15-Jul	0	0	0	0	0
TMH-low	28-Sep	0	0	0	0	0
EW1N	17-Sep	0	0	0	0	0
SHW2	25-Jun	0	0	0	0	0
Ewmid2	23-Jun	0	0	0	0	0
Ecochallenge	19-Jun	0	0	0	0	0
EW1K	16-Jul	0	0	0	0	0
SHW1	25-Jun/14-Jul/14-Aug/30-Sep	0	0	0	0	0
Mack3.2	20-Sep	0	0	0	0	0
Magone2	18-Sep	0	0	0	0	0
TMH1K	04-Oct	0	0	0	0	0
Wak7.4	16-Sep	0	0	0	0	0
Magone1	18-Sep	0	0	0	0	0
Tartan	19-Aug	0	0	0	0	0
Mack5	09-Jun	0	0	0	0	0
MRK2	04-Jun/22-Jul/28-Aug/22-Sep	8	0.0, 0.14, 0.33	284.78	1921	249.78
EZEE	12-Jun	0	0	0	0	0
SHW3	26-Jun	0	0	0	0	0
MRK1	02-Jun	1	0.15	175	55	55
EW5K	23-Jul	0	0	0	0	0
EWNW	17-Jun	2	0.24	228	225	117.50
Moosebones	04-Jul	0	0	0	0	0
Walk5.3	29-Aug	4	1.46	220.25	512	128
Mack2	16-May/27-May	2	0.0, 0.12, 0.24	198.5	172	86
TM10K	01-Oct/11-Oct	4	0.0, 0.62, 1.23	208	325	81.25
Walk7.3	26-Sep	1	0.22	221	108	108
Walk7.2	26-Sep	0	0	0	0	0
Walk7	14-May/29-May	7	1.22	174.57	411	58.71
Mack2.1	25-Sep	5	0.95	214	751	150.20
Mack2.2	02-Oct	0	0	0	0	0
Mackh10K	23-Aug	8	1.88	209.88	1076	134.5
EWN10K	13-May/26-May/10-Jul/13-Aug/24-Sep/23-Oct	28	0.0, 0.59, 1.26	223.79	3855	140.19
Walk5.2	08-May/16-Jun/10-Oct	12	0.0, 0.44, 1.33	217.92	1413	117.75
Walk5.15	22-Aug/10-Oct	11	1.71-1.80-1.88	253.19	1093	103.94
Walk6	06-May	0	0	0	0	0
Walk5.1	15-May/25-Aug	7	0-1.17-2.33	213	809	115.57
DSS10K	12-May	0	0	0	0	0
EWN210K	07-Jul	12	1.55	219.08	1319	109.92
TM20K	29-Sep	0	0	0	0	0
WW130K	07-Aug	8	.97	200.13	883	110.38
WW230K	12-Aug	14	1.65	210.86	1786	127.57
SHW30K	30-Jun/08-Oct	19	1.16-1.28-1.39	243.07	3341	177.25
EW30K	07-May/28May/24Jun/05-Aug/05-Sep/03-Oct	146	0-3.32-7.30	166.63	9266	54.81
Mack30K	03-Jul/09-Oct	21	.18-1.43-2.67	262.10	2583	228.93

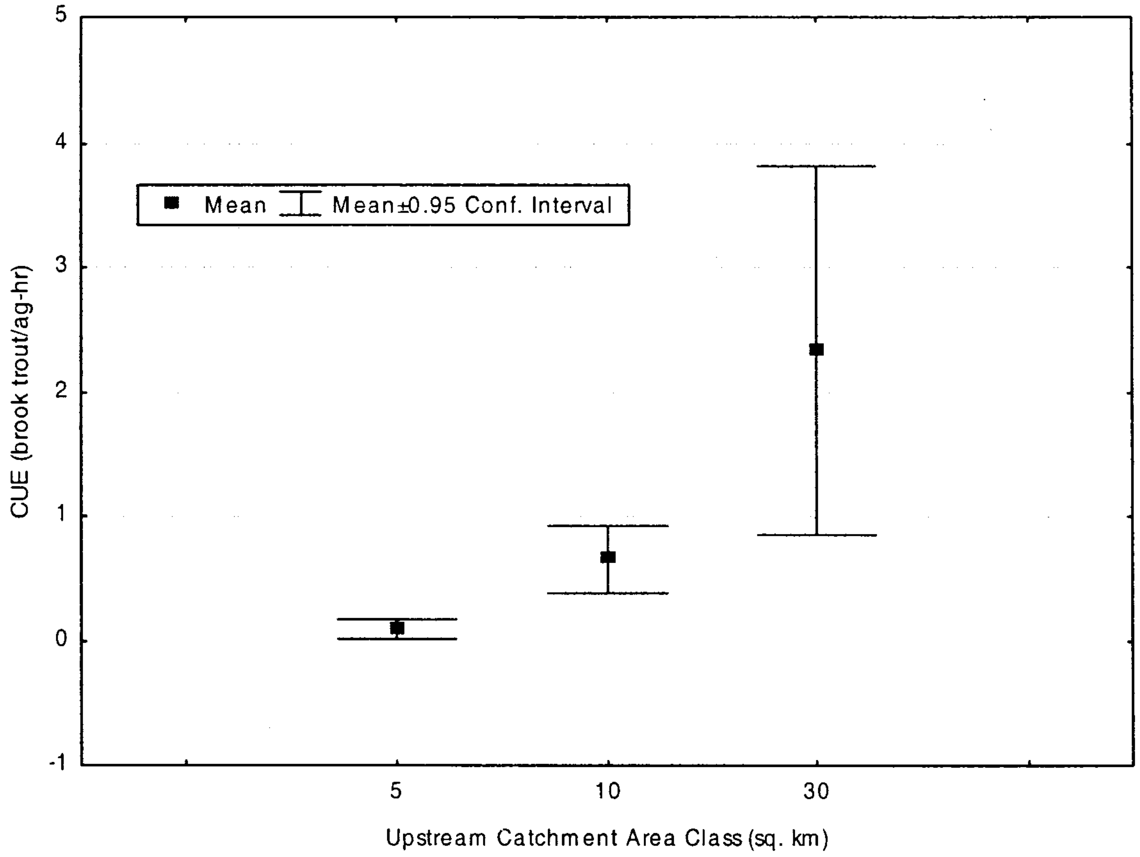


Figure 3.0.1 CUE of brook trout in beaver ponds in the study area.

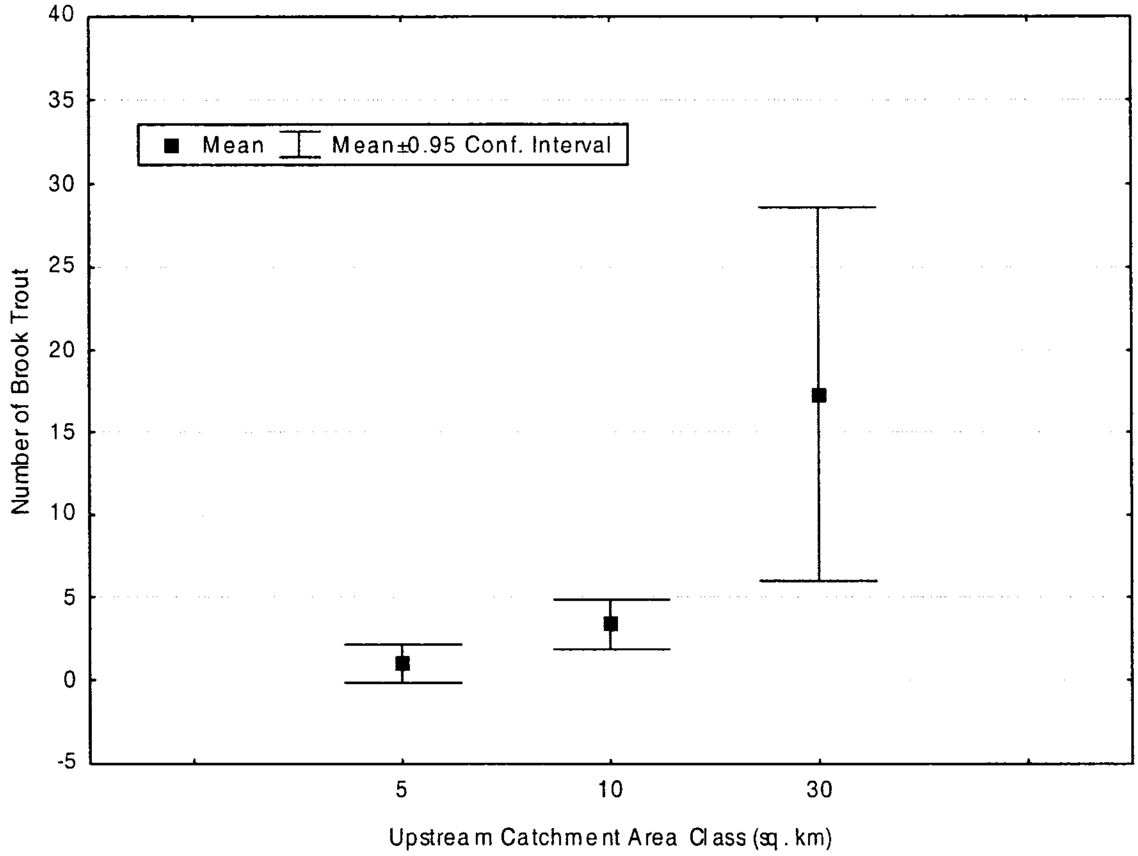
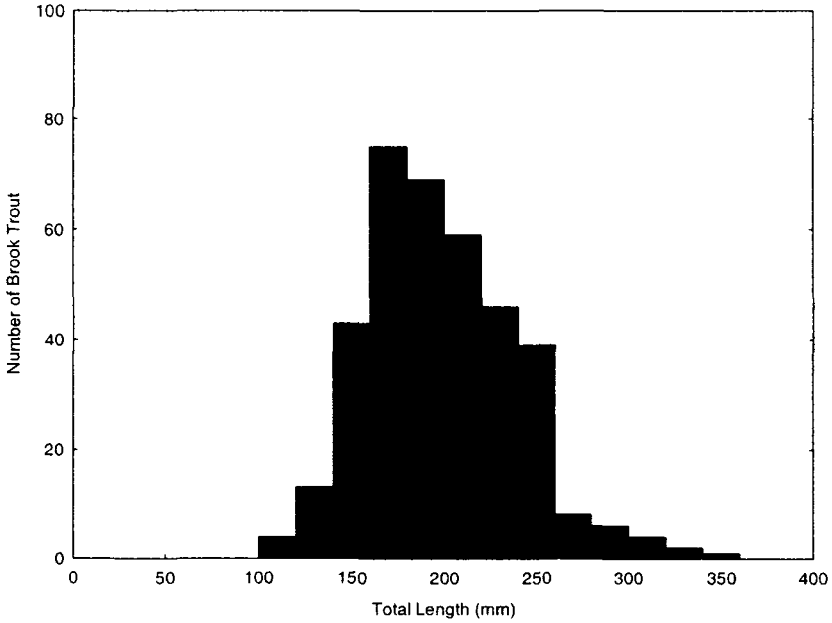


Figure 3.0.2. Mean number of brook trout captured in each UCA class in beaver ponds in the study area.

a)



b)

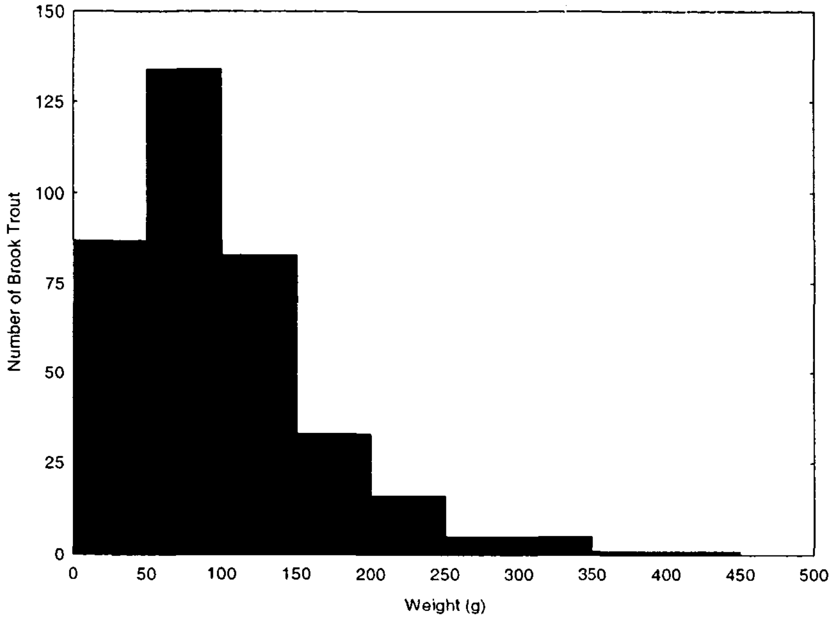


Figure 3.0.3 Total length (a) and weight (b) distributions of brook trout captured in beaver ponds in the Mackenzie River Watershed.

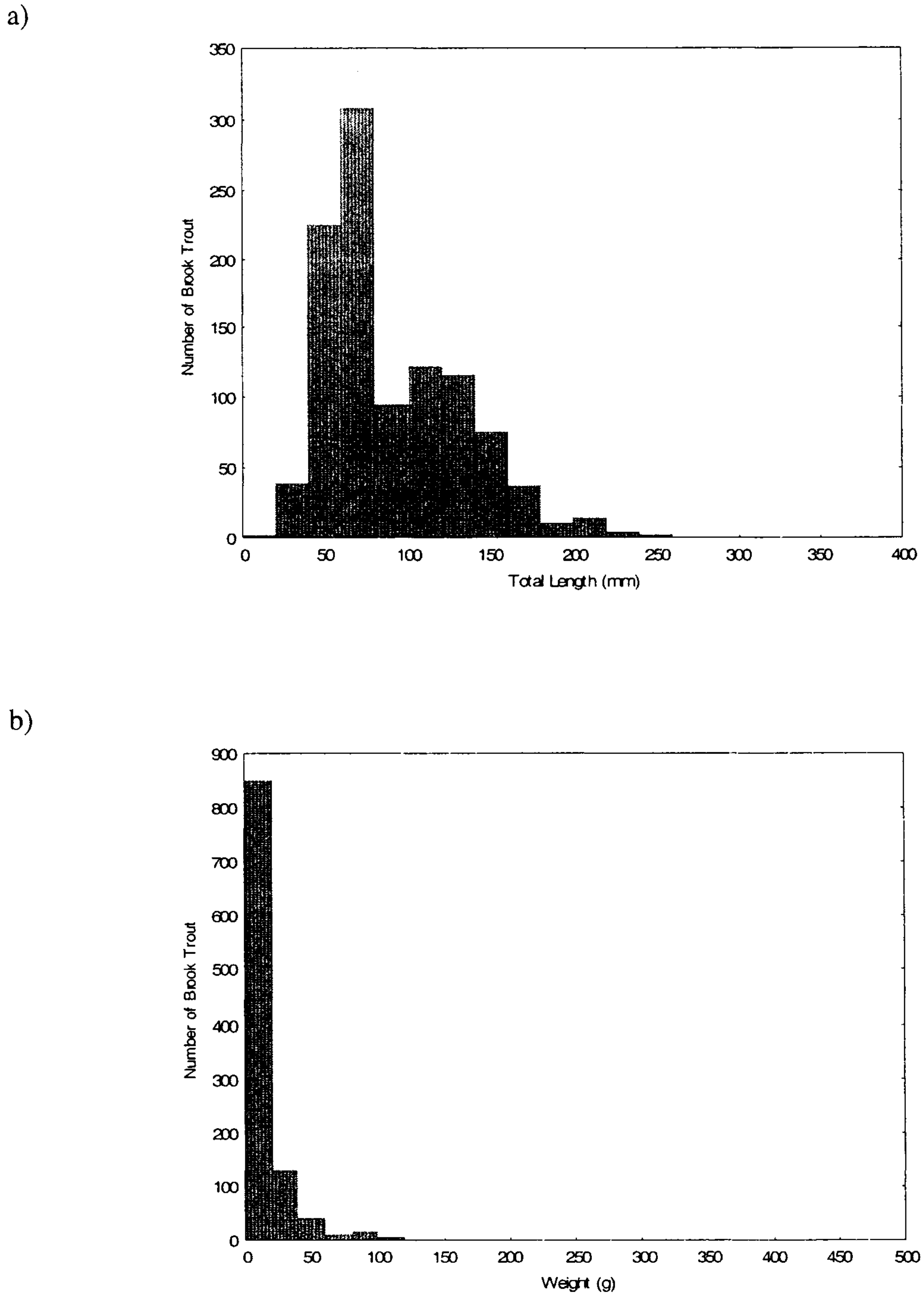


Figure 3.0.4 Total length (a) and weight (b) distributions of brook trout captured in streams in the Mackenzie River watershed.

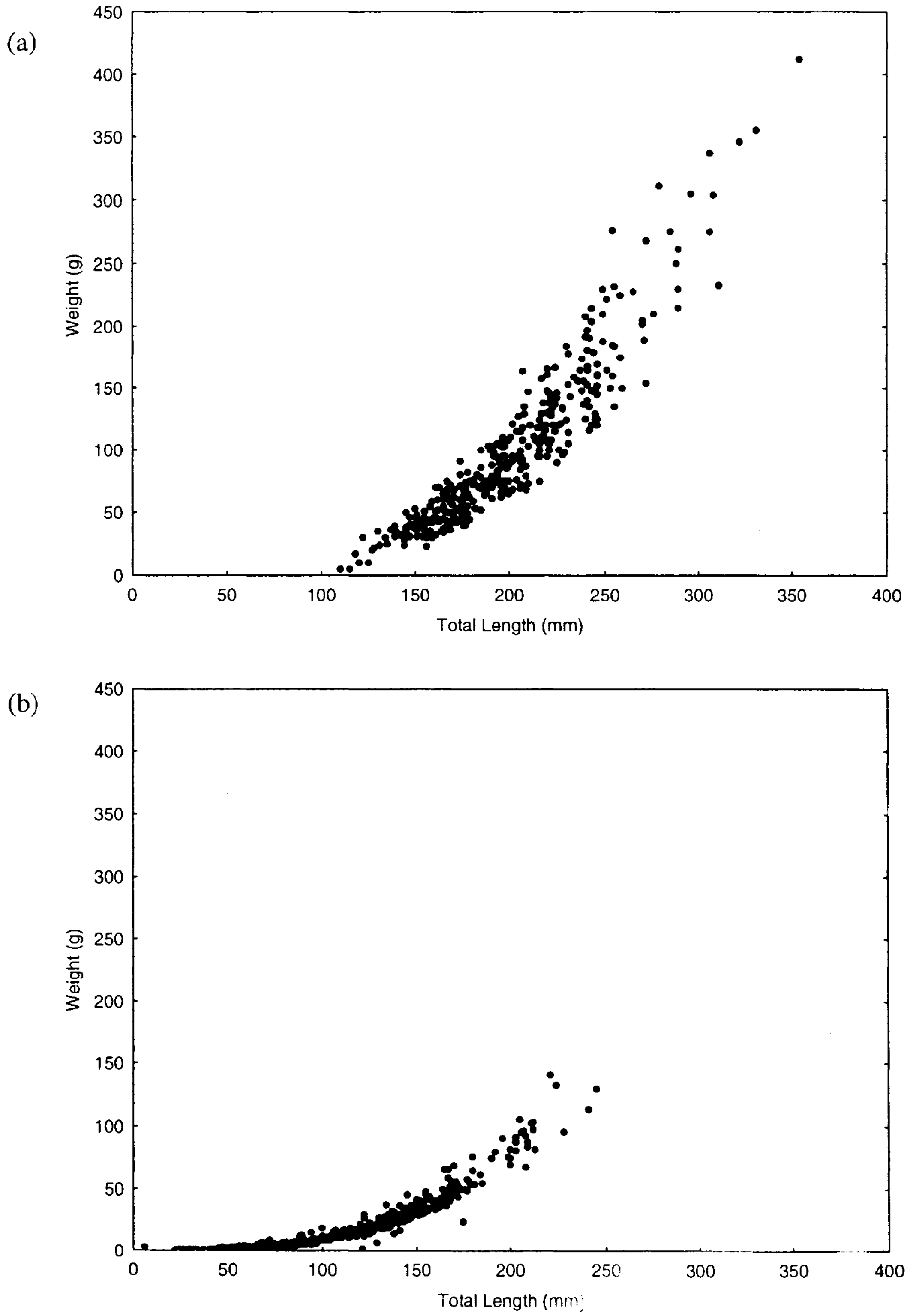


Figure 3.0.5 (a) Length - weight relationship for brook trout in beaver ponds and (b) length-weight relationship for brook trout in streams adjacent beaver ponds.

3.1 Brook Trout Size Distribution

Brook trout were never captured in beaver ponds with UCAs less than 2.9 sq. km (1 sq. km UCA category). Brook trout were captured in several 1 sq. km category streams when associated with a larger stream confluence. Brook trout captured in beaver ponds were significantly larger on average than brook trout captured in the adjacent stream among each UCA category ($F_{1, 1321} = 1658.2, P < .001$) (Figure 3.1.1). Brook trout captured in beaver ponds were, on average, 105 mm and 72 g larger in beaver ponds than in their adjacent streams. The difference was greatest in beaver ponds with 5 sq. km UCA where brook trout were on average 181 mm and 192 g larger than in the adjacent streams. The size difference was less in the larger UCA categories with brook trout being on average 119 mm and 97 g and 71 mm and 63 g larger in 10 sq. km and 30 sq. km beaver ponds than adjacent streams respectively (Figure 3.1.2 and 3.1.3). The largest brook trout captured in a stream was 245 mm in total length and 141 g in weight, whereas, the largest brook trout caught from a beaver pond was 354 mm and 412 g. Approximately 20% of the 369 brook trout caught in beaver ponds were larger than the largest brook trout captured in the stream survey.

Brook trout in beaver ponds were smaller as contributing UCA increased. Beaver ponds in the 5 sq. km UCA category had brook trout that were significantly larger on average than brook trout in 10 sq. km and 30 sq. km UCA size category ponds ($F_{2, 366} = 32.808, P < .001$) (Figure 3.1.2). Brook trout in 5 sq. km UCA beaver ponds were on average 53 mm and 91 g and 76 mm and 115 g larger than in 10 sq. km and 30 sq. km UCA ponds respectively. Similarly, brook trout in 10 sq. km UCA beaver ponds were on average 22 mm and 25 g larger than in 30 sq. km UCA ponds.

Brook trout in streams were larger as the contributing UCA increased. Brook trout in streams were significantly larger in the 30 sq. km UCA size category than brook trout in 5 sq. km and 10 sq. km UCA classes ($F_{2, 910} = 39.625, P < .001$) (Figure 3.1.3). The difference was greatest between 5 sq. km and 30 sq. km UCA streams where brook trout were on average 34 mm and 14 g larger in 30 sq. km UCA streams. The size difference was less between 10 sq. km and 30 sq. km UCA streams with brook trout being on average 25 mm and 9 g larger in 30 sq. km UCA streams.

Aging structures (otoliths, scales, and fin rays) were taken from nine brook trout following incidental mortality and scales and fin rays were taken from six additional fish that were released (Table 3.1.1). Ages of brook trout ranged from three to six years.

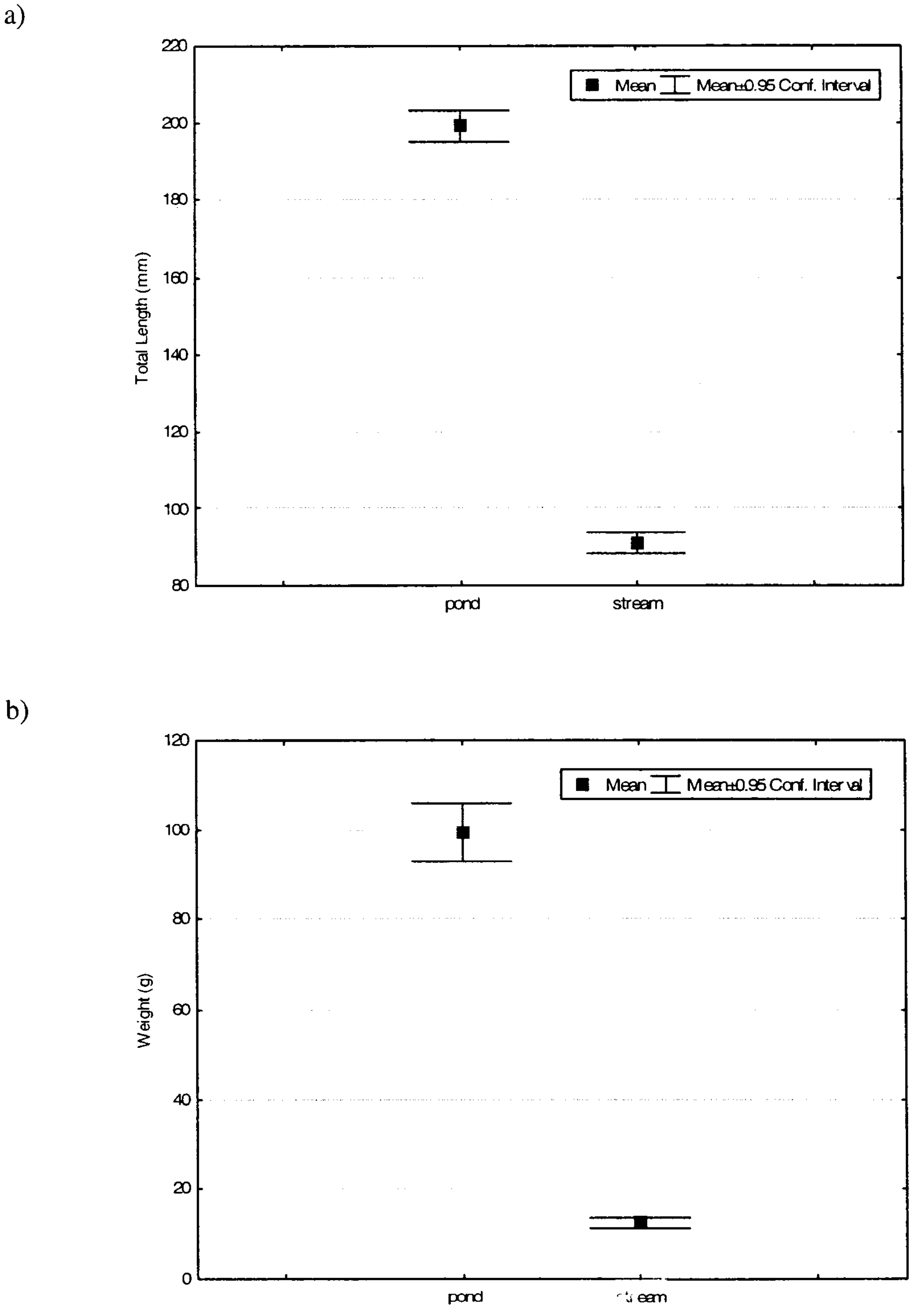
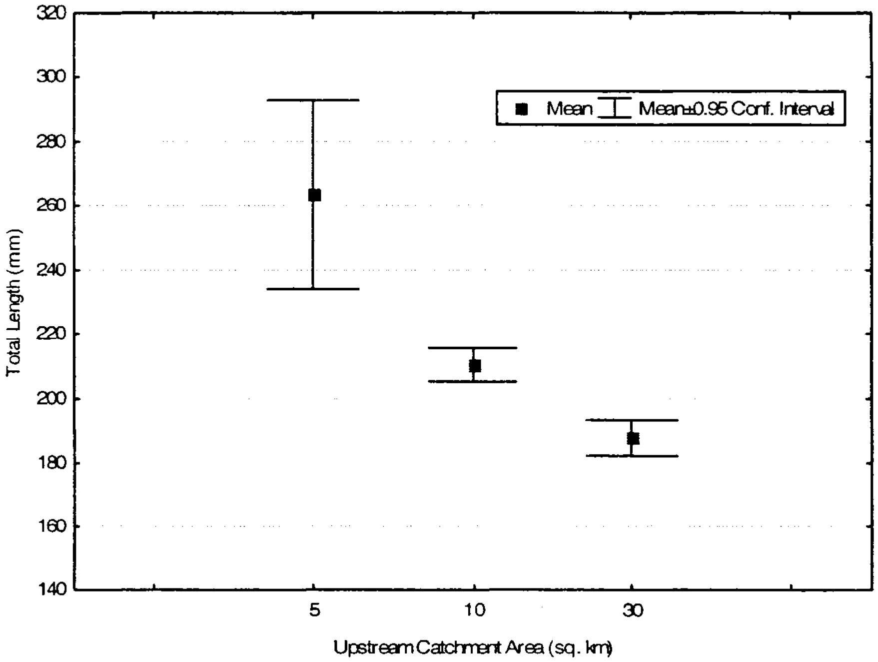


Figure 3.1.1 Mean total length (a) and weight (b) of brook trout captured in beaver ponds and their adjacent streams in the study area.

a)



b)

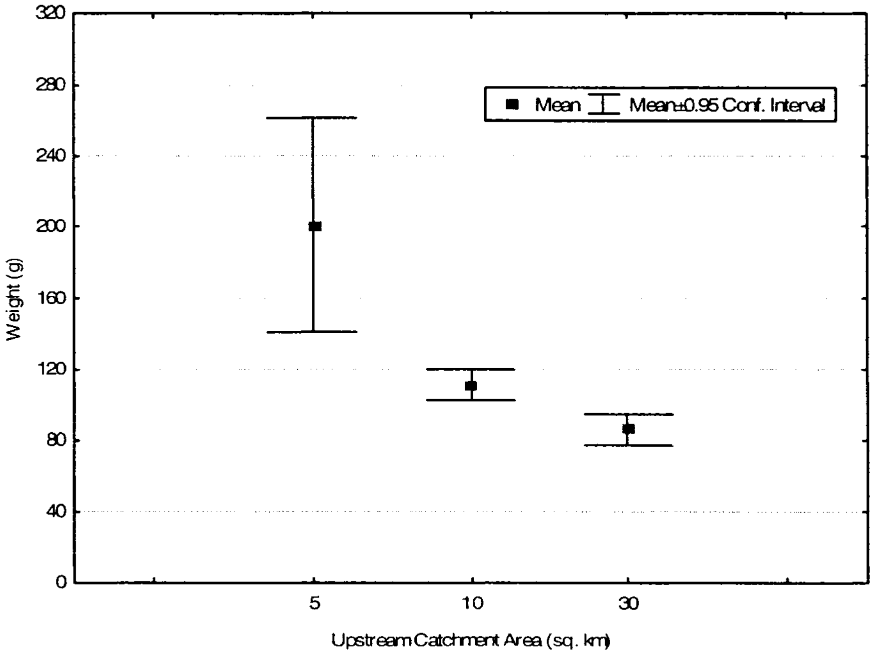


Figure 3.1.2 Mean total length (a) and weight (b) of brook trout captured in beaver ponds in the study area.

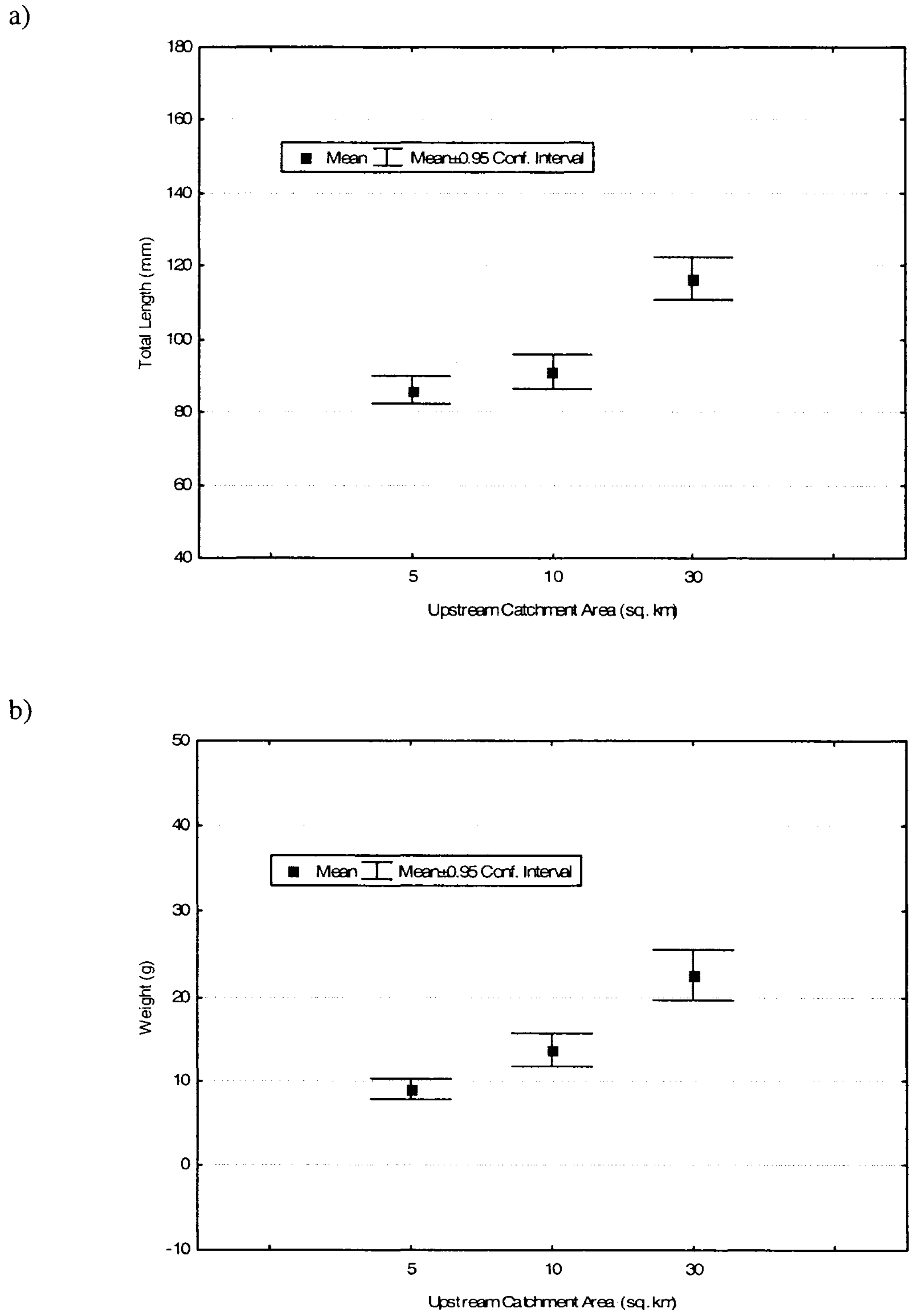


Figure 3.1.3 Mean total length (a) and weight (b) of brook trout captured in streams in the study area.

Table 3.1.1 Brook trout estimated age in beaver ponds from otoliths (oto), scales (sc), and left pectoral fin rays (fr).

Pond	Date (2003)	Total Length (mm)	Weight (g)	Structure	Estimated Age (years)
EWN10K	May 26	214	108	oto, sc	3
EWN10K	May 26	241	165	oto, sc	3
EW30K	May 28	191	61	oto, sc	3
MRK2	Jun 04	331	355	oto, sc	3
SHW30K	Jun 30	207	108	oto, sc	3
SHW30K	Jun 30	217	120	oto, sc	3
EWN210K	Jul 07	211	120	oto, sc	4
EWN10K	Aug 13	249	230	oto, sc	4
MRK2	Sept 27	293	325	oto, sc, fr	3
SHW30K	Oct 08	279	311	sc,fr	4
SHW30K	Oct 08	354	412	sc,fr	6
SHW30K	Oct 08	254	160	sc,fr	3
SHW30K	Oct 08	271	189	sc,fr	4
Mack30K	Oct 09	306	304	sc,fr	5
Mack30K	Oct 09	322	346	sc,fr	>3-4

3.2 Local and Landscape Scale Characteristics of Beaver Ponds

Local scale water quality parameters and landscape scale variables were relatively consistent among beaver ponds (Table 3.2.1 and 3.2.2). However, water temperature and dissolved oxygen levels were highly variable between seasons within ponds. Local scale habitat variables from beaver ponds with both brook trout present and absent are summarized in Table 3.2.1. Landscape scale characteristics, including upstream catchment area (UCA), pond area, wetland area, pond position, surficial geology (material and landform), and topographic index (TI) values were highly variable among beaver ponds and between beaver ponds with brook trout present and absent (Table 3.2.2). Beaver ponds with brook trout present had significantly larger UCAs than ponds without brook trout ($F_{1,49} = 2.7$, $P < .001$) (Table 3.2.4). UCA for beaver ponds with brook trout present was, on average, 10.3 sq. km greater than ponds without brook trout. This is due to the fact that brook trout were never captured in beaver ponds with UCAs less than approximately 2.9 sq. km. Beaver ponds with brook trout also had, on average, smaller surface areas and larger contiguous wetland areas.

UCAs of approximately 2.9 sq. km and smaller appear to be a threshold to brook trout presence in beaver ponds. Even after excluding ponds with UCA less than 2.9 sq. km, UCA for beaver ponds with brook trout present was still, on average, 5.3 sq. km greater than ponds without brook trout. Mean temperature of ponds with brook trout present was, on average, 3.8 °C higher than ponds without brook trout. The maximum depth of ponds with brook trout was, on average, approximately 20 cm deeper than ponds without brook trout. Beaver ponds with brook trout also had, on average, smaller surface areas and larger contiguous wetland areas. Local and landscape scale habitat variables from beaver ponds with both brook trout present and absent and with UCAs greater than approximately 2.9 sq. km are summarized in Table 3.2.5 and Table 3.2.6, respectively.

Table 3.2.1 Summary of local scale attributes of beaver ponds. Table denotes mean and (range) of values calculated from multiple sampling locations within each pond unless otherwise indicated.

Beaver Pond	Dates Sampled (2003)	Dissolved Oxygen (mg/l)	Conductivity (uS/cm)	Total Dissolved Solids (ppm)	pH	Temperature (° C)	MEI
Mackh-1K	21-Jun	7.8 (7.8)	59 (58-59)	0.03 (0.03)	6.95 (6.84-7.17)	19.53 (18.39- 20.21)	0.05
Mack3	19-Sep	10.2 (9.2-11.1)	35 (35)	0.04 (0.04)	7.08 (6.95-7.19)	17.44 ((15.90-18.32)	0.04
Ewmid	18-Jun	8.2 (8.2)	52 (46-77)	0.03 (0.03-0.04)	6.73 (6.49-7.16)	19.45 (18.17-20.68)	0.03
Mooseland	03-Jun	4.1 (0.3-8.0)	54 (48-86)	0.04 (0.03-0.06)	6.4 (6.03-6.59)	16.68 (13.46-18.8)	0.05
Mack2h1	15-Jul	5.4 (5.4)	42 (42)	0.04 (0.04)	6.94 (6.94)	20.85 (19.5-22.5)	0.04
Mack3.1	20-Sep	9.9 (9.1-10.6)	31 (31-32)	0.03 (0.03)	7.12 (7.05-7.21)	16.68 (13.31-17.62)	0.04
Mack2h2	15-Jul	6.1 (6.1)	42 (42)	0.04 (0.04)	6.94 (6.94)	20.00 (19-21)	0.05
TMH-low	28-Sep	9.8 (3.81-11.6)	37 (36-45)	0.04 (0.03-0.04)	7.17 (7.0-7.22)	8.12 (7.9-8.52)	0.07
EW1N	17-Sep	5.7 (0.2-7.9)	71 (69-83)	0.06 (0.05-0.07)	7.48 (6.9-8.29)	16.98 (14.9-17.91)	0.03
SHW2	25-Jun	7.3 (5.8-8.0)	38 (37-39)	0.04 (0.04)	6.80 (6.51-6.92)	20.47(18.97-21.92)	0.06
Ewmid2	23-Jun	6.9 (6.4-7.4)	49 (47-52)	0.04 (0.04)	6.90 (6.51-7.05)	19.94 (19.5-20.39)	0.06
Ecochallenge	19-Jun	7.3 (6.1)	50 (47-60)	0.03 (0.03-0.04)	6.90 (6.49-7.50)	19.19 (16.42-20.51)	0.04
EW1K	16-Jul	6.8 (6.1)	42 (42)	0.04 (0.04)	6.94 (6.94)	19.50(15-22.5)	0.04
SHW1	25-Jun	7.4 (6.1)	37 (37)	0.03 (0.03)	6.61 (6.61)	20.40(18.29-21.31)	0.04
Mack3.2	20-Sep	9.1 (8.5-9.4)	32 (32)	0.03 (0.03)	7.10 (6.93-7.24)	17.12(14.44-18.11)	0.04
Magone2	18-Sep	8.7 (7.1-10.1)	31 (31-32)	0.04 (0.04)	7.15 (7.01-7.21)	16.96(15.32-18.11)	0.03
TMH1K	04-Oct	10.1 (3.1-12.3)	31 (29-40)	0.03 (0.03-0.04)	7.09 (6.89-7.22)	5.40(5.03-5.68)	0.06
Wak7.4	16-Sep	8.6 (7.9-9.2)	56 (56-59)	0.05 (0.05)	7.08 (6.95-7.21)	16.59(13.99-17.95)	0.05
Magone1	18-Sep	8.3 (5.2-10.0)	33 (31-42)	0.04 (0.04-0.09)	7.00 (6.66-7.13)	16.34(9.22-18.03)	0.02
Tartan	19-Aug	4.3 (0.5-6.6)	30 (29-51)	0.02 (0.02-0.04)	6.79 (6.61-7.25)	21.84(20.03-23.29)	0.04
Mack5	09-Jun	6.9 (1.8-8.8)	36 (35-43)	0.02 (0.02-0.03)	6.49 (6.2-6.92)	16.31(13.44-16.93)	0.04
MRK2	04-Jun	9.6 (2.1-12.2)	50 (46-59)	0.03 (0.03-0.04)	6.89 (6.48-7.14)	14.30(9.86-17.77)	0.04
EZEE	12-Jun	7.5 (6.8-7.1)	51 (49-54)	0.03 (0.03-0.04)	7.04 (6.44-7.8)	14.57(10.83-16.3)	0.05
SHW3	26-Jun	6.5 (5.3-7.2)	40 (35-55)	0.03 (0.03)	6.69 (6.35-6.98)	18.32(9.96-20.69)	0.03
MRK1	02-Jun	10.1 (8.1-10.7)	48 (46-5)	0.03 (0.03)	6.94 (6.67-7.1)	13.03(11.43-14.22)	0.07
EW5K	23-Jul	3.7 (1.3-6.2)	48 (39-94)	0.03 (0.03)	5.97 (5.51-6.37)	20.29(17.99-22.1)	0.03
EWNW	17-Jun	7.3 (7.3)	59 (58-63)	0.03 (0.03-0.04)	7.04 (6.85-7.18)	19.65(16.86-20.57)	0.04
Moosebones	04-Jul	6.9 (5.2-8.3)	39 (34-51)	0.03 (0.03-0.04)	6.63 (6.41-6.99)	21.58(16.4-24.5)	0.03
Walk5.3	29-Aug	6.8 (6.0-7.6)	53 (49-57)	0.03 (0.03-0.04)	7.18 (6.99-7.66)	19.96(16.01-21.05)	0.04
Mack2	27-May	9.1 (6.9-9.9)	38 (38-39)	0.03 (0.03)	6.47 (6.36-6.8)	14.93(14.34-15.65)	0.03
TM10K	11-Oct	11.4 (9.9-12.5)	30 (30)	0.05 (0.05)	7.16 (7.01-7.33)	11.08(9.99-12.23)	0.05
Walk7.3	26-Sep	8.5 (8.1-8.9)	57 (57-59)	0.05 (0.05)	7.24 (7.19-7.29)	9.44(9.4-9.5)	0.08
Walk7.2	26-Sep	9.0 (8.8-9.6)	57 (57)	0.05 (0.05)	7.16 (7.09-7.21)	9.62(9.54-9.85)	0.10
Walk7	29-May	10.1 (9.3-11.0)	65(64-66)	0.04 (0.04)	6.94 (6.83-7.02)	13.68(10.88-15.19)	0.06
Mack2.1	25-Sep	9.2 (8.8-9.5)	28 (28-29)	0.03 (0.03)	6.89 (6.81-7.16)	9.59(9.23-10.14)	0.02
Mack2.2	02-Oct	11.1 (8.1-11.7)	22 (22-26)	0.02 (0.02-0.03)	6.85 (6.72-7.06)	3.93(3.19-4.71)	0.02
Mackh10K	23-Aug	6.9 (6.3-7.6)	66 (60-82)	0.07 (0.06-0.08)	7.19 (6.97-7.31)	18.19(11.22-21.51)	0.08
EWN10K	10-Jul	9.2 (6.1-9.6)	49 (29-30)	0.02 (0.02)	7.04 (7.04)	15.55(12.52-16.14)	0.03
Walk5.2	16-Jun	9.1 (7.5-10.2)	61 (56-72)	0.04 (0.04-0.07)	7.08 (6.88-7.41)	18.11(15.11-19.79)	0.03
Walk5.15	22-Aug	6.9 (6.2-7.2)	62 (60-64)	0.04 (0.04-0.05)	7 12 (6.95-7.26)	19.65(16.85-21.2)	0.05
Walk6	06-May	10.8 (10.0-11.9)	50 (50)	0.03 (0.03)	7.02 (6.88-7.22)	[illegible]01-7.55)	0.03
Walk5.1	25-Aug	7.2 (6.2-7.9)	63 (61-64)	0.04 (0.04-0.05)	[illegible]26 (7.09-7.4[illegible]	[illegible]35-22.12)	0.06
DSS10K	12-May	9.6 (8.8-10.2)	61 (61)	0.04 (0.04)	[illegible] (6.97-7.2[illegible]	[illegible]2-10.12)	0.05
EWN210K	07-Jul	7.2 (7.0-8.1)	41 (40-42)	0.03 (0.03)	6.94 (6.77-7.66)	[illegible]7.5-19.8)	0.02
TM20K	29-Sep	11.2 (11.0-11.4)	29 (24-31)	0.04 (0.04-0.0[illegible])	7.23 (7.1-7.45)	6.[illegible]75-7.14)	0.06
WW130K	07-Aug	5.7 (0.1-7.8)	71 (59-145)	0.05 ([illegible]04-0.09)	7.08 (6.64-7.32)	20.24(15.88-21.27)	0.05
WW230K	12-Aug	6.7 (6.2-7.7)	63 (54-74)	[illegible] (0 05-0.06)	7.15 (6.76-7.94)	17.47(6.77-21.23)	0.04
SHW30K	30-Jun	8.3 (7.4-9.4)	45 (42-48)	0.04 (0.04)	7.55 (7.18-8.08)	14.61(8.9-16.8)	0.03
EW30K	28-May	9.7 (9.3-10.0)	42 (42-43)	0.03 (0.03)	7.01 (6.98-7.40)	13.91(13.81-13.95)	0.02
Mack30K	03-Jul	6.6 (5.3-7.5)	39 (30-50)	0.03 (0.03-0.04)	7.13 (6.88-7.43)	20.01(13.8-25.4)	0.03

Table 3.2.2 Summary of landscape scale attributes of beaver ponds.

Beaver Pond	UCA (sq. km.)	UCA Class	Pond Position (m)	Mean Pond Depth (m)	Maximum Pond Depth (m)	Pond surface Area (ha)	Wetland Area (ha)	Maximum TI Value (Pond)	Maximum TI Value (Wetland)
Mackh-1K	.146	1	14707	.74	1.6	.767	3.591	11.895	11.895
Mack3	.321	1	1887	.81	1.4	.368	.68	8.517	8.517
Ewmid	.494	1	3217	.99	2.0	1.758	2.289	11.658	11.658
Mooseland	.502	1	10137	.70	1.8	2.738	3.439	13.598	13.598
Mack2h1	.502	1	8346	.78	1.3	.431	1.814	11.384	11.384
Mack3.1	.516	1	2558	.92	1.6	1.175	1.738	11.849	11.849
Mack2h2	.563	1	8073	.76	1.4	.276	.509	9.568	9.568
TMH-low	.579	1	10322	.49	1.2	.562	.992	11.45	12.694
EW1N	.595	1	8724	1.75	3.1	1.721	3.927	11.934	11.934
SHW2	.751	1	10741	.62	1.6	.363	1.092	8.542	10.295
Ewmid2	.828	1	3822	.54	1.4	.198	.202	8.929	8.929
Ecochallenge	.848	1	10939	.86	2.2	1.422	1.588	11.261	11.261
EW1K	1.084	1	3255	.91	1.9	1.839	2.846	11.785	11.785
SHW1	1.202	1	10222	.78	1.7	.525	1.790	9.719	11.913
Mack3.2	1.220	1	2344	.80	1.4	.093	1.286	5.608	10.063
Magone2	1.418	1	11983	1.22	1.8	3.848	7.221	13.326	13.326
TMH1K	1.904	1	11073	.52	1.6	.827	1.169	12.992	12.992
Wak7.4	2.171	1	1808	1.02	2.3	.779	3.347	11.400	11.468
Magone1	2.227	1	10731	1.75	3.2	5.194	10.233	12.185	12.185
Tartan	2.377	1	5275	.52	1.3	.256	.367	11.307	11.307
Mack5	2.478	1	3982	.67	1.5	1.034	1.071	10.430	10.430
MRK2	2.924	5	10697	.78	2.2	.689	.879	10.605	10.605
EZEE	2.935	5	9933	.62	1.3	.808	1.588	9.644	9.694
SHW3	3.252	5	8029	1.05	2.3	3.115	3.816	12.386	12.386
MRK1	3.507	5	9689	.42	1.2	.905	1.281	10.573	10.573
EW5K	3.768	5	12480	1.25	2.0	1.696	9.106	12.951	15.671
EWNW	4.532	5	10163	.80	1.9	.462	1.209	10.569	10.569
Moosebones	6.023	5	4921	.88	1.8	.117	474	12.389	12.389
Walk5.3	6.592	5	9085	.80	1.8	1.231	2.898	10.962	10.962
Mack2	7.065	10	3741	.81	2.1	.132	4.288	9.091	[illegible]
TM10K	7.117	10	7490	.99	2.3	.210	.241	10.940	[illegible]
Walk7.3	7.240	10	590	.69	1.3	.221	2.360	9.936	[illegible]
Walk7.2	7.333	10	449	.56	1.3	.493	1.167	10.851	12.210
Walk7	7.355	10	50	.75	1.8	.184	.269	9.526	9.526
Mack2.1	7.356	10	2844	1.36	2.4	.142	.268	7.455	10.190
Mack2.2	7.367	10	3025	1.24	2.6	.136	.214	8.23	8.23
Mackh10K	8.260	10	10809	.92	2.1	1.997	5.505	13.474	13.474
EWN10K	8.532	10	9716	1.22	2.5	.262	1.549	10.750	12.776
Walk5.2	9.884	10	7382	1.22	2.6	4.902	7.202	12.883	13.266
Walk5.15	10.240	10	7055	.92	1.7	.272	1.359	10.454	11.840
Walk6	11.076	10	9727	1.00	1.8	.224	.431	9.286	9.286
Walk5.[illegible]	11.285	10	6720	.71	1.6	.124	.48	11.933	11.933
DSS10K	[illegible]	10	6676	.82	1.6	.360	3.729	10.978	11.806
EWN210K	14.099	10	8850	1.24	2.1	.170	1.363	9.474	12.428
TM20K	18.413	10	6850	.76	1.9	.047	.50	7.915	7.915
WW130K	25.468	30	5679	1.08	1.8	.198	1.426	11.828	12.857
WW230K	25.655	30	5327	1.19	2.1	.462	1.202	12.485	13.605
SHW30K	29.397	30	1372	1.26	3.1	.468	.590	8.169	8.952
EW30K	35.932	30	2352	1.15	1.8	.154	.483	0	10.603
Mack30K	37.824	30	1228	1.07	1.9	.337	.769	9.561	9.561

Table 3.2.3 Mean and range for local scale habitat variables of beaver ponds with brook trout present and absent. The probability of means being equal (p) was calculated with univariate ANOVA for comparative purposes only.

	Brook Trout Present n = 20		Brook Trout Absent n = 30		
Variable	Mean	Range	Mean	Range	p
Temperature (°C) (Mean)	16.13	9.4 to 20.4	15.88	3.93 to 21.84	0.866
Temperature (°C) (Minimum)	12.84	6.77 to 17.50	13.62	3.19 to 20.03	0.581
DO (mg/L)	8.28	5.7 to 11.4	8.01	3.7 to 11.2	0.265
pH	7.07	6.47 to 7.55	6.91	5.97 to 7.55	0.244
TDS (ppm)	0.039	0.025 to 0.072	0.035	0.020 to 0.072	0.482
Conductivity (us/cm)	52	28 to 71	43	22 to 71	0.055
Mean Depth (m)	0.97	0.4 to 1.4	0.88	0.5 to 1.8	0.281
Maximum Depth (m)	2.02	1.2 to 3.1	1.80	1.2 to 3.2	0.121

Table 3.2.4 Mean and range for landscape scale habitat variables of beaver ponds with brook trout present and absent. The probability of means being equal (p) was calculated with univariate ANOVA for comparative purposes only.

	Brook Trout Present n = 20		Brook Trout Absent n = 30		
Variable	Mean	Range	Mean	Range	p
UCA (sq. km)	13.50	2.90 to 37.82	3.21	0.15 to 37.82	0.000
Pond Area (ha)	0.716	0.12 to 4.90	2.40	0.05 to 10.23	0.333
Wetland Area (ha)	1.78	0.24 to 7.20	1.11	0.05 to 5.19	0.357
Maximum TI (pond)	10.56	7.46 to 13.47	10.70	5.61 to 13.47	0.643
Maximum TI (wetland)	11.44	8.95 to 13.61	11.35	7.92 to 13.61	0.223

Table 3.2.5 Mean and range for local scale habitat variables of beaver ponds with an UCA greater than approximately 2.9 sq. km with brook trout present and absent. The probability of means being equal (p) was calculated with univariate ANOVA for comparative purposes only.

	Brook Trout Present n = 20		Brook Trout Absent n = 9		
Variable	Mean	Range	Mean	Range	P
Temperature (° C) (Mean)	16.1	9.4 to 20.4	12.3	3.9 to 21.6	0.022
Temperature (° C) (Minimum)	12.9	6.8 to 17.5	9.8	3.2 to 18.0	0.054
DO (mg/L)	8.3	5.7 to 11.4	8.5	3.7 to 11.2	0.528
pH	7.07	6.47 to 7.55	6.85	5.97 to 7.23	0.191
TDS (ppm)	0.039	0.025 to 0.072	0.036	0.024 to 0.053	0.794
Conductivity (us/cm)	52	28 to 71	44	22 to 61	0.226
Mean Depth (m)	0.97	0.4 to 1.4	0.91	0.56 to 1.25	0.548
Maximum Depth (m)	2.02	1.2 to 3.1	1.84	1.3 to 2.6	0.340

Table 3.2.6 Mean and range for landscape scale habitat variables of beaver ponds with an UCA greater than approximately 2.9 sq. km with brook trout present and absent. The probability of means being equal (p) was calculated with univariate ANOVA for comparative purposes only.

	Brook Trout Present n = 20		Brook Trout Absent n = 9		
Variable	Mean	Range	Mean	Range	P
UCA (sq. km)	13.50	2.92 to 37.82	8.16	2.94 to 18.41	0.175
Pond Area (ha)	0.72	0.12 to 4.90	2.29	0.05 to 3.82	0.828
Wetland Area (ha)	1.78	0.24 to 7.20	0.78	0.05 to 1.70	0.578
Maximum TI (pond)	10.56	7.46 to 13.47	10.52	7.92 to 12.95	0.539
Maximum TI (wetland)	11.44	8.95 to 13.61	11.07	7.92 to 15.97	0.305

3.3 Season and Temperature

When CUE was analyzed for all beaver ponds it appeared that brook trout catchability (abundance) was strongly influenced by water temperature. When mean water temperature in the beaver ponds was below 11 °C, CUE was much lower than at higher temperatures (Figure 3.3.1). Reference ponds sampled multiple times during different seasons demonstrated a similar pattern (Figure 3.3.2). However, there was no significant difference in mean water temperature between beaver ponds with brook trout present and absent (ANOVA, $F_{1,73} = 0.001$, $p = 0.974$). Mean water temperature was significantly higher in ponds with brook trout present (ANOVA, $F_{1,49} = 5.569$, $p = 0.022$), when only ponds with UCAs greater than 2.9 sq. km were included in the analysis. However, similar to previous observations, local scale water quality parameters were consistent among ponds whereas landscape scale characteristics were highly variable among ponds with an UCA greater than approximately 2.9 sq. km and mean pond temperature greater than 11 °C. Both local scale water quality parameters (Table 3.3.1) and landscape scale characteristics (Table 3.3.2) were relatively consistent between beaver ponds with brook trout present and absent, with the exception of UCA.

Brook trout abundance was significantly greater in beaver ponds with greater mean water temperature (ANOVA, $F_{2,48} = 4.350$, $p = 0.018$) when only beaver ponds with UCAs greater than 2.9 sq. km were included in the analysis. The number of brook trout caught when mean pond temperature was below 11 °C was 23 ($n = 24$) and when the temperature was above 11 °C was 297 ($n = 51$). When CUE and biomass curves were plotted based on mean water temperature across all seasons a threshold response appeared to exist. Brook trout relative abundance (CUE) was significantly higher in beaver ponds with a temperature that fell within the preferred thermal range of brook trout than in ponds where the water temperature fell outside of that range (ANOVA, $F_{2,48} = 5.259$, $p = 0.026$). Peak CUE occurred at approximately 14 to 18 °C.

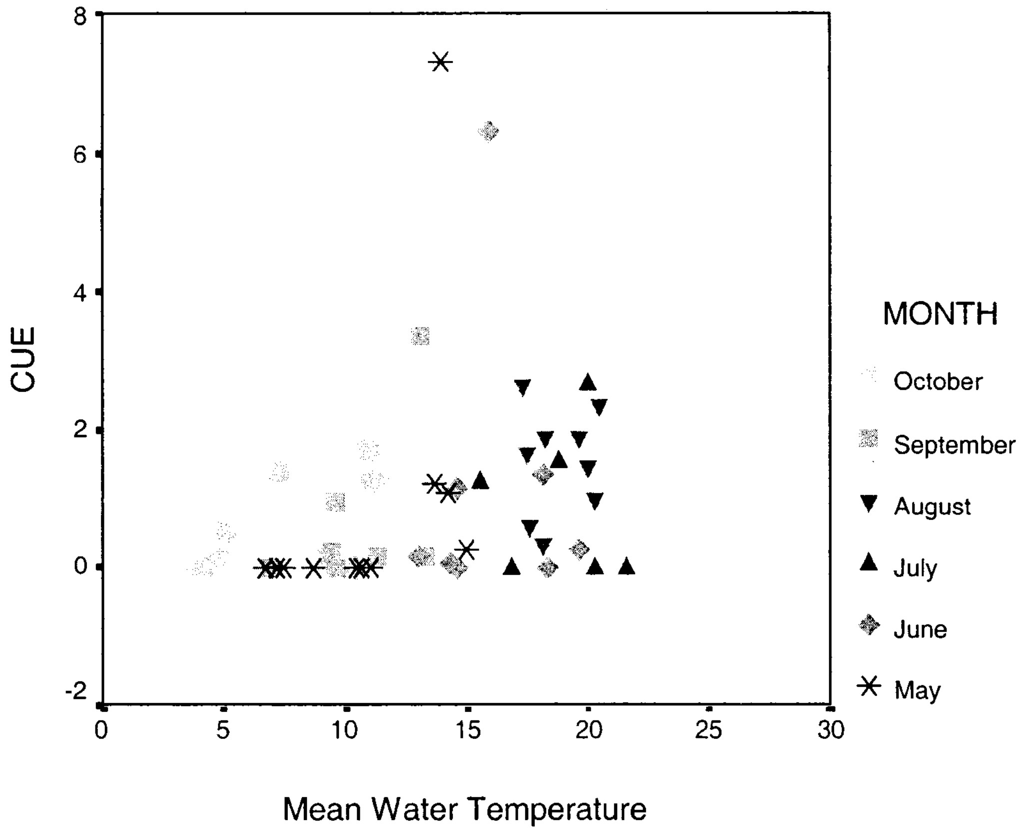


Figure 3.3.1 CUE and relative mean water temperature in beaver ponds during the 2003 sampling season.

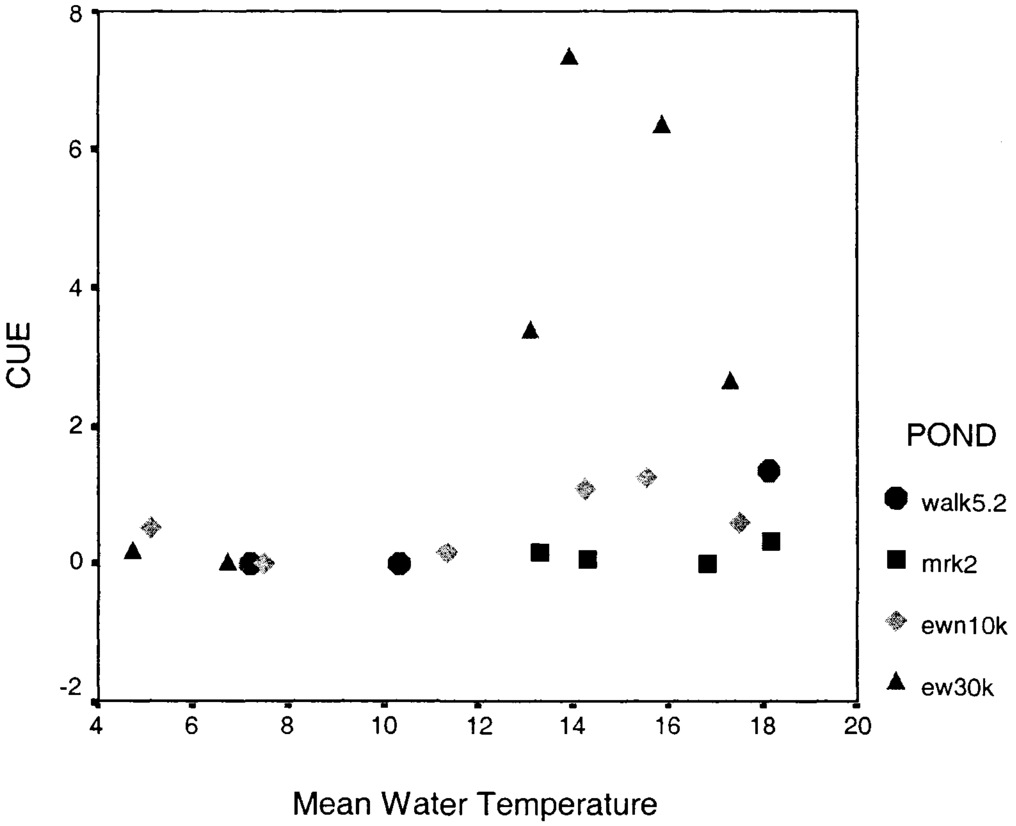


Figure 3.3.2 CUE of brook trout and mean water temperature in 4 beaver ponds sampled multiple times during the 2003 season.

Table 3.3.1 Mean and range for local scale habitat variables of beaver ponds with mean overall water temperatures greater than 11 °C and greater than 2.9 sq. km in UCA with brook trout present and absent. The probability of means being equal (p) was calculated with univariate ANOVA for comparative purposes only.

	Brook Trout Present n = 18		Brook Trout Absent n = 4		
Variable	Mean	Range	Mean	Range	P
Temperature (°C) (Mean)	16.9	11.1 to 20.4	18.7	14.6 to 21.6	0.271
Temperature (°C) (Minimum)	13.3	6.8 to 17.5	13.8	9.9 to 18.0	0.785
DO (mg/L)	8.2	5.7 to 11.4	6.2	3.7 to 6.9	0.509
pH	7.07	6.47 to 7.55	6.58	5.97 to 7.04	0.022
TDS (ppm)	0.039	0.025 to 0.072	0.032	0.030 to 0.033	0.477
Conductivity (us/cm)	53	30 to 71	45	39 to 51	0.303
Mean Depth (m)	0.96	0.42 to 1.26	0.95	0.62 to 1.25	0.926
Maximum Depth (m)	2.0	1.2 to 3.1	1.85	1.3 to 2.3	0.442

Table 3.3.2 Mean and range for landscape scale habitat variables of beaver ponds with mean overall water temperatures greater than 11 °C and greater than 2.9 sq. km in UCA with brook trout present and absent. The probability of means being equal (p) was calculated with univariate ANOVA for comparative purposes only.

	Brook Trout Present n = 18		Brook Trout Absent n = 4		
Variable	Mean	Range	Mean	Range	P
UCA (sq. km)	14.20	2.92 to 37.82	4.00	2.94 to 6.02	0.092
Pond Area (ha)	1.83	0.24 to 7.20	3.75	0.47 to 3.82	0.749
Wetland Area (ha)	0.73	0.12 to 4.91	1.43	0.12 to 3.12	0.151
Maximum TI (pond)	10.18	8.17 to 13.47	11.84	9.64 to 12.95	0.426
Maximum TI (wetland)	11.49	8.95 to 13.61	12.54	9.69 to 15.67	0.705

3.4 Differentiating Brook Trout Habitat

Local and landscape scale habitat variables differed between brook trout class (the presence or absence of brook trout) (MANOVA, $F_{15, 34} = 4.112$, $p < 0.001$). Habitat variables important in differentiating between brook trout class were identified using DFA (Table 3.4.1). Beaver ponds with and without brook trout were separated along discriminant function 1 with group centroids of -1.078 for absent and 1.616 for present (Figure 3.4.1). The significant function generated by the analysis explained approximately 64.5% of the variance among group centroids (canonical correlation = .803, Wilks' lambda = 0.355, Chi-square 41.906, df = 15, $p < 0.001$). Beaver ponds with brook trout present had positive function scores and were characterized by lower MEI, larger UCA, lower mean water temperature, higher DO, greater maximum depth, and higher conductivity. Beaver ponds with brook trout absent had negative function scores and were characterized by lower TDS, and larger wetland area.

The previous analysis was repeated using only beaver ponds with mean temperatures greater than 11 $^{\circ}$C to ensure the results were not influenced by sampling efficiency differences. Local and landscape scale habitat variables in beaver ponds with mean temperatures greater than 11 $^{\circ}$C differed significantly between brook trout classes (MANOVA, $F = 8.909_{16, 24}$, $p < .001$). Habitat variables important in differentiating between brook trout class were identified using a DFA (Table 3.4.2). Beaver ponds with and without brook trout were separated along discriminant function 1 with group centroids of -2.103 for absent and 2.687 for present (Figure 3.4.2). The significant function generated by the analysis explained approximately 85.5% of the variance among group centroids (canonical correlation = .925, Wilks' lambda = 0.144, Chi-square 60.052, df = 16, $p < 0.001$). Beaver ponds with brook trout present were characterized by greater UCA, higher DO, higher conductivity, lower maximum TI value in the contiguous wetland area, lower minimum water temperature, higher pH, greater maximum depth, and higher MEI. Beaver ponds with brook trout absent were characterized by higher mean water temperatures, lower TDS, and shallower mean depths.

Table 3.4.1 Standardized CDF coefficients generated for function 1 by the DFA.

Variable	Scale	Standardized CDF Coefficient
MEI	Local	0.994
UCA	Landscape	0.919
Water Temperature	Local	0.813
DO	Local	0.765
Maximum Depth	Local	0.728
Conductivity	Local	0.609
TDS	Local	-1.078
Wetland Area	landscape	-1.053

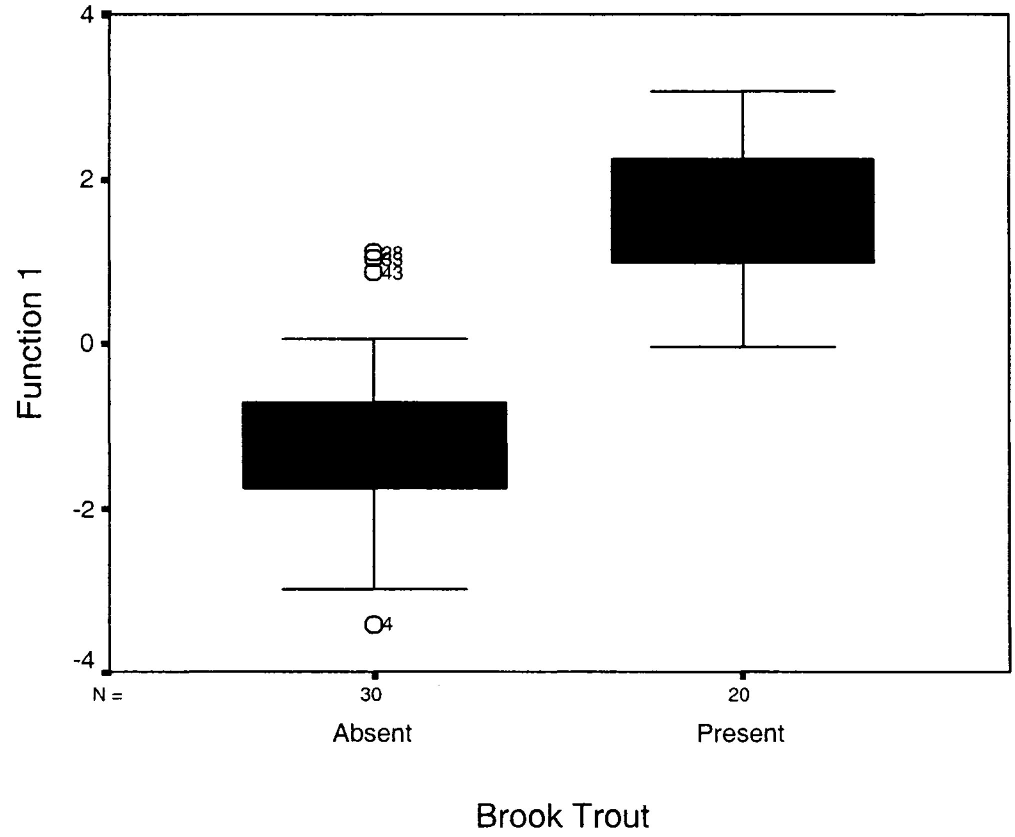


Figure 3.4.1 Box plot of DFA function 1 scores for beaver ponds characterized by local and landscape scale habitat variables. Bar indicates median, box indicates 25-75% quartile range, and whiskers indicate standard deviation. Outliers are greater than 2 quartiles from the median.

Table 3.4.2 Standardized CDF coefficients generated for function 1 by the DFA.

Variable	Scale	Standardized CDF Coefficient
UCA	Landscape	0.919
DO	Local	0.793
Conductivity	Local	0.763
Maximum Wetland TI Value	Landscape	0.700
Minimum Water Temperature	Local	0.664
pH	Local	0.486
Maximum Depth	Local	0.422
MEI	Local	0.421
Mean Depth	Local	-0.343
TDS	Local	-0.634
Water Temperature	Local	-0.668

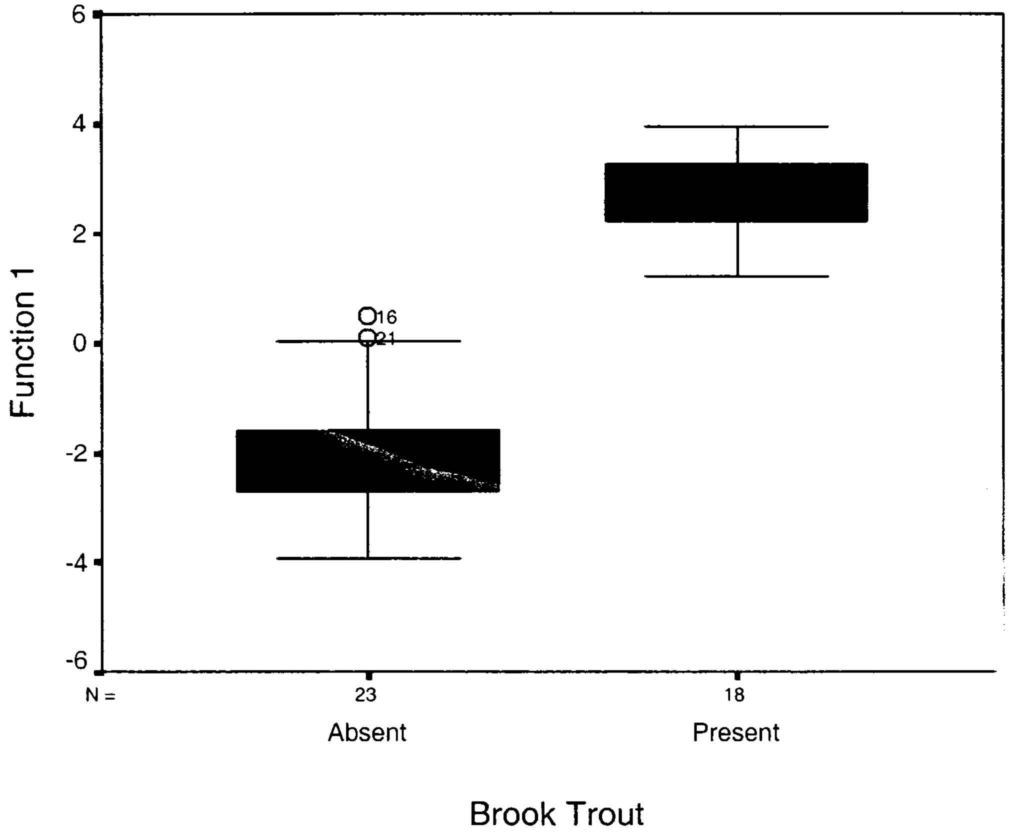


Figure 3.4.2 Box plot of DFA function 1 scores for beaver ponds with mean water temperatures greater than 11 ° C characterized by local and landscape scale habitat variables. Bar indicates median, box indicates 25-75% quartile range, and whiskers indicate standard deviation. Outliers are greater than 2 quartiles from the median.

3.5 Predicting Brook Trout Presence

The relative effectiveness of local and landscape scale variables for developing models to predict brook trout presence and absence in beaver ponds within a drainage system was tested using stepwise logistic regression following variable reduction. The logistic models were developed using a random subset of 34 sites. Model statistics are summarized in Table 3.5.1. The remaining 16 beaver ponds were used to test the efficacy of the most parsimonious model at correctly predicting brook trout presence and absence. Two models in the stepwise procedure have evidence ratio numbers less than 10, thus the relationship of variables in each model must be evaluated. Model AV-1 ($Z = 4.204 \ln(UCA) - 3.30$), which included only UCA, correctly predicted beaver pond group membership 82.4% of the time, and 81.8% for the test cases. Model AV-2, which included mean water temperature and UCA, correctly predicted beaver pond group membership 85.3%, however, predicted group membership fell to 73.0 % for the test cases.

Logistic regression models were developed using both local and landscape scale variables from only beaver ponds with mean temperatures greater than 11 °C to control for the potential influence of temperature on catch rate. Models were developed using a random subset of 28 sites with mean temperatures greater than 11 °C. To validate the models predictive capacity, the remaining 13 beaver ponds with mean temperatures greater than 11 °C were used to test the model efficacy. The attributes of each model are summarized in Table 3.5.2. Only 1 model in the stepwise procedure had an evidence ratio number less than 10. Model AV11-1 ($Z = 217.218 \ln(UCA) - 89.796 \ln(meandepth) - 135.518$), which included UCA and mean pond depth, correctly predicted beaver pond group membership 100 % for the construction cases and 83.8% for the test cases.

The single landscape scale variable, UCA, was included in each of the preceding logistic models and accounted for the majority of the variability in each model individually. Alone, UCA accounts for 77.6 % of the variability in model UCA ($Z = 4.204 \ln(UCA) - 3.30$), which is analogous to model AV-1, and correctly classified ponds by brook trout presence and absence 82.4%. In beaver ponds with a mean water temperature greater than 11 °C, UCA accounts for 97.3% of the variability in the model and correctly predicted group membership 92.9%. The discriminatory ability of model UCA-11($Z = 26.464 \ln(UCA11) - 14.876$) was 83.8 % compared to model UCA 82.4 % when tested against the remaining 16 beaver ponds.

The probability of brook trout presence in beaver ponds based on model UCA is shown in Figure 3.5.1. When only beaver ponds with an overall mean water temperature greater than 11 °C are used in the analysis the probability of brook trout presence based on UCA increases (model UCA11) (Figure 3.6.2).

Table 3.5.1 Logistic regression models developed using stepwise logistic regression with AIC_c evidence ratio numbers < 10. Smaller AICc evidence ratio numbers indicate model parsimony. Higher AUC number indicates better model fit. Shaded bottom portion of table indicates models created using subset of 28 sites with mean water temperature greater than 11 o C.

Model	**Variables in model**	**-2Log Likelihood**	**Nagelkerke R Square**	**% Correct**	**AIC_c**	**AIC_c Evidence Ratio**	**AUC**
AV-1	UCA,	25.362	0.602	82.4	57.52	1.00	0.894
AV-2	UCA, Mean Temperature	18.552	0.739	85.3	46.48	4.411	0.912
UCA	UCA	25.362	0.602	82.4	n/a	n/a	0.894
AV11-1	UCA, mean pond depth	8.03E-07	1.000	100	9.82	1.00	1
UCA-11	UCA	4.047	0.948	92.9	n/a	n/a	0.983

Table 3.5.2 The number of beaver ponds, from a subset of sites, correctly and incorrectly predicted as having brook trout present and absent using logistic regression models developed using stepwise logistic regression with AICc evidence ratio numbers < 10. Shaded bottom portion of table indicates models tested using subset of 28 sites with mean water temperature greater than 11 o C.

Model	**Variables in model**	**Number of test ponds**	**True predicted present**	**False predicted present**	**True predicted absent**	**False predicted absent**	**Predicted correctly**
AV-1	UCA,	16	7	2	6	1	81.8 %
AV-2	UCA, Mean Temperature	16	8	1	4	3	73.0 %
UCA	UCA	16	7	2	6	1	81.8 %
AV11-1	UCA, mean pond depth	13	7	1	4	1	83.8 %
UCA-11	UCA	13	7	1	4	1	83.8 %

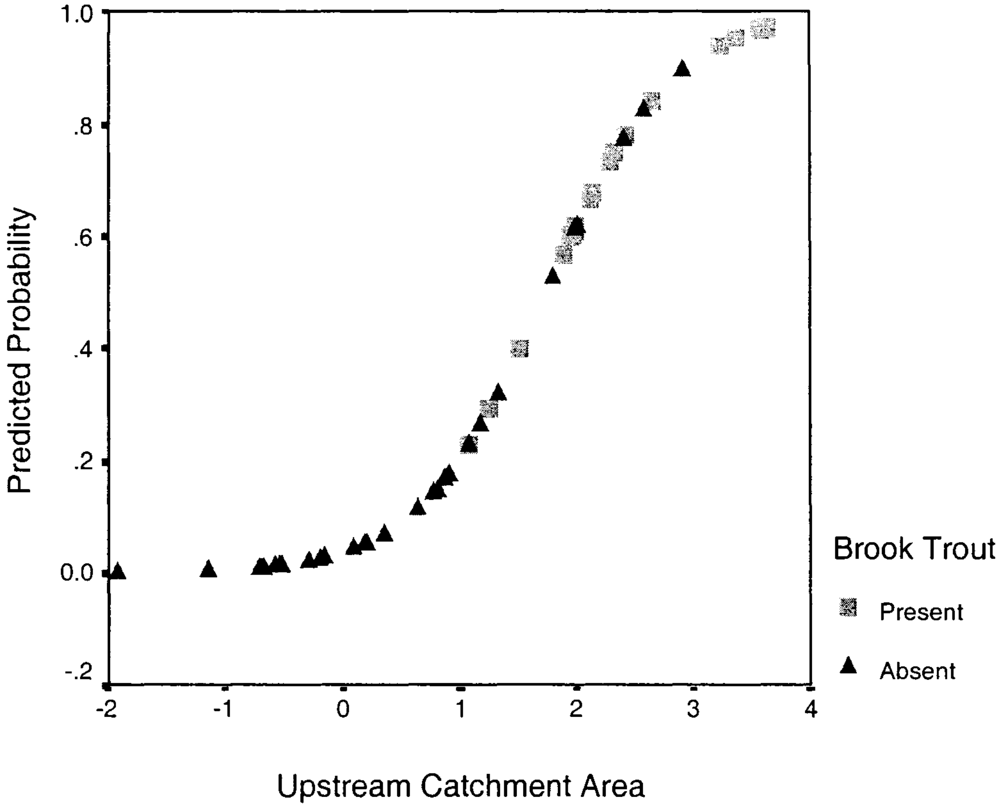


Figure 3.5.1 The predicted probability of brook trout presence in beaver ponds based on model UCA.

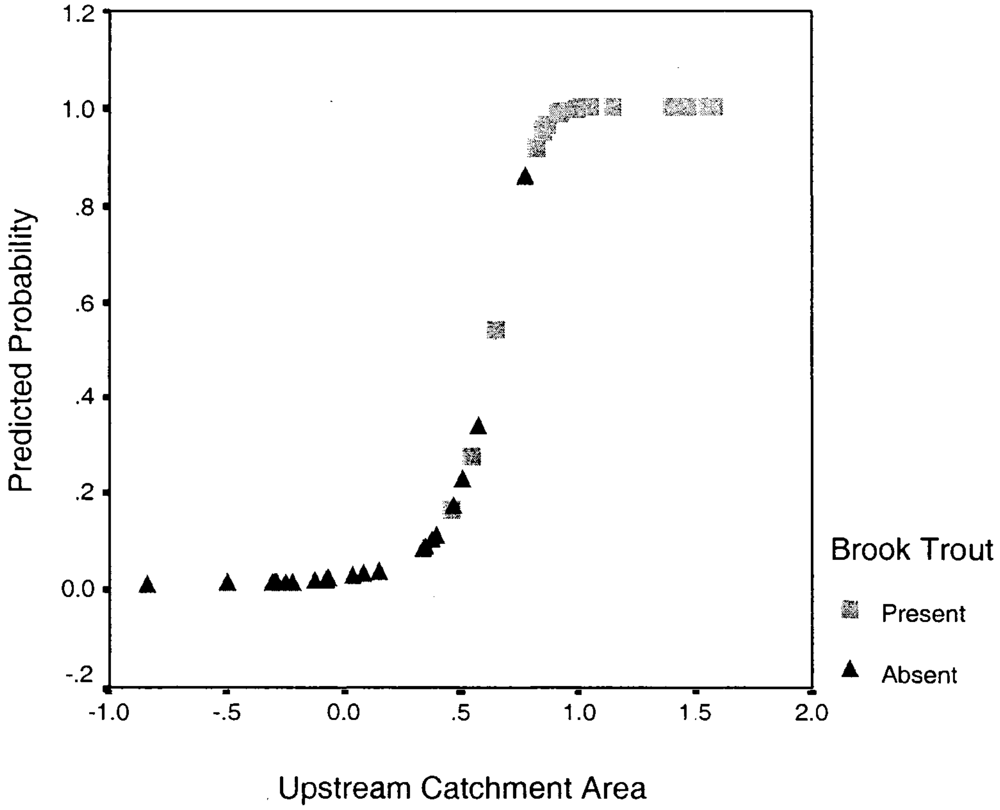


Figure 3.5.2 The predicted probability of brook trout presence in beaver ponds based on model UCA11 using only beaver ponds with an overall mean water temperature greater than 11 °C.

Using a ROC curve, the discriminatory ability of each logistic regression model was graphically evaluated using a critical threshold value (Pcrit) of 0.5 (Table 3.5.1). The Area under the curve (AUC) significantly exceeded the AUCcrit (0.7), $p<0.01$ (Hosmer and Lemeshow 2000, Bonn and Schroder 2001, Schroder 2004). The confidence limits from the bootstrap percentile method were 81.986-1.055 using the ROC plotting and AUC calculation and transferability test, version 1.3 (Schroder 2004). Thus, a Pcrit value of 0.5 is acceptable to test the results of the logistic model using the ROC curve. The ROC curve generated for each model indicates that the discriminatory ability of each model is acceptable (Hosmer and Lemeshow 2000, Schroder 2004). The predictive ability of the model increases when only beaver ponds with an overall mean water temperature greater than 11 °C were used in the analysis.

In each of the preceding analyses, model predictive ability improves when only sites with a mean water temperature greater than 11 °C are included. Each analysis indicates that UCA exerts the greatest influence over the distribution of brook trout within the watershed study area. Pond depth improved the classification of the test cases marginally when temperature is controlled for in model AVC11-1.

4.0 Discussion

Beaver ponds in small boreal stream drainages provide habitat for brook trout and may allow them to persist in marginal conditions at the periphery of their distribution. Beaver ponds are also subject to natural variation and disturbance and are abandoned and re-established over variable time periods in response to environmental variability at local and landscape scales (Lawrence 1952, Gard 1961, McComb *et al.* 1990, Barnes 1997, Snodgrass 1997, Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). The protection of brook trout habitat requires a greater understanding of local and landscape scale characteristics linking aquatic and terrestrial environments associated with the distribution of the species. My research demonstrates that beaver ponds possess characteristics that provide important brook trout habitat. Brook trout use beaver ponds within small stream drainage networks; however, brook trout do not use all ponds within the stream drainage. Similarly, brook trout relative abundance is variable among beaver ponds. My study also illustrates an association between landscape and local scale pond characteristics which in turn are associated with the pattern of distribution and relative abundance of brook trout in beaver ponds. Despite this association, it remains unclear how the linkage between these two habitat scales may influence the presence and abundance of brook trout. Complex interactions between local and landscape scale characteristics may not only influence brook trout presence and relative abundance, but also specific behavioural and functional characteristics, such as local adaptations in growth and maturity rates, maximum lifespan and size distribution. Size distribution differed among beaver ponds and between ponds and their adjacent streams. Brook trout in ponds were larger relative to those in the adjacent stream. Brook trout size distribution in ponds also differed among UCA categories with brook trout average size decreasing with increasing UCA.

Distribution and abundance of fish species has often been related to local scale or site specific characteristics that must be observed through field surveys. However, variability in these characteristics due to variation in environmental conditions and seasonality appears to affect brook trout catchability. Local scale habitat characteristics were relatively consistent among beaver ponds and between ponds with brook trout present and absent. Brook trout presence and relative abundance in beaver ponds did not appear to be related to variability associated with local scale characteristics with the exception of temperature and depth. Temperature was highly variable seasonally both within and among ponds, as was brook trout relative abundance (CUE). Brook trout were often not captured in beaver ponds where they had previously been captured. Relatively low or 0 catch rates in these ponds often corresponded to low water temperatures. Seasonal variation in beaver pond water temperature may significantly influence catch rate of brook trout at various times of the year.

Temperature appeared to be an important characteristic influencing brook trout catchability. When water temperatures in beaver ponds fell below approximately 11 °C (mean pond temperature), the catchability of brook trout was lower than at warmer temperatures. Mean water temperature, calculated for each beaver pond from multiple locations within each pond, was significantly higher in beaver ponds that had brook trout present when only beaver ponds with UCAs greater than 2.9 sq. km were included in the analysis. Similarly, mean water temperature was significantly higher in beaver ponds with greater brook trout abundance when only beaver ponds with UCAs greater than 2.9 sq. km were included in the analysis. The number of brook trout caught when mean pond temperature was below 11 °C was 23 ($n = 24$) whereas 297 ($n = 51$) were caught when the temperature was above 11 °C. Characteristic of a threshold response, low water temperatures may reduce the metabolic efficiency of brook trout and thus lead to a corresponding reduction in both foraging movements and feeding. Studies indicate that temperature influences both feeding and activity in brook trout (Baldwin 1956, Marod 1995, Drake and Taylor 1996). For instance, Baldwin (1956) demonstrated that brook trout consume half as much food at approximately 9 °C and 18 °C as they do at 13 °C. The results suggest that the sampling method may not yield reliable estimates when mean pond water temperature is less than approximately 11 °C or greater than 18 °C.

Beaver ponds with temperatures in excess of approximately 18 °C (mean pond temperature) also had a lower catch rate, though to a substantially lesser degree than ponds with mean water temperatures less than 11 °C. As water temperatures approach the critical thermal maxima of brook trout, activity decreases in response to metabolic stress and there may be a reluctance to leave thermal refugia. Marod (1995) found sustained temperatures greater than 20 °C reduced the duration of movement of brook trout during foraging. The influence of warmer mean water temperature on brook trout catchability was not as pronounced as with cooler water temperature. Cool groundwater inputs in the drainage system likely mediate higher temperature but have little effect on low water temperature. Even as surface temperature in the beaver ponds reached brook trout critical thermal maxima, large areas of thermal refugia likely existed within some ponds allowing brook trout to maintain activity levels near optimal levels. Groundwater discharge can be 5.0-7.5 °C cooler than the ambient stream temperature (Gibson 1966, McCrae and Edwards 1994, Picard *et al.* 2003). Several beaver ponds in this study had mean ambient and minimum temperature disparities as high as 10.7 °C. Cool water refugia may be an important determinant of brook trout activity rate and feeding efficiency regardless of the pond maximum temperature or overall mean temperature. In contrast, areas of cool-water discharge during the summer are areas of relatively warm-water during winter months. Groundwater discharge likely improves brook trout over-winter survival by regulating in-stream temperature and limiting ice formation creating patches of thermally stable refugial areas (Cunjak and Power 1986, Cunjak 1988, Cunjak 1996, Curry *et al.* 1997, Lindstrom and Hubert 2004). Where thermal refugia exist, brook trout may be able to persist regardless of mean ambient or maximum water temperatures.

In waterbodies where temperatures become unfavourable, brook trout may move to areas of groundwater inputs or into tributaries to exploit thermal refugial areas (Gibson 1966, Lackey 1970, Power 1980, Witzel and MacCrimmon 1983, Bowlby and Roff 1986, Curry and Noakes 1995, Cunjak 1996, Biro 1998). In the absence of cool groundwater refugia, deepwater areas in lakes are often used by brook trout during warm summer months to avoid temperatures outside of their preferred range (Baldwin 1948, Lackey 1970, Olsen *et al.* 1988, Mucha 2003). Similarly, movements into deep beaver ponds may allow brook trout to avoid stream temperatures outside of their preferred range and persist in stream systems otherwise lacking deepwater habitat. Thermal refugia in deep ponds may potentially explain higher relative abundance in deeper ponds compared to shallow ponds (Chisholm *et al.* 1987, Lindstrom and Hubert 2004).

Beaver ponds with brook trout were on average 0.22 m (maximum depth) deeper than ponds without brook trout. Lindstrom and Hubert (2004) reported similar results with brook trout and cutthroat trout (*Oncorhynchus clarkii*) utilizing beaver ponds and pools with significantly greater mean residual depths than those not used. Deeper beaver ponds had lower mean and minimum temperatures than shallower ponds. Deeper beaver ponds were on average 0.37 °C (mean temperature) and 1.75 °C (minimum temperature) colder than shallower ponds. The disparity in mean and minimum temperature between ponds with and without brook trout is greater when only ponds with a mean overall water temperature greater than 11 °C were compared. These ponds were on average 1.56 °C (mean temperature) and 2.81 °C (minimum temperature) colder than shallower ponds. Deeper ponds had larger brook trout than shallower ponds. Brook trout from ponds with a maximum depth greater than 2 m were on average 17 mm and 33 g larger than shallower ponds. The difference was greatest in ponds with an UCA of 5 sq. km, where brook trout were 75 mm and 134 g larger in deeper ponds (> 2 m) than in shallower ponds (< 2 m). Relatively large brook trout were also captured from the deeper ponds regardless of UCA. The largest brook trout was caught from a 3.1 m deep (maximum) pond with a UCA of 30 sq. km. Johnson *et al.* (1992) similarly found deep beaver ponds contained large but relatively few brook trout, whereas shallow ponds were dominated by numerous, small brook trout. Johnson *et al.* (1992) also observed that small brook trout had a greater survival potential than larger brook trout in Wyoming mountain streams likely due to the lack of deep pools and suggested deep beaver ponds may provide over-wintering habitat. Deep beaver ponds may have higher rates of hyporheic exchange due to the dynamic exchange with groundwater stored in the surrounding wetland area. As a result, even during severe winters, deep beaver ponds likely resist the formation of deep anchor ice or complete freezing, providing some form of over-wintering habitat. Chisholm (1985) observed brook trout in streams of the Snowy Mountain range migrated into deep areas of beaver ponds to over-winter. Deep ponds with groundwater discharge may possess discrete refugial areas where brook trout can remain relatively active throughout both summer and winter. The intensity of groundwater and hyporheic exchange processes are functionally linked to landscape scale geomorphic characteristics such as stream gradient, topography, and surficial geology (Grimm and Fisher 1984, Hynes 1983, Brunke and Gosner 1997, Vallett *et al.* 1997, Baxter *et al.* 1999, Power *et al.* 1999, Baxter and Hauer 2000, Franken *et al.* 2001, Borwick *et al.* 2006).

The importance of landscape scale processes within the entire stream catchment has become an important concept of lotic ecology (Vannotte *et al.* 1980, Richards *et al.* 1996, Allan and Johnson 1997, Allan *et al.* 1997, Baxter *et al.* 1999, Baxter and Hauer 2000, Fausch *et al.* 2002, Stanford *et al.* 2005, Kocovsky and Carline 2006). The view of stream ecosystems as a longitudinal continuum of habitats (Vannote *et al.* 1980) has evolved into a dynamic of habitat mosaics linking aquatic and terrestrial characteristics at local and broad landscape scales (Pringle *et al.* 1988, Schlosser 1991, Schlosser 1995a, Baxter and Hauer 2000, Schlosser and Kallemeyn 2000, Gomi *et al.* 2002, Fausch *et al.* 2002, Smith and Kraft 2005, Stanford *et al.* 2005). Local scale patterns and processes in streams are often functionally linked to landscape scale influences. Similarly, the successional nature and spatio-temporal distribution of beaver dams greatly influences fundamental geologic, hydro-morphological, and ecological processes on the landscape (Rudemann and Schoonmaker 1938, McDowell and Naiman 1986, Johnston and Naiman 1987, Johnston and Naiman 1990, Schlosser and Kallemeyn 2000, Pollock *et al.* 2004).

Landscape scale characteristics were highly variable among beaver ponds and between ponds with brook trout present and absent. My findings demonstrate that brook trout presence is strongly associated with UCA. UCA is a latent variable that represents the complex relationship among local and landscape scale characteristics and relative catchment position. Brook trout presence and relative abundance was higher in ponds with larger UCA. However, no other clear associations existed between brook trout distribution and landscape scale characteristics of ponds. Brook trout presence in ponds became patchy in ponds with smaller UCA and a threshold to upstream distribution appeared to exist at approximately 2.9 sq. km. Brook trout relative abundance was lower in ponds with smaller UCA. Mean UCA for ponds with brook trout present was on average 10.29 sq. km greater than ponds without brook trout. Brook trout were never captured in beaver ponds with UCAs less than approximately 2.9 square kilometers.

The relationship between UCA and brook trout distribution is consistent with previous studies that demonstrate stream drainage position (UCA) is an important characteristic influencing distribution and abundance of various lotic species (Vannote *et* *al.* 1980, Schlosser 1991, Matthews and Robinson 1998, Peterson and Rabeni 2001, Smith and Kraft 2005). As stream and riparian habitat characteristics change from small headwaters to larger downstream areas, so too do the characteristics of the stream fish populations (Vannote *et al.* 1980, Fausch *et al.* 2002, Smith and Kraft 2005). The composition of stream fish assemblages is also associated to some degree with UCA characteristics (Osborne and Wiley 1992, Matthews and Robinson 1998, Smith and Kraft 2005) with downstream areas generally having greater species richness (Schlosser 1987, Osborne and Wiley 1992, Schlosser and Kallemeyn 2000). The number of fish species captured in minnow traps was greater in ponds with larger UCA. Similarly, brook trout relative abundance was higher in beaver ponds and streams with larger UCAs. Typically, longitudinal patterns of distribution and abundance of fish species were thought to be influenced by local or site-specific habitat differences that occur independent of landscape scale characteristics (Creque *et al.* 2005). However, distribution and abundance are likely influenced by a complex interaction of local scale physical habitat variables and landscape scale characteristics such as geomorphology, drainage position, and groundwater potential (Bowlby and Roff 1986, Schlosser 1995a, Schlosser 1998, Baxter et al. 1999, Torgersen *et al.* 1999, Baxter and Hauer 2000, Schlosser and Kallemeyn 2000, Fausch *et al.* 2002, Smith and Kraft 2005).

The successional nature of beaver pond establishment and abandonment over millennia has created a terraced landscape (Rudemann and Schoonmaker 1938, Johnston and Naiman 1987, Johnston and Naiman 1990, Pollock *et al.* 2004) with ponds and wetland areas of various sizes throughout stream drainage networks. Variation in stream gradient and valley topography has a strong influence on beaver pond morphology (Johnston and Naiman 1987, Schlosser and Kallemeyn 2000). Beaver ponds constructed in areas of low relief generally had large contiguous wetland areas conducive to groundwater accumulation and exfiltration. Ponds constructed in areas of steep relief, such as narrow valley segments of uplifted bedrock, generally had small contiguous wetland areas. These ponds were also deeper and more heavily shaded. In ponds where bedrock dominates the surficial geology, water generally cannot penetrate to form groundwater aquifers and instead enters the stream directly as surface runoff (Freeze and Cherry 1979). The extent of groundwater storage and exfiltration in these successional ponds and beaver meadow wetlands is likely limited by individual pond topography and accumulated sediment.

The ability to identify groundwater habitat along the stream-terrestrial interface using a Topographic Index (TI) may link different habitat scales relevant for conserving brook trout habitat (Borwick *et al.* 2006). Groundwater discharge in lake basins is related to various physical habitat characteristics, including topography (Beven and Kirkby 1979), basin geomorphology (Devito *et al.* 1996, Borwick *et al.* 2006), and surficial geology (Quinn *et al.* 1991, Devito *et al.* 1996). Similar processes influencing groundwater infiltration, storage, and discharge likely exist within stream systems and affect local scale characteristics such as temperature (Baxter *et al.* 1999, Baxter and Hauer 2000, Borwick *et al.* 2006). Groundwater has been identified as an important factor structuring salmonid populations (Curry and Noakes 1995, Curry *et al.* 1997, Biro 1998, Power *et al.* 1999, Baxter and Hauer 2000) and the presence of cold groundwater inputs, indicated in this study by mean ambient and minimum temperature disparities in ponds, may enable brook trout populations to persist in otherwise thermally marginal habitats of stream drainage networks.

If groundwater discharge is related to landscape scale hydrogeological characteristics such as surficial geology and catchment topography, then brook trout were expected to be present more often in ponds with a greater potential for groundwater discharge expressed as a higher relative TI value (Buttle *et al.* 2001, Borwick *et al.* 2006). While no association appeared to exist between brook trout presence and higher relative TI value in my study, the association of TI value with groundwater discharge and temperature appears useful under appropriate conditions. For example, Borwick *et al.* (2006) found TI value was positively related to lake surface and substrate temperature differences, indicating higher TI values were associated with greater groundwater input. Borwick *et al.* (2006) also found brook trout young-of-the-year (YOY) preferred to use areas with higher TI values. Unlike Borwick *et al.* (2006) where the lake perimeter was divided into sampling units with a specific TI value for each unit, each individual beaver pond represented a sampling unit with an average TI value representative of the whole pond. Also, the small size of most ponds and the scale at which TI was assessed prevented differentiation of specific areas with higher or lower TI values. In Borwick *et* *al.* (2006), lake dwelling brook trout were able to actively move to areas with higher TI values and correspondingly lower temperatures, whereas brook trout were potentially temporally isolated in beaver ponds and were unable to move to adjacent ponds where more preferable thermal conditions may have existed. The temporal isolation of beaver ponds and their adjacent streams may complicate any association between relative TI value and presence or absence of brook trout.

The use of statistical models to predict the presence or distribution of species is an increasingly important tool for fisheries and wildlife conservation and forest management (Pearce and Ferrier 2000). In the absence of field survey data, statistical models and GIS tools may offer a method to predict the presence and absence of brook trout in beaver ponds within stream drainage systems as well as improve the ability to minimize potential perturbations to habitat from forest management activities. Using local and landscape characteristics of beaver ponds I developed a series of models to predict brook trout presence and absence. The probability of brook trout presence in a beaver pond within a stream drainage network appears to be associated with the size of the contributing UCA. In headwater streams, brook trout were predicted to be present in beaver ponds 82.4 to 100 % of the time, where they are present within the downstream drainage and are unimpeded by natural barriers to upstream movement. UCA alone correctly classified beaver ponds having brook trout present or absent 82.4 to 92.9 % of the time. Variables that accounted for the greatest amount of residual variability in the models were water temperature, depth, pond area as well as TI values in the pond and surrounding wetland area. However, only mean pond depth improved the predictive power and classification efficiency of the models relative to UCA alone.

The relative abundance of brook trout in beaver ponds was not used in the development of models in favour of presence and absence data. Relative abundance may be mistakenly construed as an indicator of habitat quality (van Horne 1983, Bonn and Schroder 2001). Relatively higher or lower abundances of brook trout may be the result of factors other than habitat preference (van Horne 1983, Pulliam 1988), such as observational difficulties (e.g. catch rate), weather conditions (e.g. temperature) or seasonal variability in discharge (Schroder 2001). Furthermore, presence and absence data provides the necessary information for the prediction of brook trout distribution within the watershed.

Mean water temperature in beaver ponds with brook trout present were higher than in ponds where brook trout were absent. Inclusion of mean water temperature in the logistic model decreased predictive capacity to 73.0 % from 82.4 % using UCA alone. When beaver ponds with a mean temperature less than 11 °C were removed from the analyses to control for possible bias in capture efficiency of brook trout at low water temperature, temperature did not contribute in any of the subsequent models developed. I predicted that temperature would be associated with brook trout distribution since it appeared to be strongly associated with catch rate. Previous studies identified temperature as an important determinant of brook trout distribution (MacCrimmon and Campbell 1969, Witzel and MacCrimmon 1983, Power *et al.* 1999) which may also be useful for discriminating between potential brook trout streams and non-brook trout streams (Picard *et al.* 2003). However, if temperature influences brook trout catchability, models may erroneously predict brook trout presence or absence if this influence is ignored, leading to spurious conclusions. Areas of discrete thermal refugia, where brook trout could occupy water temperatures at or near their preferred thermal range, were observed in several ponds where the mean pond temperature was outside of their preferred thermal limits or above their critical thermal maxima. Since brook trout foraging may be suppressed or increased under certain environmental conditions, an alternative method of capture which does not rely on foraging is required to more accurately associate individual pond temperature and brook trout relative abundance. Only looking at maximum or mean temperatures in aquatic systems ignores the spatial heterogeneity in a stream environment and the influence of thermal refugia in distributing and structuring fish populations.

The variability of brook trout distribution relative to environmental conditions, seasonal movements, and annual fluctuations in abundance makes management decisions based on presence or abundance over short time periods derisory (Platts and Nelson 1988). The variability of local scale characteristics of beaver ponds indicates that they may not be useful for accurately predicting brook trout presence or abundance. Landscape scale characteristics, such as UCA, remain relatively constant over time, whereas local scale habitat characteristics, such as temperature, may vary greatly over short time periods (Smith and Kraft 2005). The inclusion of additional variables did not significantly improve the predictive capacity of logistic models and in some instances (*i.e.* temperature) may have led to spurious conclusions regarding brook trout distribution. The utility of landscape scale characteristics, in particular UCA, as predictors of brook trout presence and absence appears obvious; however, the linkage between local and landscape scale habitat characteristics and how they affect brook trout distribution remains unclear.

Brook trout in beaver ponds were significantly larger than those in the adjacent streams throughout the drainage system. Brook trout size also differed among streams and beaver ponds with different UCAs. Although sampling methods are not directly comparable, it is clear that larger brook trout were absent in streams in the study. Angling is likely biased towards sampling larger fish in beaver ponds. However, electrofishing was assumed to provide a representative sample of the size distribution of stream dwelling brook trout. Brook trout captured in beaver ponds were, on average, 105 mm and 72 g larger in beaver ponds than in their adjacent streams. Approximately 20% of the 369 brook trout caught in beaver ponds were larger than the largest brook trout captured in the stream survey.

Brook trout were larger in beaver ponds with smaller UCAs than those captured in beaver ponds with greater UCA downstream. Brook trout were, on average, 16 mm and 25 g and 21 mm and 20 g larger in 5 sq. km UCA than those captured in 10 and 30 sq. km UCA ponds respectively. Conversely, brook trout in the adjacent stream were smaller upstream than those captured in larger downstream areas. Brook trout in 30 sq. km UCA streams were 27 mm and 10 g and 27 mm and 12 g larger than in 10 and 5 sq. km UCA streams respectively. The number of brook trout captured in downstream ponds was greater than those captured in upstream ponds with smaller contributing UCA. The average number of brook trout caught per pond was 3.25 in 5 sq. km UCA ponds, 6.73 in 10 sq. km UCA ponds and 18.8 in 30 sq. km UCA ponds. Hughes and Reynolds (1994) and Hughes (1999) observed a similar relationship with Arctic grayling (*Thymallus arcticus*) size distribution in Alaskan streams. The authors hypothesized that Arctic grayling progressively increased in size upstream due to competitive interactions with longitudinal replacement and exclusion of relatively smaller fish. Larger grayling prefer headwater areas relative to downstream areas and actively move upstream in search of optimal habitat with the largest and most robust individuals occupying the most upstream areas.

In variable habitats, brook trout that are spatially isolated can produce locally adapted populations with habitat specific behavioural and functional characteristics (Stanford *et al.* 2005). For instance, Armstrong (unpublished data, pers. comm., 2005) found brook trout in small streams in the same area are small bodied, matured as early as 1 year of age, and lived no longer than 3 years. The restricted growth, lifespan, and early maturation is likely a life history strategy to exploit the low productivity and limited nutrients characteristic of northern Ontario headwater streams. Several studies indicate that growth rate is a critical life history characteristic influencing over-winter survival (Bustard and Narver 1975, Cunjak 1988, Cunjak 1996, Cunjak and Power 1987, Quinn and Peterson 1996, Schlosser 1998, Pollock *et al.* 2004) and there is potentially a lack of over-winter or over-summer habitat in addition to limited resource availability in small headwater streams in the study area. Drake and Taylor (1996) observed a negative relationship with increasing summer water temperature and brook trout growth beyond age 2. Hunt (1969) observed a positive relationship between size and over-winter survival in brook trout and attributed it to energetic efficiency at low temperatures. Juvenile coho salmon (*Oncorhynchus kistuch*) in beaver ponds were consistently larger and had a greater over-winter survival rate than juveniles in non-impounded streams (Bustard and Narver 1975, Swales *et al.* 1986, Swales and Levings 1989). Bustard and Narver (1975) reported over-wintering survival rates of juvenile coho salmon in beaver ponds were approximately double the average of the adjacent stream system. Thus, the limiting environmental conditions experienced in these streams may restrict brook trout growth-rate and survival to older age in the absence of beaver ponds.

My observation that fewer but larger brook trout captured in ponds with smaller UCAs than in ponds with larger UCAs may indicate that ponds function as an ecological release. The highly variable stream environment may constrain the upper limit for both growth and abundance due to temporal limitations in space, nutrients and basic physiochemical requirements such as temperature, oxygen, discharge, and depth. The creation of the pond may allow fish access to more abundant resources and space leading to increased survival and higher growth-rate. In general, fish abundance and diversity decreases with decreasing UCA. Correspondingly, there were far fewer brook trout captured from beaver ponds with small UCAs. In the absence of competition in ponds with smaller UCA and relatively fewer fish, brook trout are able to utilize the pond habitat to a greater degree, attaining significantly greater size relative to the brook trout in ponds with larger UCAs.

The relatively stable habitat conditions in the pond may allow brook trout to live to older ages and larger sizes. Aging structures collected from several brook trout captured suggest that brook trout in beaver ponds live longer than those in the adjacent stream. Brook trout sampled from ponds were estimated to range in age from 3 to 6 years. Stream dwelling brook trout sampled in the same area never exceeded 3 years of age (Armstrong, unpublished data). Stream dwelling brook trout rarely exceeded 200 mm and none exceeded 246 mm, whereas the smallest fish aged from the beaver ponds was 254 mm. The difference in brook trout size was not as great between ponds and streams with greater UCAs as it was between ponds and streams with smaller UCAs. Allen (1956) hypothesized that large beaver ponds in Wyoming generally yielded large brook trout due to the increased longevity of the fish as opposed to increased growth. These results may demonstrate a density-dependent effect in response to the ecological release when the pond was constructed possibly reflecting an association between brook trout density and size (Marchand and Boisclair 1998).

Size differences between pond and stream dwelling brook trout may also be related to foraging differences within the two habitats. For example, small bodied, stream dwelling brook trout generally feed on small invertebrates (Scott and Crossman 1973, Power 1980) whereas brook trout in beaver ponds may switch to piscivory, which could account for the larger fish observed in ponds. Rapid growth and larger size of fish in lakes and ponds relative to streams may also be a result of a switch to piscivory at smaller sizes (Mittlebach and Pearsson 1998, Keeley and Grant 2001). Rupp (1955) observed the stomach contents of brook trout in beaver ponds to have a high percentage of fish and that fish abundance was greater in beaver ponds than in the adjacent stream. Numerous brook trout captured in beaver ponds regurgitated small fish upon capture

(Pers. obs.) and the stomach contents of brook trout that died accidentally contained fish, mollusks and large invertebrates. In contrast, the stomach contents of brook trout captured in stream surveys that died contained primarily small, unidentifiable invertebrate larvae (Pers. obs).

Beaver ponds in small boreal forest stream drainages exist as a mosaic of temporally variable habitat patches (Schlosser and Kallemeyn 2000) that are prone to both abandonment and re-colonization. The characteristics of beaver pond influenced stream drainages demonstrate key assumptions of metapopulation and source-sink dynamics (Hanski 1982, Hanski 1991, Hanski 1997, Pulliam 1988). Metapopulations exist at relatively large spatial scales where individuals occasionally disperse amongst isolated subpopulations (Hanski 1982, Hanski 1991, Hanski 1997, Holt 1997). Beaver ponds may not only provide a source population to re-establish stream 'sink' populations, but also provide the re-colonization potential for unoccupied pond habitat patches within the drainage. Habitat heterogeneity at the landscape scale, as result of beaver pond establishment and abandonment may provide habitat patches permitting species persistence and enhanced local species richness and abundance (Hanski 1997, Holt 1997). Survival in relatively few, but varied, habitat patches, such as beaver ponds, allows a species to persist over a broader area and range of habitats making the population at a landscape scale more resilient to stochastic environmental perturbations (Holt 1997).

It appears that brook trout may not occupy all ponds within a drainage system. For example, brook trout were not captured in relatively shallow, inactive beaver ponds which may be indicative of fish abandoning ponds as the pond ages. Winkle *et al.* (1990) state the value of beaver ponds as habitat for brook trout likely decreases as the pond ages and are eventually abandoned by beavers. In older ponds, increased sedimentation and reduced space likely have a cumulative effect by decreasing the forage density and diversity (Hodkinson 1975b), decreasing the DO levels (Baxter 1977, Fox and Keast 1990, Devito and Dillon 1993), and increasing summer temperatures (McRae and Edwards 1994). Similarly, older or shallower ponds may increase brook trout susceptibility to extirpation caused by depth and space limitations due to relatively deeper ice formation in winter (Chisholm *et al.* 1987, Hall and Ehlinger 1989, Fox and Keast

1990, Cunjak 1996). During winter 2002-2003, Thunder Bay and the surrounding area, which includes the Mackenzie River watershed, experienced the longest period of continuous sub-zero temperatures without an appreciable accumulation of snowfall on record (Environment Canada Data). Sampling conducted during 2002-2003 winter season found that many shallow, headwater streams and ponds, froze completely; potentially extirpating brook trout from many areas within the drainage system. The impact of these relatively extreme environmental conditions may explain the absence of brook trout in several ponds where they were expected to be present.

Small boreal forest streams are continually subject to natural variation and stochastic environmental disturbance that alter instream and riparian habitat conditions (Roghair *et al.* 2002, Hakala 2003) and ultimately influence the distribution and abundance of brook trout. Brook trout distribution may be continuous throughout a stream drainage system; however, at certain times during the year, distribution may become patchy due to seasonal and spatial variation in habitat conditions. Stochastic environmental perturbation such as severe storms and flooding (Roghair *et al.* 2002, Hakala 2003, Hakala and Hartman 2004, Roghair and Dolloff 2005), drought, or particularly harsh winter temperatures (Cunjak 1988, Cunjak 1996) may even temporally extirpate brook trout from areas within the drainage. However, recent studies suggest brook trout movement is common and can be extensive within stream drainages (Riley *et al.* 1992, Gowan *et al.* 1994, Gowan and Fausch 1996a, Gowan and Fausch 2002, Curry *et al.* 2002) and that re-population of defaunated stream areas can be rapid (Phinney 1975, Adams 1999, Roghair *et al.* 2002, Hakala 2003). Adams (1999) stated that invasion of unoccupied upstream areas by brook trout in Colorado streams likely occurred in pulses during optimal conditions. In a study by Phinney (1975) brook trout from the unaffected upstream area of an experimental extirpation repopulated the defaunated area after one year. Furthermore, Reice *et al.* (1990) suggest brook trout may essentially be in a constant state of recovery from disturbance due to the highly variable nature of small stream conditions. Therefore, spatial variability, observed as patchy distribution and abundance, and temporally variable extirpation and reinvasion of habitat by brook trout may be ubiquitous in boreal streams.

Small boreal forest streams are also subject to highly variable flow conditions associated with seasonal precipitation patterns. It is possible that low or zero catch rates of brook trout in beaver ponds where they were known to be present may be indicative of movements in response to higher relative discharge. Coincidently, periods of higher relative discharge generally coincide with lower water temperatures in the spring and fall. This may allow brook trout to temporarily move into complementary or supplementary stream habitat areas which are generally inaccessible. White (1940) observed a positive relationship with increased stream flow and upstream movement of brook trout. Gowan and Fausch (1996a, 1996b, 2002) observed increased movement of small stream brook trout in Colorado associated with increased precipitation and discharge. Lawrie (unpublished data) and Armstrong (unpublished data) observed upstream and downstream movement of brook trout in the study area that occurred in pulses concomitant with significant precipitation and increased stream discharge. Similarly, MacIntosh (2001) and Mucha (2003) observed upstream and downstream movement of brook trout in Lake Superior tributaries in response to increased stream flow associated with high rainfall events. In this study, brook trout migrated out of beaver ponds, presumably to spawn, during brief periods of increased stream discharge during the fall of 2002. Even though only 8 brook trout were observed, their movement out of the ponds and subsequent capture in two-way weirs coincided with high rainfall events and a corresponding increase in stream discharge. Beaver dams may be semi-permeable barriers to brook trout movement that varies with stream flow conditions. Similarly, lack of habitat in streams during low flow conditions may spatially exclude brook trout, thus isolating them in adjacent beaver ponds.

No environment is constant over time; however, some are more stable or resilient to change than others. The unique conditions created by beaver ponds likely increases the available habitat for brook trout by providing additional foraging opportunities, (Hodkinson 1975b, Smith *et al.* 1991, Clifford *et al.* 1993), pool habitat (Chisholm *et al.* 1987, Johnson *et al.* 1992) and over-wintering areas (Winkle *et al.* 1990, Johnson *et al.* 1992), temporary refugia during adverse conditions (Hanson and Campbell 1963, Chisholm *et al.* 1987, Winkle *et al.* 1990, Johnson *et al.* 1992), as well as dampen the effects of stochastic environmental perturbation (Baxter 1977, Naiman *et al.* 1986, Naiman *et al.* 1988, Naiman *et al.* 1994, Woo and Waddington 1990) in the stream drainage. In addition, beaver ponds may also act as resilient source populations from which re-colonization of periodically defaunated streams areas can occur (Schlosser 1995a, Schlosser and Kallemeyn 2000).

It is clear that beaver ponds provide habitat for brook trout that is supplementary or complementary to the adjacent stream and that ponds likely provide year-round habitat for at least some portion of the population. Beaver ponds may possess the necessary habitat attributes allowing brook trout to persist at the periphery of their natural distribution in small boreal forest stream drainages. However, further research is required to better understand the linkage between local and landscape scale characteristics influencing brook trout habitat and the influence of beaver ponds on brook trout abundance and distribution. A watershed scale approach to brook trout management could be used to tie landscape scale processes identified in a geographic information system to the protection of brook trout habitat from potentially harmful land use practices. This research may contribute to a better understanding of the importance of beaver ponds and whether they possess attributes that distinguish them as good brook trout habitat within stream ecosystems, enabling resource managers to protect these areas from possible land use impacts.

5.0 References

Adams, S. B. 1999. Mechanisms limiting a vertebrate invasion: Brook trout in mountain streams of the northwestern USA. Ph.D. Thesis, University of Montana, 221 pp.

Allan, J. D. and L. Johnson. 1997. Catchment-scale analysis of aquatic ecosystems. Freshwater Biology 37(1): 107-111

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37:149-161.

Allen, G. H. 1956. Age and growth of the brook trout in a Wyoming beaver pond. Copeia 1956: 1-9.

Allison, P.D. 1999. Logistic Regression Using the SAS System, Theory and Application. SAS Institute Inc., Cary, NC.

Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in over-dispersed capture-recapture data. Ecology 75: 1780-1793

Armstrong, K. 2005. Ontario Ministry of Natural Resources, Northwest Science and information. Thunder Bay, Ont. pers comm.

Avery, E. L. 1992. Effects of removing beaver dams upon a northern Wisconsin brook trout stream. Wisconsin Department of Natural Resources, Bureau of Research, Fish Research Section, Study 406, Madison.

Bailey, R.M., and G.R. Smith. 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes basin. Canadian Journal of Fisheries and Aquatic Science 38:1539-1561.

Baldwin, N. S. 1948. A study of the speckled trout (*Salvelinus fontinalis*) in a pre-cambrian lake. M.A Thesis, Department of Zoology. University of Toronto.

Baldwin, N. W. 1956. Food consumption and growth of brook trout at different temperatures. Transactions of the American Fisheries Society 86: 323-328.

Barnes, D. M. 1997. Beaver dams: their site selection, establishment, and impact in a northern Ontario watershed. M. Sc. Thesis. Lakehead University, Thunder Bay, Ontario.

Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany 66:40-44.

Barnes, D. M., and A. U. Mallik. 1996. Use of woody plants in construction of beaver dams in northern Ontario. Canadian journal of Zoology 74: 1781-1786.

Baxter, R. M. 1977. Environmental effects of dams and impoundments. Annual Review of Ecology and Systematics 8: 255-283.

Baxter, C. V., C. A. Frissell, and F. R. Hauer. 1999. Geomorphology, logging roads and the distribution of bull trout (*Salvelinus confluentus*) spawning in a forested river basin: Implications for management and conservation. Transactions of the American Fisheries Society 128: 854-867.

Baxter C. V., and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57: 1470-1481.

Benfey, T. J., L. E. McCabe, and P. Pepin. 1997. Critical thermal maxima of diploid and triploid brook charr, *Salvelinus fontinalis*. Environmental Biology of Fishes 49: 259-264.

Beven, K. J. and M. J. Kirkby. 1979. A physically based variable contributing area model of basin hydrology. Hydrol. Sci. Bull: 24(1): 43-69.

Biro, P. A. 1998. Behavioral thermal regulation during summer by young-of-the-year brook trout in a lake. Transactions of the American Fisheries Society 127: 212-222.

Blanchfield, P. J., and M. S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 54: 747-756.

Bonn, A. and B. Schroder. 2001. Habitat models and their transfer for single and multi species groups: a case study of carabids in an alluvial forest. Ecography 24: 483-496.

Borwick, J., J. Buttle, and M. S. Ridgway. 2006. A topographic index approach for identifying groundwater habitat of young-of-the-year brook trout (*Salvelinus fontinalis*) in the land-lake ecotone. Canadian Journal of Fisheries and Aquatic Sciences 63: 239-253.

Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in Ontario streams. Transactions of the American Fisheries Society 115: 503-514.

Brunke, M., and T. Gosner. 1997. The ecological significance of exchange processes between rivers and groundwater. Freshwater Biology 37: 1-33.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: a practical information-theortic approach, 2nd edition. Springer-Verlag, NewYork.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32: 667-680.

Buttle, J. M. 2002. Rethinking the donut: the case for hydrologically relevant buffer zones. Hydrological Processes 16: 3093-3096.

Buttle, J. M., and R. A. Metcalfe. 2000. Boreal forest disturbance and streamflow response, northeastern Ontario. Canadian Journal of Fisheries and Aquatic Sciences 57 (Suppl. 2): 5-18.

Buttle, J. M., I. F. Creed, and J. W. Pomeroy. 2000. Advances in Canadian Forest Hydrology. Hydrological Processes 14: 1551-1578.

Buttle, J. M., P. W. Hazlett, C. D. Murray, I. F. Creed, D. S. Jefferies and R Semkin. 2001. Prediction of groundwater characteristics in forested and harvested basins during spring snowmelt using a topographic index. Hydrologic Processess 15: 3389-3407.

Carlson, A. R., and A. G. Hale. 1973. Early maturation of brook trout in the laboratory. Prog. Fish-Culture 35: 150-153.

Challen, L. 2001. Impacts of Timber Harvesting on Stream Macroinvertebrate Communities at Different Spatial Scales in Ontario's Boreal Forest. M.Sc. thesis, Lakehead University, 85 pp.

Cherry, D. S., K. L. Dickson and J. Cairns. 1975. Temperatures selected and avoided by fish at various acclimation temperatures. Journal of the Fisheries Research Board of Canada 32(4): 485-491.

Cherry, D. S., K. L. Dickson, J. Cairns and J. R. Stauffer. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. Journal of the Fisheries Research Board of Canada 34: 239-246.

Chisholm, I. M. 1985. Winter stream conditions and brook trout habitat use on the Snowy Range, Wyoming. Master's Thesis. University of Wyoming, Laramie.

Chisholm, I. M., W. A. Hubert, and T. A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society 116: 176-184.

Clifford, H. F., G. M. Wiley, and R. J. Casey. 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. Canadian Journal of Zoology 71: 1439-1447.

Collen, P., and R. J. Gibson. 2001. The general ecology of beavers (*Castor spp.*), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. Reviews in Fish Biology and Fisheries 10: 439-461.

Creaser, C. W. 1930. Relative importance of hydrogen-ion concentration, temperature, dissolved oxygen, and carbon dioxide tension on habitat selection by brook trout. Ecology 11:246-262.

Creque, S. M., E. S. Rutherford, and T. G. Zorn. 2005. Use of GIS-derived landscape-scale habitat features to explain spatial patterns of fish density in Michigan rivers. North American Journal of Fisheries Management 25: 1411-1425.

Cunjak, R. A. 1988. Physiological consequences of over-wintering in streams: the cost of acclimatization. Canadian Journal of Fisheries and Aquatic Sciences 45: 443-452.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land use activities. Canadian Journal of Fisheries and Aquatic Sciences 53 (Suppl. 1): 267-282.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 43: 1970-1980.

Cunjak, R. A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology 31: 493-511.

Cunjak, R. A., R. A. Curry, and G. Power. 1987. Seasonal energy budget of brook trout in streams: Implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116(6): 817-828.

Curry, R. A., and D. L. G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1733-1740.

Curry, R. A., D. L. G. Noakes, and G. E. Morgan. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1741-1749.

Curry, R. A., and K. J. Devito. 1996. Hydrogeology of brook trout (*Salvelinus fontinalis*) spawning and incubation habitats: implications for forestry and land use development. Canadian Journal of Forest Research 26: 767- 772.

Curry, R. A., C. Brady, D. L. G. Noakes, and R. G. Danzmann. 1997. The use of small streams by young brook charr (*Salvelinus fontinalis*) spawned in a lake. Transactions of the American Fisheries Society 126: 77-83.

Curry, R. A., D. Sparks, and J. Van De Sande. 2002. Spatial and temporal movements of a riverine brook trout population. Transactions of the American Fisheries Society 131: 551-560.

Devito, K. J., and P. J. Dillon. 1993. Importance of runoff and winter anoxia to the P and N dynamics of a beaver pond. Canadian Journal of Fisheries and Aquatic Sciences 50: 2222-2234.

Devito, K. J., A. R. Hill and N. Roulet. 1996. Groundwater-surface water interactions in headwater forested wetlands of the Canadian Shield. Journal of Hydrology 181: 127-147.

Drake, M. T., and W. W. Taylor. 1996. Influence of spring and summer water temperature on brook charr, *Salvelinus fontinalis*, growth and age structure in the Ford River, Michigan. Environmental Biology of Fishes 45: 41-51.

Dunning, J. B., Danielson, B. J., and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52: 483-498.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of predicting errors in conservation presence/absence models. Environmental Conservation 24: 38-49.

Fox, M. G., and A. Keast. 1990. Effects of winterkill on population structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. Canadian Journal of Zoology 68: 2489-2498.

Francis, M. M., R. J. Naiman, and J. M. Melillo. 1985. Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*). Hydrobiologia 121: 193-202.

Franken, R. J. M., R. G. Storey, and D. D. Williams. 2001. Biological, chemical and physical characteristics of downwelling and upwelling zones in the hyporheic zone of a north-temperate stream. Hydrobiologia 444: 183-195.

Fraser, J. M. 1982. An atypical brook charr (*Salvelinus fontinalis*) spawning area. Environmental Biology of Fishes 7: 385-388.

Freeze, R. A., and J. A. Cherry. 1979. Groundwater. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Fry, F. E. J., J. S. Hart, and K. F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). University of Toronto Studies, Biological Series 54. Publication of the Ontario Fisheries Research Laboratory 66: 9-35.

Gard, R. 1961. Effects of beaver on trout in Sagehen Creek, California. Journal of Wildlife Management 25: 221-242.

Garrett, J. W., and D. H. Bennett. 1995. Seasonal movements of adult brown trout relative to temperature in a coolwater reservoir. North American Journal of Fisheries Management 15: 480-487.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Reviews of the Cambridge Philosophical Society. 34: 221-242.

Gibson, R. J. 1966. Some factors influencing the distribution of brook trout and young Atlantic salmon. Journal of the Fisheries Research Board of Canada 23: 1977-1980.

Gomi, T., R. C. Sidle and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. BioScience 52: 905-916.

Gowan, G. C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51: 2626-2637.

Gowan G. C., and K. D. Fausch. 1996a. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences. 53: 1370-1381.

Gowan, C. and K. D. Fausch. 1996b. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6: 931-946.

Gowan G. C., and K. D. Fausch. 2002. Why do foraging stream salmonids move during summer? Environmental Biology of Fishes 64: 139-153.

Grande, M. and S. Andersen. 1991. Critical thermal maxima for young salmonids. Journal of Freshwater Ecology 6: 275-279.

Grimm, N. B., and S. G. Fisher. 1984. Exchange between interstitial and surface water: implications for stream metabolism and nutrient cycling. Hydrobiologia 111: 219-228.

Hagglund, A., and G. Sjoberg. 1999. Effects of beaver dams on the fish fauna of forest streams. Forest Ecology and Management 115: 259-266.

Hakala, J. P. 2003. Factors Influencing Brook Trout (*Salvelinus fontinalis*) Abundance in Forested Headwater Streams with Emphasis on Fine Sediment, Master's Thesis, West Virginia University

Hakala, J. P., and K. J. Hartman. 2004. Drought effect on stream morphology and brook trout(*Salvelinus fontinalis*) populations in forested headwater streams. Hydobiologia 515: 203-213.

Hall, D. J., and T. J. Ehlinger. 1989. Perturbation, planktivory, and pelagic community structure: the consequences of winterkill in a small lake. Canadian Journal of Fisheries and Aquatic Sciences 46: 2203-2209.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210-221.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models, and observations. Biological Journal of the Linnean Society 42: 17-38.

Hanski, I. A. 1997. From Metapopulation Dynamics to Community Structure: Some Consequences of Spatial Heterogeneity. In: Hanski, I. A., and M. E. Gilpin, (Eds.). Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, San Diego, pp. 149-165.

Hanson, W. D., and R. S. Campbell. 1963. The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a North Missouri stream. American Midland Naturalist 69: 136-149.

Harris, A. G., S. C. McMurray, P. W. C. Uhlig, J. K. Jeglum, R. F. Foster and G. D. Racey. 1996. Field guide to the wetland ecosystem classification for northwestern Ontario. Ontario Ministry of Natural Resources. NWST. Thunder Bay, Ont. Fild Guide FG-01, 74p. + Append.

Hartviksen, C. and W. Momot. 1989. Fishes of the Thunder Bay Area on Ontario: A Guide for Identifying and Locating the Local Fish Fauna. Wildwood Publications, Thunder Bay, Ont. 71 pp.

Hendricks, S. P., and D. S. White. 1991. Physiochemical patterns within a hyporheic zone of a northern Michigan river, with comments on surface water patterns. Canadian Journal of Fisheries and Aquatic Science 48: 1645-1654.

Hodkinson, I. D. 1975a. Energy flow and organic matter decomposition in an abandoned beaver pond ecosystem. Oecologia 21: 131-139.

Hodkinson, I. D. 1975b. A community analysis of the benthic insect fauna of an abandoned beaver pond. Journal of Animal Ecology 44: 533-551.

Hokanson, K. E. F., J. H. McCormick, B. R. Jones and J. H. Tucker. 1973. Thermal requirements for maturation, spawning, and embryo survival of the brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Resources Board of Canada 30: 975-984.

Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. In: Metapopulation Biology. Hanski, I. A., and M. E. Gilpin, (Eds.), Academic Press, San Diego, pp. 149-165.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression, 2nd edition. John Wiley& Sons, Inc., New York, USA.

Hughes, N. F. 1999. Population processes responsible for larger-fish-upstream distribution patterns of Arctic grayling (*Thymallus arcticus*) in interior Alaska runoff rivers. Canadian Journal of Fisheries and Aquatic Science 56: 2292-2299.

Hughes, N. F., and J. B. Reynolds. 1994. Why do of Arctic grayling (*Thymallus arcticus*) get bigger as you go upstream? Canadian Journal of Fisheries and Aquatic Science 51: 2154-2163.

Hunt, R. L. 1969. Over-winter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board of Canada 26: 1473-1483.

Hurvich, C. M. and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika, 78: 297-307.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology 74: 673-684.

Hutchings, J. A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. Ecoscience 3: 25-32.

Hynes, H. B. N. 1983. Groundwater and stream ecology. Hydrobiologia 100: 93-99.

Johnson, S. L., F. J. Rahel, and W. A. Hubert. 1992. Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. North American Journal of Fisheries Management 12: 118-124.

Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorpholgy. Landscape Ecology 1: 47-57.

Johnston, C. A., and R. J. Naiman. 1990. Browse selection by beaver: effect on riparian forest composition. Canadian Journal of Forest Resources. 20: 1036-1043.

Klotz, R. L. 1998. Influence of beaver ponds on the phosphorus concentration of stream water. Canadian Journal of Fisheries and Aquatic Sciences 55:1228-1235.

Knudsen, G. J. 1962. Relationships of beaver to forests, trout and wildlife in Wisconsin. Wisconsin Conservation Department Technical Bulletin 25.

Kocovsky, P, M. and R. F. Carline. 2006. Influence of landscape-scale factors limiting brook trout populations in Pennsylvania streams. Transactions of the American Fisheries Society 135: 76-88.

Labbe, T. R. and K. D. Fausch. 2000. Dynamics of Intermittent Stream Habitat Regulate Persistence of a Threatened Fish at Multiple Scales. Ecological Applications 10(6): 1774-1791.

Lackey, R. T. 1970. Seasonal depth distributions of landlocked Atlantic salmon, brook trout, landlocked alewives, and American smelt in a small lake. Journal of the Fisheries Research Board of Canada 27: 1656-1661.

Lawrence, W. H. 1952. Evidence of the age of beaver ponds. Journal of Wildlife Management.16: 69-79.

Leidholt-Brunner, K., D. E. Hibbs, and W. C. McComb. 1992. Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two costal Oregon streams. Northwest Science 66: 218-223.

Lindstrom, J. W. and W. A. Hubert. 2004. Ice processes affect habitat use and movements of adult cutthroat and brook trout in a Wyoming foothills stream. North American Journal of Fisheries Management 24: 1341-1352.

MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 26: 1699-1725.

MacIntosh, K. 2001. Habitat use and movement by brook trout (*Salvelinus fontinalis*) and Rainbow Trout (*Oncorhynchus mykiss*) in three tributaries and Nipigon Bay, Lake Superior. M.Sc. thesis, Lakehead University, 104 pp.

Marchand, F., and D. Boisclair. 1998. Influence of fish density on the energy allocation pattern of juvenile brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 55: 796-805.

Margolis, B. E., M. S. Castro, and R. L. Raesly. 2001. The impact of beaver impoundments on the water chemistry of two Appalachian streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 2271-2283.

Marod, S. M. 1995. The influence of temperature and discharge on movement patterns of brook trout (*Salvelinus fontinalis*) in the Ford River, Dickinson County, Michigan. M. S. thesis, Michigan State University, 95 pp.

Matthews, W. J. and H. W. Robinson. 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the interior highlands of Arkansas. American Midland Naturalist 139: 1-19.

Mazerolle, M. J. 2004. Mouvements et reproduction des amphibiens en tourbières perturbées. Ph.D thesis. Université Laval. Faculté de Forestrerie et de Géomatique.

McComb, W. C., Sedell, J. R., and T. D. Buchholz. 1990. Dam site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50: 273-281

McDowell, D. M., and R. J. Naiman. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). Oecologia 68: 481-489.

McRae, G., and C. J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. Transactions of the American Fisheries Society 123: 641-656.

Meisner, J. D. 1990. Potential loss of thermal habitat for brook trout due to climatic warming in two southern Ontario Canada streams. Transactions of the American Fisheries Society 119: 282-291.

Menard, S. 1995. Applied Logistic Regression Analysis. Thousand Oaks, CA. Sage Publications, Inc.

Mittlebach, G, G, and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55: 1454-1465.

Mollard, D. G., and J. D. Mollard. 1981a. Kaministikwia Area (NTS 52A/NW), District of Thunder Bay; Ontario Geological Survey, Northern Ontario Engineering Geology Terrain Study 57, 27 pp. Accompanied by Map 5045, scale 1:100 000.

Mollard, D. G., and J. D. Mollard. 1981b. Black Bay Area (NTS 52A/NE and part of NTS52A/SE), District of Thunder Bay; Ontario Geological Survey, Northern Ontario Engineering Geology Terrain Study 58, 30 pp. Accompanied by Map 5046, scale 1:100 000.

Moore, C. 2000. http://www.arches.uga.edu/~ctmoore/prof/CVLRnotes.html

Mucha, J. M. 2003. Habitat use, movement patterns, and home ranges of coaster brook trout in Nipigon Bay, Lake Superior. M.Sc. thesis, Lakehead University, 81 pp.

Murtaugh, P. A. 1996. The statistical evaluation of ecological indicators. Ecological Applications 6: 132-139.

Naiman, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watershed. Ecological Monographs 53: 73-94.

Naiman, R. J, J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67: 1254-1269.

Naiman, R. J., C. A. Johnston, and J. C. Kelly. 1988. Alteration of North American streams by beaver. Bioscience 38: 753-762.

Naiman, R. J., G. Pinay, C. A. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75: 905-921.

Olsen, R. A., J. D. Winter, D. C. Nettles and J. M. Haynes. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario, USA. Transactions of the American Fisheries Society 117: 552-559.

Osborne, L. L. and M. J. Wiley. 1992. Influence of tributary spatial position on the structure of warmwater fish communities. Canadian Journal of Fisheries and Aquatic Sciences 49: 671-681.

Pearce, J. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modeling 133: 225-245.

Peterson, R. H. 1973. Temperature selection of Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) as influenced by various chlorinated hydrocarbons. Journal of the Fisheries Research Board of Canada 30: 1091-1097.

Peterson, J. T. and C. F. Rabeni. 2001. Evaluating the physical characteristics of channel units in an Ozark stream. Transactions of the American Fisheries Society 130: 898-910.

Phinney, D. E. 1975. Repopulation of an eradicated stream section by brook trout. Transactions of the American Fisheries Society 104: 685-687.

Picard, C. R., M. A. Bozek and W. T. Momot. 2003. Effectiveness of using summer thermal indices to classify and protect brook trout streams in northern Ontario. North American Journal of Fisheries Management 23: 206-215.

Pinder L. C. V. and I. S. Farr. 1977. Biological surveillance of water quality. Temporal and spatial variation in the macroinvertebrate fauna of the River Frome, a Dorset chalk stream. Archiv Fur Hydrobiologie 109:321-331

Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross, and R. M. Hughes. 1989. Rapid bioassessement protocols for use in streams and rivers: benthic macroinvertebrates and fish. Assessment and Water Protection Division, U.S. Environmental Protection Agency, Report EPA/440/4-89- 001. Washington, D.C.

Platts, W. S., and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluations. North American Journal of Fisheries Management 8: 333-345.

Pollock, M. M., G. R. Pess, T. J. Beechie, and D. R. Montgomery. 2004. The importance of beaver ponds to coho salmon production in the Stillaguamish River basin, Washington, USA. North American Journal of Fisheries Management 24: 749-760.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. In Charrs, Salmonid fishes of the Genus *Salvelinus*. E. K. Balon, Dr W. Junk, Publishers. pp. 141-203.

Power, G. 2002. Charrs, glaciations and seasonal ice. Environmental Biology of Fish 64: 17-35

Power, G., R. S. Brown, and J. G. Imhof. 1999. Groundwater and fish: insights from North America. Hydrological Processes 13: 401-422.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme and M. J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7: 503-524.

Pulliam, H. R. 1988. Sources, sinks and population regulation. American Naturalist 132: 652-661.

Pye, E. G. 1969. Geology and Scenery, North Shore of Lake Superior. Ont. Dept. Mines, Geol. Guide Book 2. 144 pp.

Quinn, T. P. and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53: 1555-1564.

Quinn, P., K. Beven, P. Chevallier, and O. Planchon. 1991. The prediction of hillslope flow paths for distributed hydrogeological modelling using digital terrain models. Hydrological Processess 5: 59-80

Raleigh, R. F. 1982. Habitat suitability index models: brook trout. U. S. Fish and Wildlife Service FWS-OBS-82/10.24.

Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14: 647-659.

Rempel, L. L. and D. G. Smith. 1998. Postglacial fish dispersal from the Mississippi refuge to the Mackenzie River basin. Canadian Journal of Fisheries and Aquatic Sciences 55: 893-899.

Reynolds, W. W., and M. E. Casterlin. 1979. Behavioural thermoregulation and the 'Final Preferendum' paradigm. American Zoologist 19: 211-224.

Richards, C., L. B. Johnson and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 295-311.

Ricker, W. E. 1934. Studies of speckled trout (*Salvelinus fontinalis*) in Ontario. Ontario Fisheries Research Laboratory Publications 44: 69-110.

Riley, S. C., K. D. Fausch and C. Gowan. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1: 112-122.

Roghair, C. N. and C. A. Dolloff. 2005. Brook trout movement during and after recolonization of a naturally defaunated stream reach. North American Journal of Fisheries Management. 25: 777-784.

Roghair, C. N., C. A. Dolloff, and M. K. Underwood. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society 131: 718-730.

Ruedemann, R., and W. J. Schoonmaker. 1938. Beaver-dams as geologic agents. Science 88: 523-525.

Rupp, R. S. 1955. Beaver-trout relationship in the headwaters of Sunkhaze stream, Maine. Transactions of the American Fisheries Society 84: 75-85.

Rutherford, W. H. 1955. Wildlife and environmental relationships of beavers in Colorado forests. Journal of Forestry 53: 803-806.

Ryder, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Transactions of the American Fisheries Society 94: 214-218.

Schlosser, I. J., 1987, A conceptual framework for fish communities in small warmwater streams, pp. 17-24. *In*: W. J. Matthews & D. C. Heins (ed.), Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41: 704-712.

Schlosser, I. J. 1995a. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia. 303: 71-81.

Schlosser, I. J. 1995b. Dispersal, boundary processes, and trophic level interactions in streams adjacent to beaver ponds. Ecology 76: 908-925.

Schlosser, I. J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. Oecologia 113: 260-268.

Schlosser, I. J. and L. W. Kallemeyn. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. Ecology 81: 1371-1382.

Schroder, B. 2004. http://brandenburg.geoecology.unipotsdam.de/users/schroeder/download.html

Scott, W. B. and E. J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin of the Fisheries Research Board of Canada 184: 966p.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. Environmental Management 14: 711-724.

Shtatland, E. S., M. B. Barton, and E. M. Cain. 2001. The perils of stepwise logistic regression and how to escape them using information criteria and the output delivery system. SUGI '26 Proceeding, Paper 222-26, Cary, NC: SAS Institute, Inc.

Shtatland, E. S., K. Kleinman, and E. M. Cain. 2003. Stepwise methods in using SAS PROC LOGISTIC and SAS ENTERPRISE MINER for prediction. SUGI '28 Proceeding, Paper 258-28, Cary, NC: SAS Institute, Inc.

Shtatland, E. S., K. Kleinman, and E. M. Cain. 2004. A new strategy of model building in PROC LOGISTIC with automatic variable selection, validation shrinkage and model averaging. SUGI '29 Proceeding, Paper 191-29, Cary, NC: SAS Institute, Inc.

Simonoff, J. S. 2000. http://www.biostat.wustl.edu/archives/html/s-news/2000-11/msg00184.html

Sims, R. A., W. D. Towill, K. A. Baldwin, P. Uhlig and G. M. Wickware. 1997. Field guide to the forested ecosystem classification for northwestern Ontario. Ont. Min. Natur. Resour., Northwest Sci. & Technol. Thunder Bay, Ont. Field Guide FG-03. 176 pp.

Smith, T. A. and C. E. Kraft. 2005. Steam fish assemblages in relation to landscape position and local habitat variables. Transactions of the American Fisheries Society 134: 430-440.

Smith, M. E., C. T. Driscoll, B. J. Wyskowski, C. M. Brooks, and C. C. Cosentini. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. Canadian Journal of Zoology 69: 55-61.

Smock, L. A., G. M. Metzler, and J. E. Gladden. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. Ecology 70: 764-775.

Snodgrass, J. W. 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, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79: 928-942.

Snodgrass, J. W., and G. K. Meffe. 1999. Habitat use and temporal dynamics of blackwater stream fishes in and adjacent to beaver ponds. Copeia 3: 628-639.

Sprules, W. M. 1940. The effect of a beaver dam on the insect fauna of a trout stream. Transactions of the American Fisheries Society 70: 236-248.

Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. Verh. Internat. Verein. Limnol. 29: 123-136.

Swales, S., and C. D. Levings. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46: 232-242.

Swales, S., R. B. Lauzier, and C. D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. Canadian journal of Fisheries and Aquatic Sciences 64: 1506-1514.

Swets, J. A. 1986. Indices of discrimination or diagnostic accuracy: their ROCs and implied models. Psych. Bull. 99: 100-117.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science 240: 1285-1293.

Tonn, W. M. and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149-1166.

Tucker S., and J.B. Rasmussen. 1999. Using radiocesium (137Cs) to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) in the field. Canadian Journal of Fisheries and Aquatic Sciences 56: 875-887.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Vallett, H. M., C. N. Dahm, M. E. Campana, J. A. Morrice, M. A. Baker, and C. S. Fellows. 1997. Hydrologic influences on groundwater-surface water ecotones: heterogeneity in nutrient composition and retention. Journal of the North American Benthological Society 16: 239-247.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Wang, Z. 2000. Model selection using Akaike information criterion. STATA Technical Bulletin, 54: 47-49.

Warren, M. L. and M. G. Pardew. 1998. Road crossings as barriers to small-stream fish movement. Transactions of the American Fisheries Society 127: 637-644.

White, H. C. 1940. Life history of sea-running brook trout (*Salvelinus fontinalis*) of Moser River, N. S. Journal of the Fisheries Research Board of Canada 5: 176-186.

White, D. S. 1990. Biological relationships to convective flow patterns within stream beds. Hydrobiologia 196: 149-158.

Wickware, G. M. and C. D. A. Rubec. 1989. Ecoregions of Ontario, Ecological Land Classification Series, No. 26. Sustainable Development Branch, Environment Canada. Ottawa, Ontario.

Wilder, D. G. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* Mitchell). Journal of the Fisheries Research Board of Canada 9: 169-203.

Wilson, C. C. and P. D. N. Hebert. 1996. Phylogeographic origins of lake trout (*Salvelinus namaycush*) in eastern North America. Canadian Journal of Fisheries and Aquatic Sciences 53: 2764- 2775.

Wilson, C. C. and N. E. Mandrak. 2004. History and evolution of lake trout in Shield lakes: past and future challenges. In: Boreal Shield Watersheds: Lake Trout Ecosystems in a Changing Environment. J. M. Gunn, R. J. Steedman and R. A. Ryder (eds.) pp. 21-35.

Winkle, P. L., W. A. Hubert, and F. J. Rahel. 1990. Relations between brook trout standing stocks and habitat features in beaver ponds, southeastern Wyoming. North American Journal of Fisheries Management 10: 72-79.

Witzel, L. D., and H. R. MacCrimmon. 1983. Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. Canadian Journal of Zoology 61: 1783-1792.

Woo, M. K. and J. M. Waddington. 1990. Effects of beaver dams on subarctic wetland hydrology. Arctic 43: 223-230.

Zoltai, S. C. 1961. Glacial History of Part of Northwestern Ontario. Proceedings of the Geological Association of Canada. 13: 61 - 83.

Zoltai, S. C. 1963. Glacial features of the Canadian Lakehead area. Canadian Geographer VII (3): 101-115.

Zoltai, S. C. 1965. Glacial features of the Quetico-Nipigon area, Ontario. Canadian Journal of Earth Sciences 2: 247-269.

Zoltai, S. C. 1967. Glacial features of the North-Central Lake Superior Region, Ontario. Can. J.Earth Sci. 4: 515-528.