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**SEASONAL MOVEMENT AND HABITAT USE OF  
WILD BROOK TROUT (*SALVELINUS FONTINALIS*)**

A Thesis in

Wildlife and Fisheries Science

by

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## ABSTRACT

Eastern brook trout *Salvelinus fontinalis* populations face a myriad of threats throughout the species' native range in the eastern United States. Anthropogenic alterations to the landscape, in particular, have the potential to degrade and fragment brook trout habitat. Therefore, understanding wild brook trout movement patterns and habitat requirements is essential for conserving existing populations, and for restoring habitats that no longer support self-sustaining populations. Radio biotelemetry is one approach commonly used to quantify fish movements and habitat use. Until recently, however, telemetry research targeting small stream-dwelling salmonids has been limited by the relatively large size of transmitters and short battery life (i.e., only larger fish were tagged and tracked over relatively short time frames). Recent advances in radio biotelemetry allows for smaller fishes to be tracked for longer time periods (i.e., for months rather than weeks), and thus provides the opportunity to gain additional insight into the ecology of stream-dwelling salmonids. To address uncertainties related to wild eastern brook trout movements and habitat use, I radio-tagged and tracked 36 fish in a headwater stream system in central Pennsylvania during the fall and early winter of 2010 – 2011. I used generalized additive mixed models to identify relationships between brook trout movement and covariates. I also surveyed thalweg profiles of the study area to quantify available stream habitat and used discrete choice models with random effects to evaluate habitat use, a novel modeling approach for fish habitat use studies.

There was a large amount of among-fish variability in movement patterns; however, most of the activity was associated with the onset of the spawning season (late September – early October), including several long-distance ( $> 1$  km) movements. Some of the among-fish variability could be explained by the size of individual fish, because the larger main-stem brook

trout were more active, on average. In addition to a positive relationship between fish size and movement, modeling results also indicated that movement was positively correlated with higher stream flow. However, these effects of fish size and stream flow stage varied seasonally.

Although movement during the spawning season was variable, little movement was observed across all brook trout once stream temperatures dropped below 7 °C in early December. Lastly, the larger brook trout that were tagged in the main-stem utilized lower regions of only one of the tributaries during spawning season, despite other tributaries being nearby and accessible. These results suggest that not all tributaries provided equal-quality habitat and individual tributaries may contribute disproportionately to reproduction and sustainability of brook trout in this system.

Although there was a general preference for pool versus non-pool habitats, there was a large amount of among-fish heterogeneity in habitat use. Specifically, there was variability in preference for intermediate (0.26 – 0.44 m deep) and deep (0.44 – 1.06 m deep) residual pools, while all fish showed a similar selection for shallow (0.10 – 0.26 m) residual pools compared to non-pool habitats. In addition, habitat use was nonlinear, both seasonally and in relation to the length of specific habitat types. Seasonally, there was a selection for shallow residual pools during spawning season, followed by a selection for deep residual pools as winter approached. This nonlinear seasonal selection likely reflected brook trout spawning and overwintering behavior. Brook trout were also found to show a threshold-effect for pool use with respect to pool length: habitat use for pools tended to increase as the average length of pools increased up to a point and then use declined rapidly for very long pool habitats.

The heterogeneity and nonlinear dynamics of movement and habitat use of the wild brook trout observed in this study underscores two important points: (1) linear models may not provide an accurate description of movement and habitat use, which can have implications for

management, and (2) the importance of maintaining stream connectivity when managing self-sustaining populations. These results also demonstrate the importance of diversity, in terms of the physical stream environment, when protecting or restoring instream habitat. A way of preserving stream connectivity and providing quality instream habitat is to use a watershed approach when managing resident brook trout populations.

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## Chapter 1

### INTRODUCTION

The eastern brook trout *Salvelinus fontinalis*, a coldwater fish species native to eastern North America, has a southern range that begins in northern Georgia and extends northward along the Appalachian Mountains and across the Great Lakes region through a large portion of Canada to the Arctic Circle (MacCrimmon et al. 1971). Regionally, brook trout have ecological, social, and economic importance; however, populations are declining over much of their native range. Declines have largely been attributed to degradation of instream habitat, loss of vegetated riparian areas and surrounding forested watersheds, and the introduction of the nonnative salmonids, specifically brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* (EBTJV 2008). As a result of habitat loss and fragmentation and nonnative species, many remaining eastern brook trout populations are isolated and restricted to headwater stream systems (EBTJV 2008; Hudy 2008). The loss of stream connectivity and habitat corridors further increases the risk of losing these populations to environmental stressors and stochastic events by preventing recolonization (Letcher et al. 2007; Roghair and Dolloff 2005) and reducing genetic diversity (Zwick 1992; Amelio et al. 2008). In addition, potential thermal and hydrological changes resulting from global climate change will further threaten brook trout populations and create additional challenges for conservation and management (Eaton and Scheller 1996; Clark et al. 2001; Fausch et al. 2002).

*Brook trout in Pennsylvania.* – Brook trout can live in a variety of habitats and have variable life-histories. For example, there are potamodromous (migrating within freshwater) “coaster” populations in Lake Superior that utilize nearby streams for spawning (Amelio et al. 2008;

Mucha and Mackereth 2008) and anadromous “sea-run” or “salter” populations that spawn in inland streams in eastern Canada and the northeast United States (Jones et al. 1997; Doucett et al. 1999). In Pennsylvania, however, brook trout are resident (i.e., non-migratory) fishes that grow approximately 200-300 mm in length (Detar 2007). Brook trout populations in Pennsylvania are relatively short-lived, with a life-span of three to four years, becoming sexually mature at age 1 or age 2 (Detar 2007). Although brook trout conservation is important throughout its native range, management of brook trout populations in Pennsylvania is of particular interest due to their ecological and recreational importance. In recent years, concerns over the status of wild brook trout populations resulted in the species being added to Pennsylvania’s Wildlife Action Plan. In fact, Hudy et al. (2008) evaluated brook trout habitat and distribution in the eastern United States and determined that Pennsylvania was one of the areas of greatest concern. At one time brook trout likely inhabited nearly every coldwater stream in Pennsylvania (MacCrimmon and Campbell 1969); however, brook trout populations in Pennsylvania, like populations throughout much of its native range, are now fragmented and generally limited to upper headwater regions of stream systems (EBTJV 2008).

*Brook trout movement and habitat use.* - An important aspect of eastern brook trout ecology that lacks a complete understanding is seasonal movement dynamics and habitat use. In particular, there is a paucity of information on how movement and habitat use vary over space and time, and there is uncertainty with respect to how much heterogeneity exists in movement and habitat use among populations and among individuals within populations. Understanding movement dynamics and habitat requirements is essential for brook trout conservation and management, especially when considering that many of the current threats to brook trout populations (e.g.,

natural gas exploration and extraction) have the ability to affect both movement potential within and among populations, as well as instream habitat. Incomplete information pertaining to the ecology and life history of a fish species can lead to erroneous conclusions about population dynamics, genetic isolation of populations, and success of fisheries management activities (Gowan et al. 1994; Riley and Fausch 1995); whereas, an understanding of movement dynamics and habitat selection can identify conditions that facilitate a species' establishment, persistence, and dispersal (DeGrandchamp et al. 2008). Specifically, knowledge of movement tendencies of brook trout combined with fish-habitat relationships can be used to help (1) direct conservation efforts to areas with habitat conditions deemed necessary for sustaining brook trout populations, (2) assist with restoration programs by providing targets for stream restoration efforts, and (3) predict the consequences of potential habitat changes and management actions (Scheuerell et al. 2006; Knudby et al. 2010). It is also important to consider the influence of the physical stream habitat on fish movement and habitat use tendencies, as it has been established that it shapes the environment in which aquatic organisms evolve, adapt, and interact (Southwood 1977; Gorman and Karr 1978; Zwick 1992).

Additionally, there is some contradiction in the literature as to the potential mobility of stream-dwelling brook trout (i.e., how far might an individual move during its lifespan?). Conventional stream ecology has generally viewed resident stream fishes as sedentary species that spend a majority of their lives in reaches of less than 50 m (Bangham and Bennington 1939; Gerking 1959; Hill and Grossman 1987). This perception of limited mobility (often referred to as the "restricted movement paradigm"; Gowan et al. 1994) has also been applied to resident brook trout (Leclerc and Power 1980). However, there are more recent studies that have documented movements by stream-dwelling brook trout of several kilometers (Gowan and Fausch 1996;

Roghair and Dolloff 2005), with reports of movements up to 17 km (Rodríguez 2002). This contradiction may be due to sampling methods and/or to technological limitations in studying smaller stream fishes.

Although research has been devoted to understanding eastern brook trout ecology (e.g., Hokanson et al. 1973; Fausch and White 1981; Cunjak and Green 1983; Dewald and Wilzbach 1992; Marschall and Crowder 1996), few studies have examined seasonal movement dynamics. In addition, much of the past research, including movement and habitat use studies, have largely focused on nonnative brook trout in western United States streams (e.g. Chisholm et al. 1987; Riley et al. 1992; Gowan and Fausch 1996; Lindstrom and Hubert 2004) or on “coaster” brook trout (e.g. Amelio et al. 2008; Mucha and Mackereth 2008). Recently, however, there have been some published studies focused on wild brook trout movement in the eastern United States (Baker et al. 1996; Baird and Krueger 2003; Roghair and Dolloff 2005; Hansbarger et al. 2010). Although these studies provide useful insight into brook trout ecology, their temporal duration was often limited to less than 2 months and the information was coarse with respect the physical habitat. As a result, there remains a lack of information related to some of their basic life history requirements.

*Drivers of brook trout movement and habitat use.* - A variety of factors potentially influence movement and habitat selection of brook trout. For instance, increased activity has been observed in the fall when compared to summer months (Gowan and Fausch 1996; Curry et al. 2002; Peterson and Fausch 2003; Lindstrom and Hubert 2004; Petty et al. 2005; Hansbarger et al. 2010). This increased movement during the fall corresponds to changing water temperatures,

when temperatures decrease into the range of thermal preference for brook trout (between 11 – 16 °C; Coutant 1977) and spawning activities.

Spawning of brook trout typically occurs in headwater regions of streams, with important characteristics for redd-site selection including lower flow velocity and coarser substrate (Witzel and MacCrimmon 1983; Bernier-Bourgault and Magnan 2002). Also, brook trout have been consistently observed selecting areas of groundwater upwelling to construct redds in field studies (Witzel and MacCrimmon 1983; Snucins et al. 1992; Curry and Noakes 1995a), laboratory experiments (Webster and Eiriksdottir 1976), and study ponds (Carline 1980). The importance of upwelling is thought to be related to improved egg survival, as these areas provide more thermal stability and increased dissolved oxygen (Snucins et al. 1992; Curry and Noakes 1995b). Although there is substantial evidence suggesting that upwelling may be important to brook trout for successful spawning, the exact role it plays in redd site selection is not entirely understood (Curry and Noakes 1995a).

In addition to time of year, other factors that may influence stream-dwelling fish movement and habitat use include fish size (Riley et al. 1992; Bunnell et al. 1998; Albanese et al. 2004; Quinn and Kwak 2010) and stream flow (Chisholm et al. 1987; Gowan and Fausch 1996; Albanese et al. 2004; Murchie and Smokorowski 2004). Although both fish size and flow have been positively correlated with activity, their role in seasonal movement and habitat selection of wild brook trout is not well defined. The gradient of a stream also may influence brook trout movement, as greater stream slope has been associated with less movement in stream salmonids (Chisholm et al. 1987; Adams et al. 2000; Kahler et al. 2001).

*Brook trout movement predictions.* - Based on the published literature, I predicted that brook trout movement would be mostly seasonal and that the effects of other covariates would be related to the time of year. Specifically, I examined how fish size, flow, and a change in water temperature was related to brook trout movement (see below for details), and I predicted that the influence of these factors would be most pronounced in the fall, during spawning season. As winter approached, I predicted a trend of decreasing movement across all fish, regardless of changes and differences within the other factors (i.e., there would be an interaction between fish size, flow, and temperature with time of year).

I expected larger fish to exhibit more mobility than smaller fish and increased brook trout movement to be related to higher flows. Also, I examined how short-term variations within a seasonal temperature range might be related to brook trout movement. The range of water temperature a fish experiences is relative to the time of year (i.e., warmer in the summer and colder in the winter). Thus, movement tendencies based on the actual water temperature would be correlated to a time effect when modeling movement. Therefore, I predicted that brook trout movement would be a function of a *change in water temperature*, independent of the actual water temperature. Specifically, I predicted an increase in movement with larger increases or decreases in water temperature. Lastly, I expected that there would be a difference in fish movement among the study streams due to differences in stream gradient. I predicted less movement in stream reaches with greater slope.

*Radio biotelemetry.* - Electrofishing and mark-recapture methods provide researchers and managers with useful information about fish populations. However, both have intrinsic limitations when used to evaluate movement and habitat use. The inherent invasive nature of

electrofishing may cause habitat use models to overemphasize deep water pools and overhead cover, since fish are often driven into areas of refuge (Young 1996). Whereas in mark-recapture studies, a large number of marked fish often are never recaptured, which results in the inability to make any inferences related to those individuals (Gowan et al. 1994; Gowan and Fausch 1996; Rodríguez 2002).

Radio biotelemetry is an alternative for evaluating movement and habitat use of fishes. Because sampling (locating) fish can be done with minimal disturbance to the fish, locations and habitat preferences can be determined without driving fish into areas of refuge, and the fate of each individual can be determined with a relatively high degree of certainty. In addition, neither electrofishing nor most mark-recapture methods allow for continuous tracking, which makes it logistically difficult to identify seasonal changes in movement and habitat use patterns and to collect sufficient data to utilize fish/habitat statistical modeling approaches. By utilizing biotelemetry, the stream habitat can be viewed as a landscape network, as opposed to discrete habitat units. Viewing streams as landscape networks also allows for fish movements and habitat use to be viewed as a continuous process (Schlosser 1991, 1995; Fausch et al. 2002; Allan 2004; Smith and Kraft 2005). For example, this can help to better understand the potential mobility of a fish species, since recapturing an individual in the same area it was marked can not necessarily be correctly interpreted as a lack of movement (i.e., the fish could have moved and then returned to the area). Also, it is important, in terms of management and conservation, to determine if a fish species requires a variety of habitats to complete its life cycle (Saiget et al. 2007).

In the past, a disadvantage of using radio transmitters in small fishes, such as stream-dwelling brook trout, was a short battery life. This limited studies to tracking individual fish over relatively short time periods (e.g. 1 to 2 months or less). However, advances in radio

biotelemetry technology have led to the availability of smaller transmitters with relatively long life expectancies (e.g., up to 5 months for a 60 g fish). And although we have a basic understanding of movement and habitat use for some stream fishes, these improvements in biotelemetry technology, along with the development of new statistical modeling approaches (e.g., see *Brook trout habitat use modeling approach* below), allows for new insights.

*Brook trout habitat use modeling approach.* - Although there are a variety of approaches that can be used to model animal habitat use (e.g., Manly et al. 2002), I considered the following questions prior to deciding on an analytical approach:

- Can the model identify disproportionate use of a certain habitat? For example, if deep pools were less common than shallow pools in a reach of stream, can the model evaluate if usage of the deep pools is excessive in relation to their availability?
- Does habitat selection differ when available habitat is quantified at different spatial scales, i.e., to what degree was selection spatially dependent?
- Did habitat usage and selection change temporally?
- Can differences in habitat selection by an individual fish be attributed to covariates that are characteristics of the fish or of the habitat type? Also, was the relationship between habitat use and these covariates linear in nature or should nonparametric relationships be examined?
- Does the model account for correlations between measurements due to repeated observations on the same individual fish?

A statistical modeling approach that allows for explicit consideration of the above aforementioned questions is discrete choice models with random effects (Kneib et al. 2009).

Discrete choice models can be used to evaluate population- level and individual-level selectivity based on the available choice sets, and the choice set can change over space and time. Despite its flexibility and ability to accommodate the complexities inherent in habitat selection data, to the best of my knowledge this statistical modeling framework has not been used to study habitat selection in fishes.

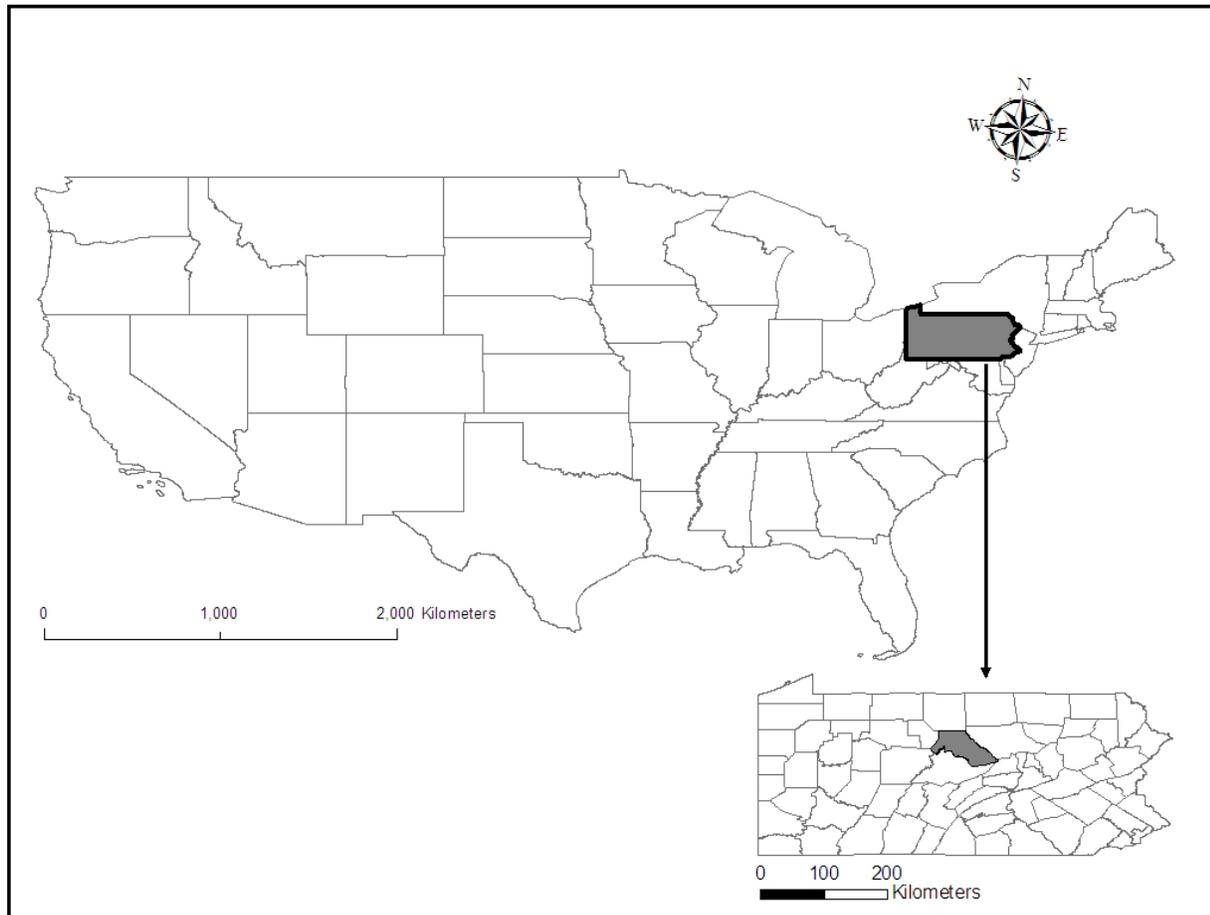
*Research goals and objectives.* The overall goal of my study was to evaluate seasonal movement and habitat use patterns of wild brook trout in central Pennsylvania from late summer through early winter. This allowed me to identify movement and habitat use trends for brook trout during both spawning season and during the time of year when water temperatures transition from warmer to cooler. My first objective was to address uncertainties of eastern brook ecology related to movement (e.g., do they move and how far?). I also was interested in whether or not main-stem fish would utilize smaller tributaries, especially during spawning season, and if movement trends varied among streams or individuals. To address this objective, I employed radio biotelemetry to collect movement data on brook trout in the study area. My second objective was to evaluate my predictions of potential influences on wild brook trout movement. To address the second objective, I used generalized additive mixed models (GAMMs) to identify relationships between brook trout movement and aforementioned covariates. Lastly, my third objective was to evaluate brook trout habitat selection based on available pool habitat and quantify variation in habitat use among individuals. To address this last objective, I surveyed thalweg profiles of the study streams and analyzed habitat use using discrete choice models with random effects.

## Chapter 2

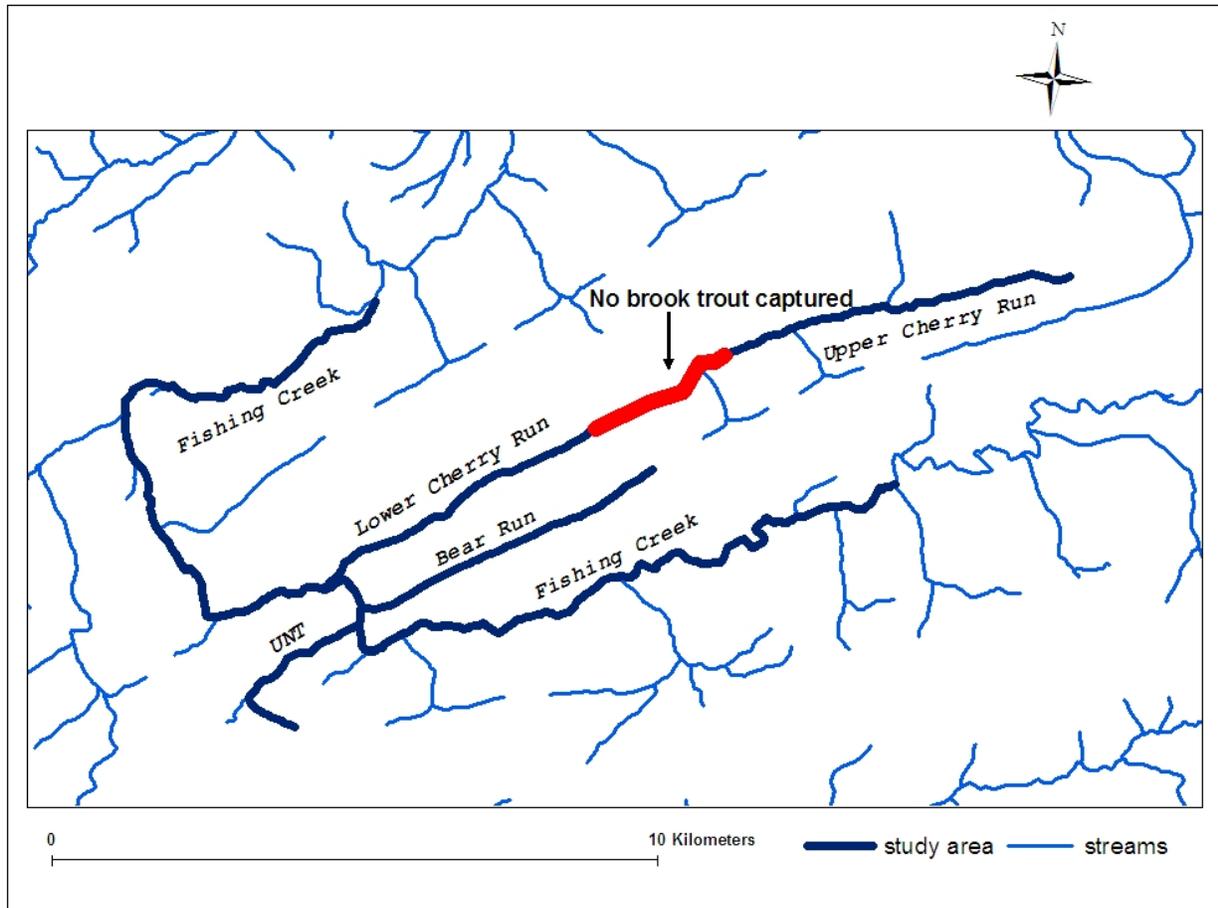
### STUDY AREA

This research was conducted in central Pennsylvania, USA (Figure 1). The main-stem of the stream system was Fishing Creek, a 69 km long limestone-influenced stream located in southern Clinton County. Sections of Fishing Creek, including the study area, are designated as Class A wild trout streams by the Pennsylvania Fish and Boat Commission (PFBC). A Class A wild trout stream in Pennsylvania is not stocked and "supports a population of naturally produced trout of sufficient size and abundance to support a long-term and rewarding sport fishery" (PFBC 2011). Although this system is dominated by brown trout (estimated biomass of 268 kg/ha), self-sustaining wild brook trout populations are present in Fishing Creek (estimated biomass of 2 kg/ha) and in several of the tributaries (PFBC 2009). In addition to Fishing Creek, the study area included three headwater tributaries: Cherry Run, Bear Run, and the unnamed tributary #22515 (hereafter referred to as UNT; Figure 2). Unlike Fishing Creek, these tributaries lack a limestone influence in the geology of the underlying aquifer. A common characteristic of limestone streams is that they are influenced by groundwater input, which results in less variability in the stream environment due to stable flow, thermal, and chemical conditions (Sear et al. 1999). Cherry Run will sometimes be referenced to as both upper Cherry Run (the upstream portion) and lower Cherry Run (the downstream portion). This division of Cherry Run was a reflection of where brook trout were sampled. As a result of access points, fish were captured in the both the lower 5 km and the upper 5 km of the stream, with no sampling efforts in the middle reach (see Figure 2). Although no fish were sampled in this middle reach, there were no barriers that would prevent fish movement between the upper and lower reaches.

The study area was heavily forested with a mix of eastern hemlock *Tsuga canadensis* and various deciduous hardwood tree species. Cabins occupied some of the riparian area along Fishing Creek and lower Cherry Run. A state road runs along Fishing Creek for much of the study area and crosses Cherry Run about 1 km from its mouth. Interstate 80 and the town of Lamar, PA are located near Fishing Creek downstream of the study area and agricultural areas occur upstream of the study area.



**Figure 1.** Map of the United States showing the location of Pennsylvania in gray and a map of Pennsylvania showing the location of Clinton County in gray (map data source: [www.esri.com](http://www.esri.com)).



**Figure 2.** Map of the study area in Clinton County, PA showing Fishing Creek and the tributaries Cherry Run, unnamed tributary #22515 (UNT), and Bear Run, shown in bold. The red area of Cherry Run indicates the approximate area where no brook trout were sampled. Upstream of this area was considered upper Cherry Run and downstream of this area was considered lower Cherry Run (map data source: [www.pasda.psu.edu](http://www.pasda.psu.edu)).

### Chapter 3

#### METHODS

*Quantifying stream habitat.* - Thalweg profiling is a surveying method, useful for assessing fish habitat in small streams, that measures stream channel morphology to create a longitudinal profile of physical stream habitat (Bauer and Ralph 2001; Mossop and Bradford 2006). There are advantages of thalweg profiling over more traditional approaches to quantifying instream habitat (e.g., assessing habitat at randomly placed transects) including: (1) thalweg profiles can be quantified for an entire stream or stream segment, thus providing a continuous quantification of stream habitat across an entire study area (Bauer and Ralph 2001), and (2) they provide a quantitative measure of habitat that is independent of flow stage and stream discharge (Lisle 1987).

Although numerous metrics can be derived from thalweg profiles (see Mossop and Bradford 2006 for details), I used this methodology to identify and quantify residual pools and to calculate the slope of a stream reach. Residual pools were measured as changes in elevation, rather than water depth, and can theoretically be thought of as pools that would still exist if there were no flow in a stream (Lisle 1987). To identify a residual pool, streambed elevation was measured longitudinally along the thalweg (i.e., the deepest point of the stream channel). A change in elevation (i.e., depth) of  $\geq 0.1$  m was classified as a residual pool. This criterion was used to eliminate minor irregularities in the streambed as being considered pool habitat (Mossop and Bradford 2006). I focused my efforts on quantifying residual pools because of the importance of pool habitat for salmonids (e.g., House and Boehne 1986; Bowlby and Roff 1986; Hearn 1987; Nickelson et al. 1992; Solazzi et al. 2000; Hakala and Hartman 2004).

I surveyed thalweg profiles of the study streams employing standard surveying techniques (Harrelson et al. 1994). A two-person crew worked upstream and recorded the elevation and distance along the thalweg of the stream channel at predetermined intervals, using a laser level, stadia rod, and a measuring tape. Measurements were taken every 5 m or at a break (reduction in elevation) in the slope of the stream channel. This break indicated the “edge” of a potential residual pool. I also ensured that the deepest point (i.e., the greatest reduction in elevation from the “edge”) was recorded, along with the upstream point that coincided as closely as possible with the elevation of the “edge”. This allowed me to record the maximum residual pool depth and residual pool length for each residual pool. A GPS waypoint was recorded either every 50 m of longitudinal stream distance or when the channel took an abrupt change of direction.

Longitudinal profiles were developed for the entire reach of Cherry Run (12.2 km) and the UNT (2.4 km). The reach of Fishing Creek between the mouth of Cherry Run and the mouth of the UNT also was surveyed (1.0 km; Figure 2). Using the linear distance between the GPS points, I assigned a latitude and longitude to each elevation measurement of the thalweg profile and incorporated the data into a GIS layer. Spatially referencing thalweg profile measurements created a digital map of the stream channel that detailed residual pool habitat. These data were used for quantifying and classifying stream habitat and also for calculating movement between fish locations.

*Surgical implantation of radio transmitters.* - Between 20 September 2010 and 2 October 2010, a field crew captured 36 brook trout weighing 48 - 348 g (mean  $\pm$  SD,  $98 \pm 67$  g). All of the brook were age 1 or older and considered sexually mature. However, a confident determination of sex

was not possible for most of the fish. I surgically-implanted the brook trout with Lotek (Lotek Wireless Inc., Newmarket, Ontario, Canada) NanoTag series digitally encoded transmitters (model NTC-3-2 – 1.2 g/124 d life expectancy). The crew used pulsed-DC backpack electrofishing to capture brook trout in lower Cherry Run (9 fish), upper Cherry Run (10 fish), and UNT (9 fish). We sampled fish throughout these stream reaches in order to have brook trout distributed as evenly as possible, with respect to stream distance between individuals. I chose to surgically-implant fish based on spatial distribution, rather than fish size, because I did not expect considerable variation in fish size in these streams. Elevated water temperatures of 20° C in Cherry Run, followed by a high flow event on 28 September 2010, delayed some of the sampling and surgical procedures. Consequently, I did not surgically-implant 7 of the brook trout in Cherry Run until after the high flow event. Fishing Creek, being a larger stream, required different logistic considerations in terms of sampling. Fish biologists from the PFBC assisted the field crew and provided the use of a tow boat electrofishing unit. Due to time constraints, all of the brook trout (8 fish) were captured and released in the same area 1 km upstream of Cherry Run. No brook trout were surgically-implanted with radio transmitters in Bear Run, but it was monitored during the entire study period to identify any use by radio-tracked fish.

I used the shielded-needle technique (Ross and Kleiner 1982), a commonly used method for implanting radio transmitters internally in fishes, in the surgical procedure. The brook trout were anesthetized using MS-222 prior to the surgery. During the procedure, oxygenated water containing a maintenance dose of MS-222 was pumped over the gills. An incision was made anterior to the pelvic girdle to implant the radio transmitter in the peritoneal cavity and was closed with nylon sutures, using a simple interrupted suture pattern. Also, I employed recommendations made by Mulcahy (2003) to minimize infection and stress on the fish. I

released the brook trout as soon as they had recovered from the surgical procedure to minimize residual stress (Jepsen et al. 2002; Mulcahy 2003). The capture and handling of fish followed protocols approved by The Pennsylvania State University Institutional Animal Care and Use Committee (IACUC # 33760).

A suggested guideline for fish biotelemetry is that the mass of the transmitter in air should be less than 2% of the body mass of the fish (Winter 1983). Ten of the brook trout violated this guideline, but the weight of the tag did not exceed 2.5% of the fish's body weight. There are studies that have demonstrated that an internally implanted transmitter exceeding 2% of the fish's body mass does not affect growth or behavior in salmonids (e.g., Adams et al. 1998; Jakober et al. 1998; Bélanger and Rodríguez 2001; Muhlfeld and Marotz 2005) and no effects on the swimming performance of salmonids have been observed using transmitters up to 12% of the body mass of the fish (Brown et al. 1999).

*Radio-tracking.* - During summer 2010, I conducted a pilot study in order to optimize radio-tracking methods. This involved surgically-implanting 5 brook trout with transmitters and radio-tracking their movement from June to August 2010. These fish exhibited a tendency to return to the location of capture, regardless of where they were released in the stream. Thus, to avoid any fish movement calculations being influenced by where the fish had been released relative to where it was captured, I released all of the brook trout in September and October 2010 as closely as possible to their capture location. In addition, I did not track the fish during the first 48 h after the surgery to allow them to recover from the surgical procedure. The radio transmitters came equipped with a 12 h on/off feature and were active between 700 hours and 1900 hours each day.

I tracked the brook trout on foot, with a truck used solely to move within range of the signals from the radio transmitters. Once I identified an individual fish, the exact location was estimated as precisely as possible. As I approached the stream, I maintained a distance that would minimize the likelihood of being seen by the brook trout. Initially, I attempted to visually identify the brook trout's location. If that proved unsuccessful, I used the strength of signal from the radio transmitter to estimate the location of the fish. The estimated error using the strength of signal is  $< 2$  m of the actual location of the brook trout. This estimate is based on successful visual locations of a fish, the location of a shed tag, and trials where a tag was hidden by a crew member. The estimated error in my location of a fish was less than the estimated GPS error of 5 m in Cherry Run and Fishing Creek and 10-20 m in UNT. Young (1996) demonstrated that measurements of instream habitat taken after fish were located by biotelemetry had no apparent effect on the subsequent location choice of cutthroat trout *Oncorhynchus clarki pleuriticus*, as many were located repeatedly in the same locations and some were observed feeding less than 5 m from the researchers.

I located each individual brook trout two to three times per week during October and November 2010. Locations gradually reduced to one to two times per week as stream temperatures dropped below 6 °C in December 2010 and fish movement began to decrease and eventually cease in January 2011. Although attempts were made to keep the number of locations per fish approximately equal, irregularities in transmitter battery life, poor driving conditions on access roads in January 2011, and shed tags led to some variability

*Brook trout movement calculations.* - To calculate the distance moved for each brook trout, each GPS fish location was placed into the nearest thalweg profile point using the "proximity tool" in

ArcMap (version 10.0, 2010; Environmental Systems Research Institute, Inc., Redlands, CA, USA). The distance between two fish locations was then calculated from the thalweg profile data (i.e., the measured longitudinal stream distance between the two corresponding elevation measurements). For brook trout locations that were outside of the thalweg profile, the GPS points were projected onto the “Networked Streams of Pennsylvania” GIS layer (Pennsylvania Spatial Data Access 1998). The distance between fish locations was then calculated by measuring along the stream using the “measure tool” in ArcMap. “Movement” between locations and total movement for each brook trout was reported as distance moved, regardless of direction. “Net movement” for each brook trout was reported with respect to stream flow direction. Upstream movement was considered positive and downstream movement was considered negative. I categorized individual brook trout based on where they were found at their last location as Fishing Creek, lower Cherry Run, upper Cherry Run, or UNT (see Study Area for details and Figure 2). I used this criterion to classify the 5 brook trout that had been located in both Fishing Creek and lower Cherry Run on the assumption that they had used Cherry Run primarily for spawning. Also, in terms of the number of days spent in each stream for these fish, more time was spent in Fishing Creek than Cherry Run during the tracking period.

The movement measurement methods described above were used as a way to report brook trout movement as stream distance, as opposed to linear distance. However, it is important to note that these calculations represent only estimates of the actual movement. Furthermore, these movement estimates are conservative because an individual fish was seldom located on two consecutive days during the study and diel movements of the fish were not monitored (Swanberg 1997; Young 1999). As a result, estimates of ‘zero’ movement between locations may not represent true zeros. All means are presented  $\pm$  SD.

*Water temperature and stream flow.* - I monitored water temperature and stream flow during the study period. HOBO ProV2 temperature loggers (Onset Computer Corporation, Bourne, MA, USA) deployed at locations of approximately equal distances in Fishing Creek, Cherry Run, and UNT recorded water temperature at 30 min intervals. I also measured water temperature at each brook trout's location. I recorded the stream flow stage daily from a staff gauge that had been installed in each of the streams in order to create flow indices. All means are presented  $\pm$  SD.

*Brook trout movement modeling.* - I developed competing *a priori* models (hypotheses) describing seasonal movement of wild brook trout and used generalized additive mixed models (GAMMs) to examine both linear and nonlinear relationships between wild brook trout movement and the covariates time, fish size, flow stage, and a change in water temperature. Using the gamm function in the mgcv package in R (version 2.8.1, R Developmental Core Team 2008; Wood 2004, 2006, 2008, 2010) I fitted GAMMs with thin plate regression splines using a generalized cross-validation procedure. An individual fish-specific random effect included in all models accounted for correlations between measurements because of repeated observations on the same individual fish.

I expressed brook trout movement in the models as the movement between locations for each brook trout (see Brook trout movement calculations for details). A positive value represented both upstream and downstream movements. I did not differentiate between upstream and downstream movement because I was not attempting to model brook trout movement in relation to direction. Movement data were highly skewed as a result of a small number of large movements (e.g., movements of several kilometers) made by a few brook trout compared to a

large number of small movements. As a result of the skewed distribution, movement was natural-log transformed. A small constant of 1 m was added to all the movement calculations prior to the transformation to accommodate zeros in the dataset. The addition of the 1 m preceding log-transformation implies that the zero movement estimates were not true zeros, which is a reasonable assumption given that it is highly unlikely a fish did not move at all between telemetry locations (see Brook trout movement calculations). “Time” was represented in the models as the day of the study (i.e., first day of the study was 1, second day was 2, and so on). To improve model convergence, time was grand mean centered ( $time_i - \overline{time}$ ).

Prior to fitting and comparing competing movement hypotheses, I evaluated two additional modeling considerations. First, I tested the assumption that the residual errors were independent from one time point to the next. To evaluate this temporal independence assumption, I fitted a model containing only the effect of time (model MM1) and compared it to a model that only differed in that it explicitly modeled temporal correlation among residuals (model MM1b). I compared the models using Akaike Information Criterion corrected for small sample size ( $AICc = -2(\log\text{-likelihood}) + 2K + 2K(K + 1) / n - K - 1$ , where  $K$  is the number of estimable parameters and  $n$  is the number of observations (Burnham and Anderson 2002)). Specifically, I used a spherical model to accommodate potential temporal autocorrelation (Pinheiro and Bates 2000). I investigated the spherical correlation model instead of the more commonly used autoregressive model (e.g., AR-1) because it can better accommodate missing values and irregularly spaced data (Zuur et al. 2009). In addition to investigating if temporal movement varied among streams, I fitted an additional model to examine if there were detectable differences in movement over time across the study streams by allowing a smoother to be fitted to each stream separately (model MM1c). This model was investigated because I expected

movement trends to differ in relation to the gradient of the streams (Fishing Creek: <1% stream slope in the study area, lower Cherry Run: 1.5% stream slope, upper Cherry Run: 2.0% stream slope, and UNT: 5.0% stream slope). Model MM1c was then compared to Model MM1 using AICc.

In addition to models MM1, MM1b, and MM1c, which were fitted to evaluate the need to accommodate temporal autocorrelation and multiple smoothers, I developed the following *a priori* models describing brook trout movement. Since my expectation was that movement would be primarily related to season, a time effect was included in all models. The first hypothesis was that movement was only a function of time (Model MM1, above). The second hypothesis, Model 2 (MM2), predicted that movement was related to fish size and the time of year. Fish size was expressed as the natural-logarithm of the weight in grams of the individual brook trout. Model 3 (MM3) evaluated the relationship between stream flow stage and the time of year with brook trout movement. “Flow” was expressed in the models as the corresponding increase or decrease in flow index between consecutive brook trout locations. Since the flow index could only provide the stream flow stage at a point in time, any change in flow index within 2 d of a fish location were recorded for that location to account for lag-time in capturing a change in stream flow. Once a flow value was assigned to a fish location, it was considered a continuous covariate. Model 4 (MM4) evaluated the relationship between a change in water temperature and the time of year with brook trout movement. A change in water temperature was expressed in the models as the corresponding increase or decrease in water temperature between brook trout locations and was calculated as the greatest positive or negative change in water temperature between two consecutive fish locations. Once a change in temperature value was assigned to a fish location, it was considered a continuous covariate.

In the next set of models, I hypothesized that fish size, flow, and a change water temperature, and time of year were not additive in their relationship with brook trout movement. These models explored interactions between the covariates in explaining brook trout movement. Model 5 (MM5) evaluated a fish size and time of year interaction on brook trout movement. Model 6 (MM6) evaluated a stream flow and time of year interaction on brook trout movement. Model 7 (MM7) evaluated a change in water temperature and time of year interaction on brook trout movement.

The last set of models explored more complex interactions between the covariates hypothesized to explain variation in brook trout movement. Model 8 (MM8) evaluated the interaction between stream flow, a change in water temperature, and the time of year on brook trout movement. Model 9 (MM9), the most complex model, evaluated the interaction between stream flow, a change in water temperature, fish size, and the time of year on brook trout movement.

I used AICc to compare competing models (Burnham and Anderson 2002). Although there are inherent difficulties when using AICc to compare models with random effects (due to uncertainties in counting the number of parameters estimated), I used AICc because of the interest in making inferences about population-level parameters, across all fish, as opposed to inferences about particular fish in the data set (Vaida and Blanchard 2005). The models were ranked based on AICc differences ( $\Delta_i$ ), where  $\Delta$  for model  $i$  was calculated as  $\Delta_i = \text{AICc}_i - \text{AICc}_{\min}$ , where  $\text{AICc}_{\min}$  was the smallest AICc value in the model set. Akaike weights ( $w_i$ ) were calculated for each of the  $r$  models as  $w_i = \exp(-0.5\Delta_i) / \sum_{r=1}^R \exp(-0.5\Delta_r)$ .

*Discrete choice models.* The discrete choice model with random effects is a multinomial logit model that assumes there are  $k$  different habitats types. At different points in time (but not necessarily at equal intervals) observations are collected for  $n$  fish. The probability that habitat type  $r$  is chosen at time  $t$  by fish  $i$  is denoted by  $\pi_{it}^{(r)}$  and is related to fish-specific and habitat-specific covariates by the model:

$$(1) \quad \pi_{it}^{(r)} \propto A_{it}^{(r)} \exp(\eta_{it}^{(r)})$$

where  $\propto$  indicates proportionality up to a multiplicative constant with  $\eta_{it}^{(r)}$  being an additive predictor of the model:

$$(2) \quad \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + x_{it}'\gamma^{(r)} + \sum_{j=1}^{p1} f_j^{(r)}(u_{ij}) + \sum_{j=1}^{p2} f_j(v_{ij}^{(r)})$$

Following Kneib et al. (2009), the components in model (1) and model (2) are described as:

$A_{it}^{(r)}$  is the availability of habitat type  $r$  at time  $t$  for fish  $i$ . This is a known constant proportional to the habitat fraction of the available space and is referred to as an offset, which accounts for the varying availability of habitat types. The inclusion of availability allows us to elucidate whether habitat use is selective and, therefore, disproportionate to availability (Kneib et al. 2009). The available habitat used in the model can be calculated at any spatial scale within the observation area.  $\beta^{(r)}$  are parameters that indicate the overall habitat preference for the brook trout after accounting for the effects of covariates and habitat availability. A positive parameter estimate would indicate increased use of the corresponding habitat type compared to its availability in the choice set.  $b_i^{(r)}$  are individual fish-specific random effects to account for correlations between multiple observations on a given fish. The random effects are assumed to be independent and identically distributed as  $b_i^{(r)} \sim N(0, \tau_r^2)$ , with category-specific variances  $\tau_r^2$ . By assuming the

random effects of different animals are independent, it is implied that correlations exist for observations on the same fish, but observations made on other fish remain independent (Kneib et al. 2009).  $\gamma^{(r)}$  are parameters corresponding to the linear effects of time or fish-specific covariates  $x_{it}'$ .  $f_j^{(r)}(u_{ij})$  are parameters corresponding to nonparametric effects of time or fish-specific continuous covariates  $u_{ij}$ , where the nonparametric functions are habitat category-specific and the covariates are defined globally.  $f_j(v_{ij}^{(r)})$  are parameters corresponding to nonparametric effects of habitat category-specific continuous covariates  $v_{ij}^{(r)}$ , where the effect is defined globally (see Kneib et al. 2009 for additional details).

Of particular interest to this research, and an important reason for using discrete choice modeling, was to account for changes in the available habitat among fish and time (i.e., when a fish moves to a different location, the available habitat set changes). This approach differs in scale from other modeling approaches (e.g., logistic regression), which assumes all habitat is “available” to all fish over the entire study period, regardless of where the fish is located: for stream-dwelling fish this assumption may not be reasonable.

### **Habitat use modeling in Cherry Run**

I used discrete choice models with random effects to examine habitat use of 20 wild brook trout that were located in Cherry Run. This included the 5 fish that I last located in Fishing Creek, but were located in Cherry Run during spawning season. Although I had thalweg profile data for UNT and a portion of Fishing Creek, habitat modeling was not employed for the fish locations in those portions of the study area. In UNT, a larger degree of GPS error (up to 20 m), along with shorter habitat lengths, reduced my confidence in accurately assigning fish locations

to a specific habitat type. In Fishing Creek, most of the brook trout moved out of the area that was surveyed for habitat. Further, using the thalweg profile to evaluate habitat use in a larger stream such as Fishing Creek would not have been appropriate since the relationship between residual pool depth and salmonids applies specifically to smaller streams, where pool availability may be more limiting (Mossop and Bradford 2006).

*Quantifying available habitat and creating habitat classes.* - Discrete choice models require the habitat in the study area to be quantified in such a way that allows for the percentages of each habitat type to be calculated in each choice set. The map of residual pool habitat for Cherry Run, derived from the longitudinal thalweg profile (see Quantifying stream habitat), met this requirement. Specifically, the thalweg profile was used to create habitat categories based on the maximum depth of the residual pools. Because I did not have any *a priori* rationale for choosing specific residual pool depth categories, the categories were determined using a change-point analysis. The change-point analysis found thresholds in the distribution of maximum residual pool depth values. By plotting each maximum residual pool depth measurement on the  $x$ -axis of a frequency histogram, the change-point analysis detected shifts in the mean number of pools in each length bin (Figure 3). This procedure grouped the residual pools into three categories, which were described as shallow (0.10 – 0.26 m), intermediate (0.26 – 0.44 m), and deep (0.44 – 1.06 m). Using the change-point analysis yielded similar results to using the 25<sup>th</sup> and 75<sup>th</sup> quantiles of residual pool depth values. Regardless of the approach used, the analysis was not sensitive to the exact cutoff between ‘shallow’, ‘intermediate’ and ‘deep’ pools. Habitat that was not identified as a residual pool in the thalweg profile was categorized as non-pool. These categories (shallow, intermediate, deep, and non-pool) were the parameters of main interest

(i.e.,  $\beta(r)$ ) in the discrete choice models and were used to identify used habitat for each fish location and quantify available habitat relative to the location.

*Used habitat.* – The used habitat for each brook trout location was classified as shallow, intermediate, deep, or non-pool. I assigned fish based on the corresponding habitat category the fish was found in for each telemetry location (see brook trout movement calculations). The used habitat category was based on the thalweg profile data, the same data used for determining available habitat.

*Choice sets.* - Since the habitat data set included the entire 12.2 km reach of Cherry Run, I was able to calculate a unique available habitat set for every fish location, regardless of its movement within the observation area. Thus, each time a fish moved, the available habitat (the proportion of shallow, intermediate, deep, and non-pool habitats) was recalculated. It has also been demonstrated that habitat use of stream salmonids may be scale-dependent (Baxter and Hauer 2000; Feist et al. 2003). So, to evaluate if brook trout habitat use differed across multiple spatial scales, I varied the amount of stream that was considered available at any given point in time. Specifically, I evaluated four different scales of available habitat based on the longitudinal distance with respect to each fish location: 250 m, 500 m, 1,000 m and at the “landscape” scale. The available habitat was calculated using an equal stream distance upstream and downstream of a fish’s location to arrive at the corresponding longitudinal distance for that level (i.e., at the 250 m scale, the available habitat was comprised of the habitat 125 m upstream and 125 m downstream of each fish location.) The landscape model allowed the entire reach of Cherry Run to be considered available habitat for each brook trout location.

*Brook trout habitat use models.* – I fitted six competing, *a priori*, models that represented hypotheses describing habitat selection of wild brook trout for three of the spatial scales (250, 500, and 1,000 m) used to quantify available habitat. Because the landscape-scale model differed in how the available habitat was quantified (i.e., available habitat did not vary over space and time), it was considered separately below. I predicted that brook trout would be found predominantly in residual pool habitat and that the models would indicate a selection by brook trout for all three residual pool categories over the non-pool category. Accordingly, the reference category for all models was set as the non-pool habitat category. This allowed me to compare selection between the three residual pool categories in each of the models compared to non-pool habitat.

Model 1 – Because of the importance of pool habitat for brook trout and that residual pool depth has been shown to be a useful habitat feature to evaluate populations of stream salmonids (Horan et al. 2000; Mossop and Bradford 2006), Model 1 (HM1) was an unconditional model that hypothesized brook trout habitat selection was based solely on residual depth of the available habitat. The predictor was of the form:

$$(3) \quad \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)}$$

Model 2 - Although depth is generally the pool characteristic of interest in studies concerning stream salmonids, the length of a pool may also be important in terms of habitat use. Some studies consider the area or volume of a pool habitat in relation to brook trout population densities (e.g. Bowlby and Roff 1986; Roghair et al. 2002; Hakala and Hartman 2004) or habitat use (e.g. Chisholm et al. 1987; Lindstrom and Hubert 2004), which inherently include length in the metrics. However, using discrete choice models allowed for habitat-specific covariates to be examined independently of other habitat variables. Accordingly, Model 2 (HM2) hypothesized

that the average length of the pool category, along with residual depth, influenced brook trout habitat selection. Although I expected to locate brook trout primarily in residual pool habitat, non-pool habitat comprised a portion of the available habitat in the choice sets. The length of all habitat classes must be included in discrete choice models, since the sum of the length of the habitat patches must equal the total length of the available habitat (see Kneib et al. 2009). However, the results reflect habitat selection in relation to the average length of the habitat class where the brook trout was located within the choice set. Habitat patch length was evaluated independently of residual depth and is expressed as a habitat-category specific nonparametric effect in the model. The predictor was of the form:

$$(4) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + \sum_{j=1}^{p_2} f_j(v_{itj}^{(r)})$$

Model 3 - Brook trout habitat selection may differ based on the time of year. Different habitat types (i.e., residual pool depths) may be preferred for spawning when compared to late summer or overwinter habitat. It has been suggested that depth may be important in redd site selection by brook trout (Witzel and MacCrimmon 1983; Essington et al. 1998). Moreover, no studies to my knowledge have utilized residual depth measurements to evaluate brook trout habitat selection during spawning season.

Model 3 (HM3) hypothesized that habitat selection by brook trout *at a certain time of year* was based on residual pool depth. Time was represented as the day of the study (i.e., first day of the study is 1, second day is 2, and so on) and was standardized

$\left( \frac{time_i - \overline{time}}{SD(time)} \right)$  to aid model convergence. Time was a continuous covariate and

expressed as a nonparametric effect in the model. The predictor was of the form:

$$(5) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + \sum_{j=1}^{p_1} f_j^{(r)}(u_{itj})$$

Model 4 –Model 4 (HM4) hypothesized that brook trout habitat selection *at a certain time of year* was based on both residual pool depth and pool length. Pool length was expressed as a category specific nonparametric effect and time was a continuous covariate and expressed as a nonparametric effect in the model. The predictor was of the form:

$$(6) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + \sum_{j=1}^{p_1} f_j^{(r)}(u_{itj}) + \sum_{j=1}^{p_2} f_j^{(r)}(v_{itj})$$

Model 5 – Preference for certain habitats may also be influenced by the size of a fish. Larger stream fishes are usually associated with deeper habitats and smaller ones with shallower habitats (Grossman and Freeman 1987; Schlosser 1987; Harvey and Stewart 1991). Accordingly, it is reasonable to assume that larger brook trout would select for relatively deeper residual pools. However, it is important to consider that spawning habitat use may be similar across size classes of brook trout, since this may be related to a life history trait independent of fish size. Selection for specific habitat, based on residual pool depth and pool length, may also, in part, explain the increased mobility that has been documented in larger stream-dwelling salmonids (see drivers of movement and habitat use).

Model 5 (HM5), hypothesized that brook trout habitat selection *at a certain time of year* was influenced by residual pool depth, habitat length, and the fish's weight. Fish weight was natural log-transformed prior to analysis. The natural log of fish weight was expressed as a nonparametric fish-specific covariate in the model. The predictor was of the form:

$$(7) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + \sum_{j=1}^{p_1} f_j^{(r)}(u_{itj}) + \sum_{j=1}^{p_2} f_j^{(r)}(v_{itj})$$

Model 6 –Because there was also observed variation in mobility between fish of similar sizes, I classified each of the brook trout into either a disperser or a non-disperser category. This determination was based on net movement. Each fish that moved 500 m or more, either upstream or downstream from the release point, was classified as a disperser. I chose this criterion since there was a natural break in the data at 500 m (i.e., net movement of greater than 500 m was generally of a kilometer or more).

Model 6 (HM6) hypothesized that brook trout habitat selection *at a certain time of year* was influenced by both residual pool depth and pool length, the natural log of the fish’s weight, and whether a fish was a ‘disperser’. The disperser/non-disperser category was expressed as a fish-specific covariate in the model. The predictor was of the form:

$$(8) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + x_{it} \gamma^{(r)} + \sum_{j=1}^{p_1} f_j^{(r)}(u_{itj}) + \sum_{j=1}^{p_2} f_j^{(r)}(v_{itj})$$

### Landscape models

The fourth spatial scale evaluated was the landscape scale. In this model the habitat over the entire length of Cherry Run was available for every fish location. The same hypotheses used for the other three spatial scales apply to the landscape models. However, I could not include pool length as a covariate in landscape models because there was only a single covariate value for pool length for each category. In addition, the models would not converge when fish weight was considered as a covariate. Consequently, only three models were fitted at the landscape-scale.

Landscape model 1 (LHM1) was the unconditional model that assumed brook trout habitat selection was based solely on residual depth of the available habitat. The predictor was of the form:

$$(9) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)}$$

Landscape model 2 (LHM2) hypothesized that habitat selection by brook trout *at a certain time of year* was based on residual pool depth. Time was represented as the day of the study and was standardized as previously described. Time was a continuous covariate and expressed as a nonparametric effect in the model. The predictor was of the form:

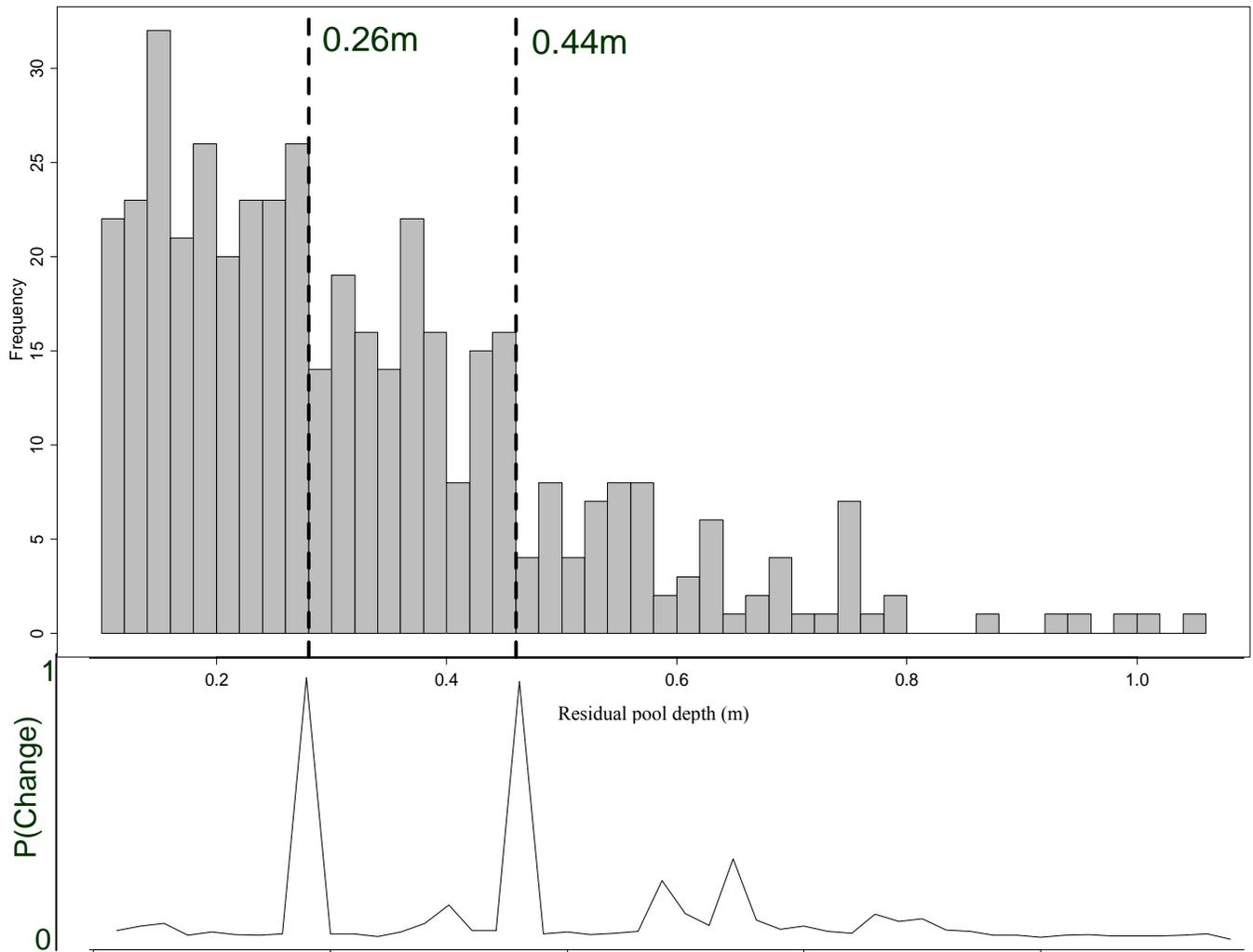
$$(10) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + \sum_{j=1}^{p_1} f_j^{(r)}(u_{itj})$$

Landscape model 3 (LHM3) hypothesized that brook trout habitat selection *at a certain time of year* was influenced by residual pool depth and whether or not a fish was classified as a disperser. The disperser/non-disperser category was expressed as a fish-specific covariate in the model. The predictor was of the form:

$$(11) \eta_{it}^{(r)} = \beta^{(r)} + b_i^{(r)} + x_{it} \gamma^{(r)} + \sum_{j=1}^{p_1} f_j^{(r)}(u_{itj})$$

### Model comparison

The discrete choice models for the 20 brook trout were ranked at each of the four spatial scales using Akaike Information Criterion (AIC). To take into account the difficulties in counting the number of parameters estimated when fitting random effects models, the equivalent degrees of freedom was used as a measure of the effective number of parameters in the regression models (see Kneib et al. 2009 for details). Accordingly, AIC was calculated using the effective degrees of freedom as a measure of model complexity. The models were ranked based on AIC differences and Akaike weights ( $w_i$ ) were calculated as previously described. All discrete choice models were fitted using BayesX (BayesX, version 2.0.1, 2009).



**Figure 3.** Change-point analyses used to identify thresholds in the distribution of pool habitat based on maximum residual depths in Cherry Run in Clinton County, PA. Top panel is histogram of maximum residual pool depths. Dashed vertical lines indicate thresholds identified in change-point analysis. Bottom panel shows the probability of a threshold occurring [P(Change)] based on the change-point analysis. Changes in the mean number of pools in the length bins of the frequency histogram were identified at 0.26 m and 0.44 m.

## Chapter 4

### RESULTS

*Brook trout radio-tracking and movement summary.* – The total number of locations, across all fish, during the tracking season was 715. The number of days tracked and number of locations for each brook trout ranged from 10 – 129 d and from 3 – 42 locations, respectively (Table 1). For all 36 brook trout, movement between locations ranged from 0 – 4,800 m with a median of 10 m and a mean of  $100 \pm 375$  m. Fishing Creek brook trout were the most mobile, followed by lower Cherry Run brook trout, upper Cherry Run brook trout, and UNT brook trout. For Fishing Creek brook trout (11 fish, 336 locations), movement between locations ranged from 0 – 4,800 m, with a median of 10 m and a mean of  $125 \pm 490$  m. For lower Cherry Run brook trout (6 fish, 133 locations), movement between locations ranged from 0 – 2,100 m, with a median of 10 m and a mean of  $150 \pm 350$  m. For upper Cherry Run brook trout (10 fish, 162 locations), movement between locations ranged from 0 – 775 m, with a median of 5 m and a mean of  $50 \pm 115$  m and for UNT brook trout (9 fish, 84 locations), movement between locations ranged from 0 – 315 m, with a median of 0 m and a mean of  $20 \pm 40$  m. For all 36 brook trout, the mean total movement ranged from 50 – 9,000 m, with a mean of  $1,990 \pm 2,470$  m (Table 1).

Throughout the tracking, I did not locate any lower Cherry Run brook trout in upper Cherry Run or any upper Cherry Run brook trout in lower Cherry Run. Also I did not locate any brook trout in the middle reach of Cherry Run where brook trout had not been sampled (see Figure 2). Although no fish entered the middle reach of Cherry Run, I surveyed the entire stream during the thalweg profiling and I did not observe any physical barriers that would have prevented fish from moving between upper and lower Cherry Run.

The total duration spent tracking fish also varied slightly by stream. For example, I lost contact with UNT brook trout on 23 December 2010. Only one fish had been located in UNT during previous tracking, as this stream had a higher rate of apparent predation (i.e., transmitters found on land) and shed transmitters. Also, two of the UNT brook trout were implanted with transmitters that had been recovered during the pilot study in summer 2010 and consequently had a shorter battery life. Tracking concluded on 30 December 2010 in upper Cherry Run because access roads were not maintained, resulting in very poor driving conditions. I had not observed any movement of more than 100 m in upper Cherry Run brook trout since late November 2010. With the exception of two fish, all were found repeatedly in exact locations during this time. I tracked brook trout in the remainder of the study area into January 2011. I gradually lost contact with the remaining 10 brook trout (around two per week) on 24 January 2011. At this time there were only two fish that I was still successfully locating. Since I had not observed any movement greater than 100 m in any of the brook trout during January 2011, it was decided that effort, time, and expenses outweighed any remaining data that could be collected.

As expected, there was a trend of decreasing brook trout movement from late fall through winter. A notable decrease in activity occurred across all fish in late November to early December 2010, with fish movements between locations ceasing nearly completely by late December 2010. Although two brook trout were observed moving 50 – 80 m between 28 December 2010 and 24 January 2011 (fish #110 and #131), most fish were found repeatedly in the same location. This decreased mobility by the brook trout coincided with water temperatures dropping below 6 °C, with movement generally ceasing when water temperatures dropped below 4-5°C. However, one brook trout (#124) did move downstream in lower Cherry Run ~2.5 km during late December into the confluence of Cherry Run and Fishing Creek and was located

there repeatedly throughout the remainder of the tracking. The water temperature in this confluence was consistently around 2 °C warmer than the average water temperature in lower Cherry Run during this time period

Although the Fishing Creek brook trout, which were the larger fish (mean weight  $177 \pm 75$ g), overall exhibited the most mobility and traveled the furthest distances, there was variability in net movement among Fishing Creek brook trout, as well as among brook trout in the other three study areas (Figure 4). The average fish size was similar between lower Cherry Run (mean weight  $60 \pm 16$ g), upper Cherry Run (mean weight  $64 \pm 12$ g), and UNT (mean weight  $64 \pm 12$ g; Table 1).

*Water temperature and stream flow.* - Both water temperature and stream flow varied considerably throughout the study period. The water temperature in Fishing Creek ranged from 2.8 – 16.5 °C, with a mean daily water temperature of  $7.8 \pm 3.1$  °C. The water temperature in lower Cherry Run ranged from 0.1 – 17.0 °C, with a mean daily water temperature of  $5.9 \pm 4.6$  °C, while the water temperature in upper Cherry Run ranged from 2.0 – 16.2 °C, with a mean daily water temperature of  $8.2 \pm 3.2$  °C. The water temperature in the UNT ranged from 3.4 – 15.0 °C, with a mean daily water temperature of  $8.5 \pm 2.8$  °C (Figure 5). Mean daily stream temperatures did not vary more than 2° C between temperature loggers that were deployed in the tributaries and 4° C in between temperature loggers in Fishing Creek. Fluctuations (i.e., day-to-day increases and decreases) were similar across all the temperature loggers in each stream. There were two high flow events during the study period, which occurred on 30 September 2010 and 1 December 2010. There were also several smaller increases in flow during October and

November 2010 (Figure 6). The trends in stream flow stage were similar for all of the study streams.

*Brook trout movement modeling.* – The results of model MM1b (AICc = 2966.12,  $\Delta$ AICc = 0.93, log-likelihood = -1475.98, number of estimable parameters ( $K$ ) = 7) compared to model MM1 (AICc = 2965.19,  $\Delta$ AICc = 0.0, Log-likelihood = -1477.56,  $K$  = 5) did not suggest that a more complex model that included an autocorrelated error structure was warranted. Therefore, I fitted all subsequent models under the assumption that the residual errors were independently normally distributed. In other words, residuals from different points in time did not co-vary in the models, suggesting that brook trout movement (or lack of movement) at one location was not influenced by brook trout movement (or lack of movement) at the previous location. In addition, contrary to my expectation, the results of model MM1c (AICc = 2968.37,  $\Delta$ AICc = 3.18, log-likelihood = -1472.99,  $K$  = 11) when compared to model MM1 indicated little evidence to suggest that temporal movement trends varied among streams. Therefore, subsequent movement models did not estimate separate smoothers for each stream.

The top-ranked movement model was MM5 ( $w_i=0.31$ ), which included an interaction term of time and fish weight (Table 2). The second-ranked model was MM6 ( $w_i= 0.22$ ), which included an interaction term of time and flow. Model MM1, which contained only time, was the fourth-ranked model ( $w_i= 0.12$ ; Table 2). Because all three top-ranked models included an interaction with time of year or a time of year main effect, these results suggest factors that influence brook trout movement in this system were largely time-dependent.

The top ranked model (MM5) suggested that larger fish tended to move more in early fall, corresponding with brook trout spawning season (Figure 7). Similarly, the second ranked

model (MM6) suggested that large movements observed early in the season tended to occur during high flow events, with the amount of movement associated with higher flows declining over time (Figure 8). These results were expected based on what was observed in the field. The large-scale movements of several kilometers observed during the study were by the largest brook trout. Yet, the trend of decreasing movement (see Brook trout movement summary) was observed across all fish. In addition, during the first high flow event on 28 September 2010, a large portion of the brook trout in all of the streams moved 200 m or more, with several movements of >1 km. During the second high flow event on 1 December 2010 there was little to no movement (generally 50 m or less), with the largest single movement being 250 m.

*Brook trout habitat use models.* – Across the entire reach of Cherry Run, residual pool habitat percentages, calculated as the total length of each habitat category, were 14 percent shallow, 18 percent intermediate, 17 percent deep, and 51 percent non-pool. Unconditional models were fitted for each spatial scale (250, 500, 1,000 m, and landscape-scale) to evaluate overall selection of residual pool habitat categories compared to non-pool habitats and to quantify heterogeneity in selection among individual fish. Based on all the unconditional models, there was an expected selection for residual pool habitat compared to non-pool habitats (Table 3). However, there was considerable variability among individual fish in their selection for intermediate and deep pools across all spatial scales, whereas there was little or no variability among individual fish for selection of shallow pool habitats (Table 3 variances and Figures 9 – 12).

After the addition of time, habitat-level, and fish-level covariates, the top-ranked model at the 250 m and 1,000 m scales was model HM4 ( $w_i = 0.66$  and  $0.39$ , respectively), which included the nonparametric covariate time and the nonparametric habitat-specific covariate of

habitat mean length (Table 4). The top-ranked model at the 500 m scale was HM5 ( $w_i = 0.69$ ), which included the nonparametric covariates time, the fish-specific covariate of natural log-transformed fish weight, and the nonparametric habitat-specific covariate of habitat mean length (Table 4). For the landscape model, the top-ranked model was LHM2 ( $w_i = 0.72$ ), which included the nonparametric covariate time (Table 5).

Parameter estimates, standard deviations, 95% confidence intervals, and individual specific random effects for the top-ranked model at each spatial scale are provided in Table 6. The parameter estimates and variances were similar to the unconditional models across the spatial scales. This indicated that, even when covariates were included in the models, there was comparable selection between the residual pool categories by brook trout as well as little variability between individual fish in the use of shallow residual pools, and larger variability among individual fish in the use of intermediate and deep residual pools.

Because all of the covariates in the top-ranked models were modeled nonparametrically, parameter estimates were not provided in Table 6. Rather, graphical representations are provided (Figures 13 – 20). The nonparametric effect of habitat patch length was included in the top-ranked models at the 250 m, 500 m, and 1,000 m. Since I located brook trout almost exclusively in residual pool habitat (99.7% of the locations), the results were interpreted as the selection of patch length in relation to residual pool habitat. At the 250 m scale, there was an increasing selection for residual pool habitat of around 20 – 40 m in patch length with a decrease in selection of habitats greater than 40 m in length (Figure 13). At the 500 m scale, there was an increasing selection for residual pool habitat of around 20 – 30 m in length with a sharp decrease in selection for habitat patches greater than 35 m in length (Figure 14). At the 1,000 m scale,

there was an increasing selection for residual pool habitat of around 20 – 30 m in patch length (Figure 15).

The nonparametric effect of time was included in the top-ranked model at all spatial scales. Although there was a slight indication of seasonal variation in the use of shallow and deep residual pools at the 250 m scale, illustrated by the curvilinear fitted lines (Figure 16), this seasonal effect was much more pronounced at the 500 m, 1,000 m and landscape scales. At these larger spatial scales, an increased selection of shallow residual pools occurred between October to early to mid-November (time -1.5 and -0.5 on the figures), which encompassed much of brook trout spawning season (Figures 17-19). This trend leveled off with the end of spawning season in early November (around time zero). During this same period, between early October to early November (time -1.5 and zero), there was a decrease in selection of deep residual pools and then a subsequent sharp increase during the time period that corresponded with the onset of winter conditions. Selection of intermediate residual pools increased in a linear manner over time at these three spatial scales.

The nonparametric effect of the natural log-transformed fish weight was included in the top-ranked model at the 500 m spatial scale. There was an increased selection for shallow residual pools by larger fish with a nonlinear effect for intermediate residual pools, as selection increased with fish size and then decreased. There was essentially no effect of fish size on selection for deep residual pools (Figure 20).

**Table 1.** Individual summary for 36 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed in Clinton County, PA. Fish ID is the radio-tag number, length is the total length of the fish in mm, weight is the weight of the fish in g. Class is the site classification of each fish based on where the fish was found at its last location. (FC = Fishing Creek, LCR = lower Cherry Run, UCR = upper Cherry Run, and UNT = unnamed tributary). Days is the number of days the fish was tracked, locations is the number of times a fish was relocated after being tagged and released, total movement is the total movement the fish moved. Net movement is the distance in meters of the last location for the fish with respect to its release point, with '+' indicating upstream and '-' indicating downstream. Furthest upstream and furthest downstream is the furthest distance upstream and downstream in meters that the fish was located with respect to its release point, respectively.

Fish ID	Length (mm)	Weight (g)	Class	Days	Locations	Total Movement (m)	Net movement (m)	Furthest upstream (m)	Furthest downstream (m)
101	228	115	FC	11	5	865	+810	810	0
110	213	95	FC	129	42	3145	+795	885	15
119	289	233	FC	81	31	670	+40	165	15
120	345	348	FC	115	34	6090	-5355	0	5400
127	240	133	FC	107	36	890	+105	215	65
133	248	154	FC	95	35	2920	+1460	1480	20
111	260	165	FC*	39	18	2950	+645	1745	570
125	295	245	FC*	123	39	9000	+2090	2860	570
102	263	162	FC*	115	33	7595	-6910	195	6910
108	215	104	FC*	85	30	3790	-3220	0	3425
131	267	192	FC*	115	35	4650	-3475	240	3565
109	212	91	LCR	51	18	7475	+735	1545	525
112	182	66	LCR	93	22	1570	-945	275	945
123	184	55	LCR	114	30	5760	-1225	1200	1660
124	168	48	LCR	115	25	3290	-3000	35	3010
130	173	48	LCR	71	18	1035	+95	310	0
132	172	53	LCR	78	20	585	-125	210	135
104	182	56	UCR	84	19	105	-5	20	5

106	192	63	UCR	15	4	800	+610	690	10
107	212	94	UCR	84	19	2070	+75	455	20
113	187	64	UCR	26	7	1710	-145	730	155
114	185	62	UCR	78	18	295	-245	0	270
115	185	50	UCR	84	19	180	0	38	0
118	198	64	UCR	84	19	1095	-175	100	265
122	192	70	UCR	91	20	50	+10	30	0
128	201	62	UCR	78	18	240	-5	90	10
136	175	57	UCR	84	19	1480	-10	320	10
103	181	62	UNT	77	16	45	+35	35	0
105	202	77	UNT	30	8	135	-15	30	15
121	167	48	UNT	35	9	130	0	60	0
126	195	71	UNT	15	4	85	-5	40	5
129	187	73	UNT	10	3	20	-20	0	20
134	175	52	UNT	30	8	225	-95	0	150
135	201	77	UNT	72	16	475	-295	40	295
213	184	63	UNT	46	11	190	0	75	20
214	176	49	UNT	35	9	120	-20	0	30

\* Fish was located in both Fishing Creek and lower Cherry Run during study period, but last location was in Fishing Creek.

**Table 2.** Candidate generalized additive mixed models for describing movement of 36 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed in Clinton County, PA (see Methods for description of models MM1 – MM9). AICc is AIC corrected for small sample size,  $\Delta_i$  = AICc differences,  $w_i$  = Akaike weights,  $K$  is the number of estimable parameters, Log-lik is the log-likelihood. Models are listed in descending order from top- to lowest-ranked model. A “+” indicates the covariates are additive in the model. An “x” indicates an interaction between two or more covariates in the model; temp = temperature (°C); weight = natural log of fish’s weight (g), and flow is a stream flow index; see Methods for a detailed description of covariates.

<b>Model</b>	<b>Description</b>	<b><math>K</math></b>	<b>Log-lik</b>	<b>AICc</b>	<b><math>\Delta_i</math></b>	<b><math>w_i</math></b>
MM5	time x weight	6	-1475.56	2963.23	0.00	0.31
MM6	time x flow	6	-1475.92	2963.97	0.73	0.22
MM3	time + flow	7	-1475.21	2964.58	1.35	0.16
MM1	time	5	-1477.55	2965.19	1.96	0.12
MM2	time + weight	7	-1475.56	2965.27	2.04	0.11
MM7	time x temp	6	-1477.27	2966.66	3.42	0.06
MM4	time + temp	7	-1477.27	2968.70	5.47	0.02
MM8	time x temp x flow	13	-1472.60	2971.73	8.50	0.00
MM9	time x temp x flow x weight	18	-1468.50	2973.98	10.75	0.00

**Table 3.** Parameter estimates, standard deviations, 95% confidence intervals, and habitat-specific variances (individual fish-specific random effects) for the unconditional discrete choice habitat use models for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA at the 250 m, 500 m, 1,000 m, and landscape spatial scale. The reference category for all models was “non-pool” habitat.  $\hat{\beta}$  is the estimated preferences for each of the pool habitats classified by maximum residual depth, SD is the standard deviation, 95% CI is the 95% confidence interval, and  $\hat{\tau}_r^2$  is the habitat-specific variance describing variability in selection among individual fish.

<b>Spatial scale</b>	$\hat{\beta}$	<b>SD</b>	<b>95% CI</b>	$\hat{\tau}_r^2$
<b><u>250 m</u></b>				
Shallow pool	4.08	0.51	3.07-5.08	0.00
Intermediate pool	3.50	0.69	2.15-4.84	3.41
Deep pool	3.70	0.66	2.41-4.98	2.81
<b><u>500 m</u></b>				
Shallow pool	4.10	0.46	3.20-5.00	0.00
Intermediate pool	3.60	0.66	2.30-4.88	3.75
Deep pool	3.85	0.61	2.65-5.05	2.73
<b><u>1,000 m</u></b>				
Shallow pool	4.13	0.46	3.23-5.03	0.00
Intermediate pool	3.55	0.65	2.27-4.83	3.68
Deep pool	3.81	0.60	2.64-4.99	2.50
<b><u>Landscape</u></b>				
Shallow pool	4.29	0.47	3.37-5.20	0.13
Intermediate pool	3.61	0.66	2.32-4.90	3.77
Deep pool	3.91	0.63	2.67-5.15	3.24

**Table 4.** Candidate discrete choice models with random effects describing habitat use for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA (see Methods for description of models HM1 – HM6) at the 250 m, 500 m, and 1,000 m spatial scales.  $df$  is the corresponding equivalent degrees of freedom,  $-2l$  is  $-2 \times$  log-likelihood,  $\Delta_i$  is the AIC difference, and  $w_i$  is the Akaike weight. Models are listed in descending order from top- to lowest-ranked model.

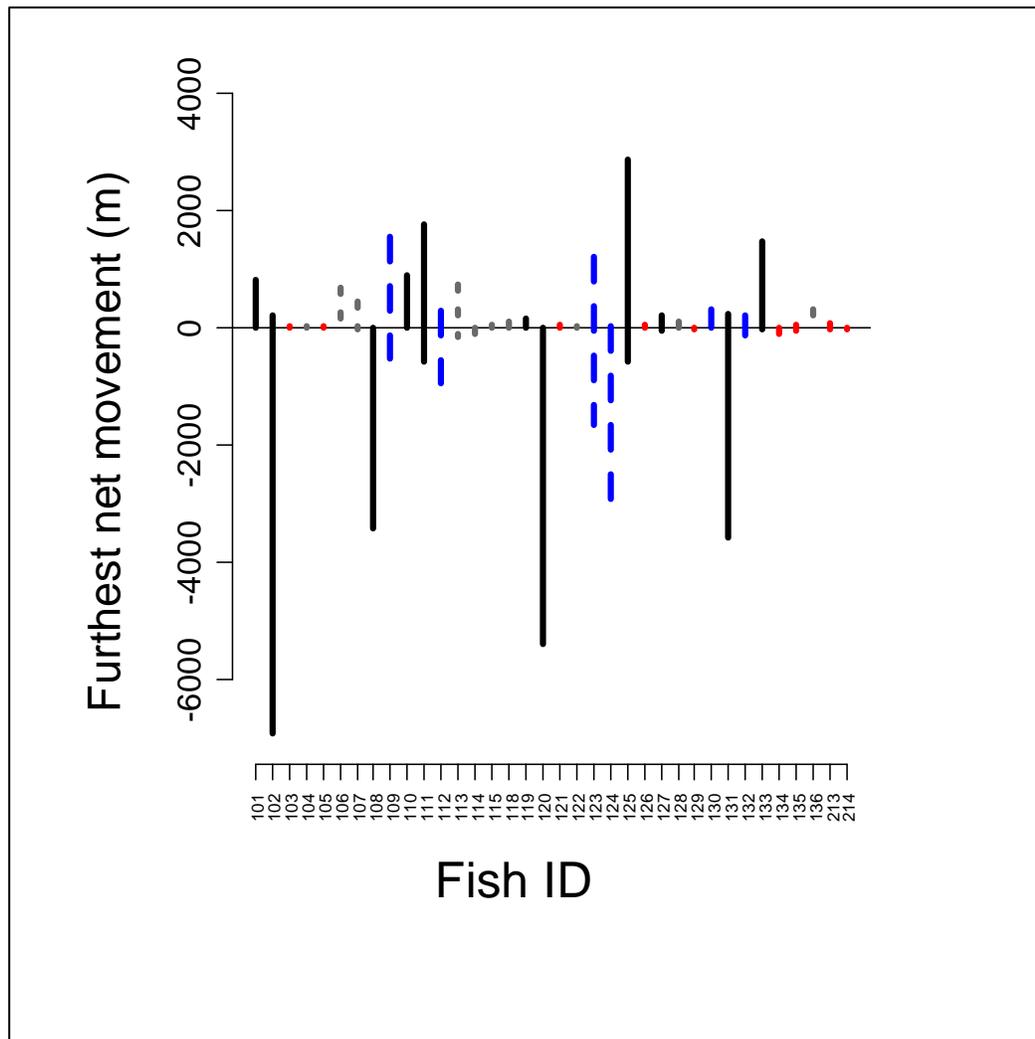
<b>Spatial scale</b>	<b><math>df</math></b>	<b><math>-2l</math></b>	<b>AIC</b>	<b><math>\Delta_i</math></b>	<b><math>w_i</math></b>
<b><u>250 m</u></b>					
HM4	37.40	273.35	348.13	0.00	0.66
HM5	39.12	271.97	350.21	2.07	0.24
HM6	40.45	271.10	351.99	3.85	0.10
HM2	31.65	294.91	358.22	10.09	0.00
HM3	37.41	300.05	374.87	26.73	0.00
HM1	30.65	326.17	387.46	39.33	0.00
<b><u>500 m</u></b>					
HM5	44.53	344.67	433.73	0.00	0.69
HM6	46.21	343.40	435.82	2.10	0.24
HM4	42.35	353.61	438.31	4.58	0.07
HM3	40.24	371.53	452.00	18.28	0.00
HM2	35.32	384.72	455.37	21.64	0.00
HM1	31.98	415.90	479.85	46.13	0.00
<b><u>1,000 m</u></b>					
HM4	41.86	374.78	458.50	0.00	0.39
HM5	43.74	372.02	459.50	1.00	0.24
HM3	40.21	379.27	459.70	1.19	0.22
HM6	44.95	370.53	460.42	1.92	0.15
HM2	32.89	421.36	487.14	28.64	0.00
HM1	31.94	423.93	487.80	29.30	0.00

**Table 5.** Candidate discrete choice models with random effects describing habitat use for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA (see Methods for description of models HM1 – HM6) at the landscape scale.  $df$  is the corresponding equivalent degrees of freedom,  $-2l$  is  $-2 \times \log$ -likelihood,  $\Delta_i$  is the AIC difference, and  $w_i$  is the Akaike weight. Models are listed in descending order from top- to lowest-ranked.

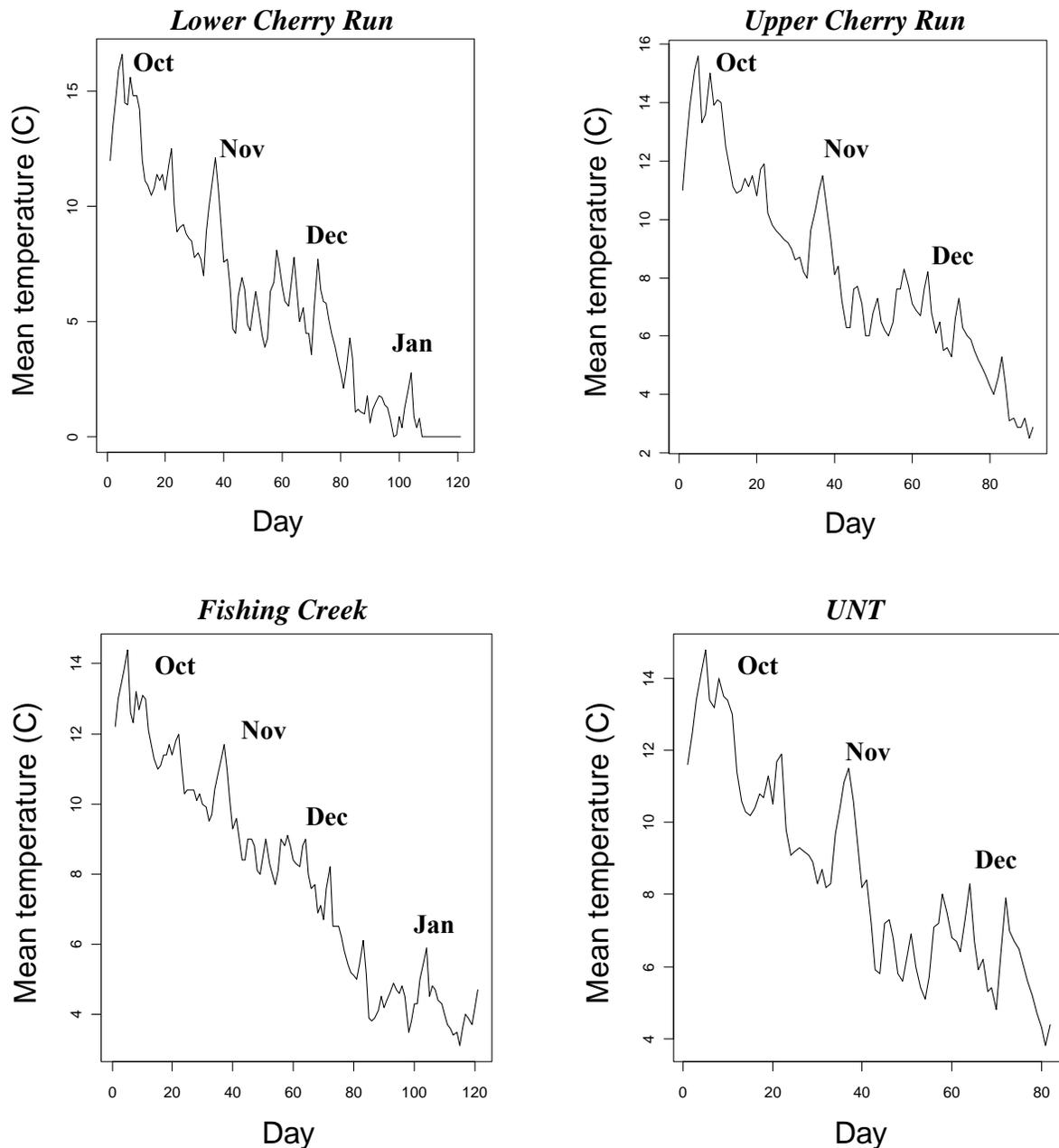
	$df$	$-2l$	AIC	$\Delta_i$	$w_i$
LHM2	42.02	377.91	461.95	0.00	0.72
LHM3	44.23	375.37	463.82	1.86	0.28
LHM1	33.45	425.65	492.55	30.60	0.00

**Table 6.** Parameter estimates, standard deviations, 95% confidence intervals, and habitat-specific variances (individual-specific random effects) for the top-ranked discrete choice habitat use models for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA at the 250 m, 500 m, 1,000 m, and landscape spatial scale (see Tables 4 and 5). The reference category for all models was “non-pool” habitat.  $\hat{\beta}$  is the estimated preferences for each of the pool habitats classified by maximum residual depth, SD is the standard deviation, 95% CI is the 95% confidence interval, and  $\hat{\tau}_r^2$  is the habitat-specific variance describing variability in selection among individual fish. Covariate parameter estimates are not provided because all covariate effects were modeled nonparametrically. See Figures 13-20 for graphical representation of effects.

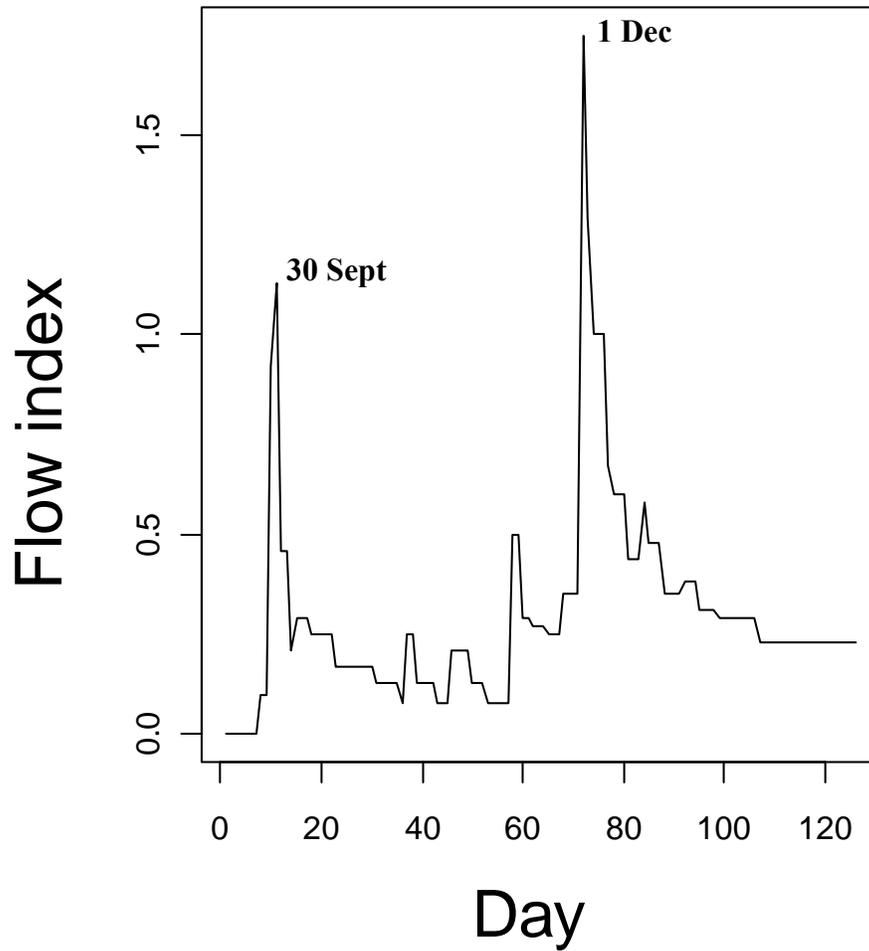
<b>Spatial Scale</b>	$\hat{\beta}$	<b>SD</b>	<b>95% CI</b>	$\hat{\tau}_r^2$
<b><u>250 m</u></b>				
Shallow pool	5.83	1.13	3.61-8.04	0.00
Intermediate pool	5.06	1.20	2.72-7.40	3.38
Deep pool	4.63	1.18	2.32-6.95	3.36
<b><u>500 m</u></b>				
Shallow pool	4.67	0.96	2.80-6.54	0.00
Intermediate pool	4.42	1.02	2.41-6.43	3.67
Deep pool	3.66	1.03	1.64-5.68	2.66
<b><u>1,000 m</u></b>				
Shallow pool	4.53	0.96	2.65-6.41	0.08
Intermediate pool	4.60	1.01	2.62-6.58	4.29
Deep pool	4.30	1.01	2.31-6.29	1.92
<b><u>Landscape</u></b>				
Shallow pool	5.12	0.89	3.37-6.87	0.12
Intermediate pool	4.80	1.00	2.85-6.75	4.75
Deep pool	4.95	1.00	3.00-6.90	3.77



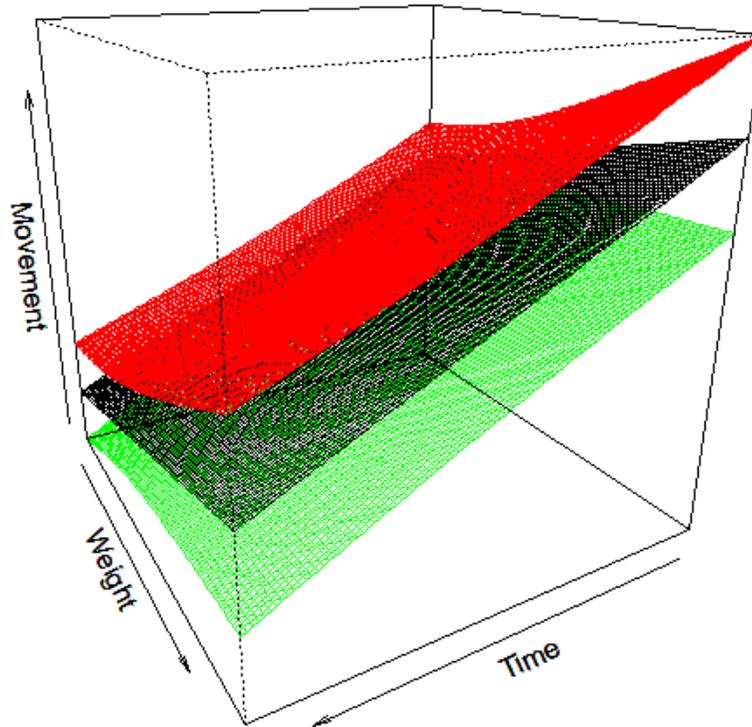
**Figure 4.** Net movement for 36 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed in Clinton County, PA. The  $x$ -axis is the fish identifier (corresponding to the Fish ID in Table 1) and the  $y$ -axis indicates the furthest upstream (+) and downstream (-) location for each fish. The solid black line represents Fishing Creek brook trout, the dashed blue line represents lower Cherry Run brook trout, the dashed gray line represents upper Cherry Run brook trout, and the red line represents UNT brook trout. Brook trout were classified based on where the fish was found at its last location.



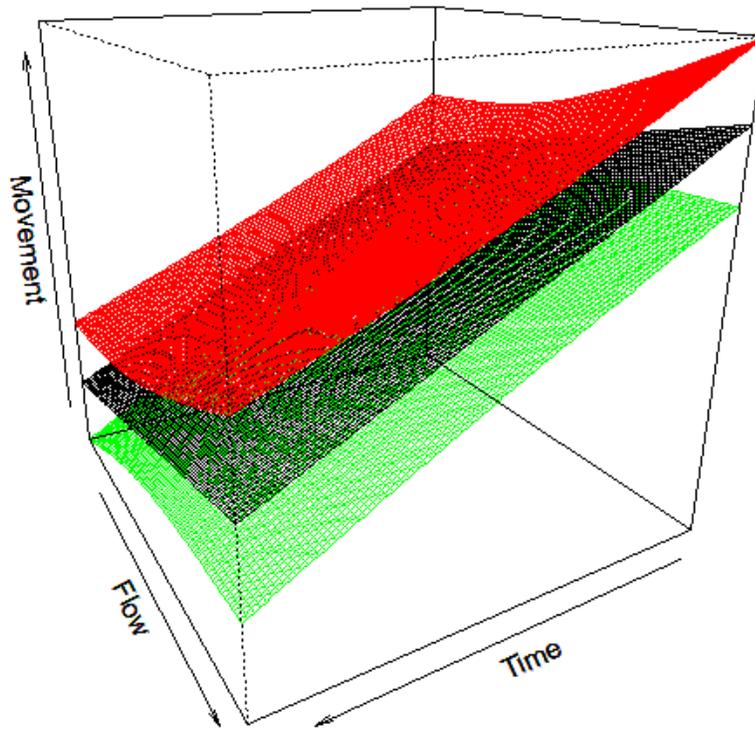
**Figure 5.** Mean daily water temperature in °C recorded from HOBO ProV2 temperature loggers (Onset Computer Corporation, Bourne, MA, USA) in Fishing Creek, lower Cherry Run, upper Cherry Run, and an unnamed tributary (UNT) in Clinton County, PA from 21 September (Day 1) 2010 – 19 January 2011 (Day 121). The beginnings of the months from October 2010 to January 2011 are indicated on the graphs to aid in visualizing temporal trends.



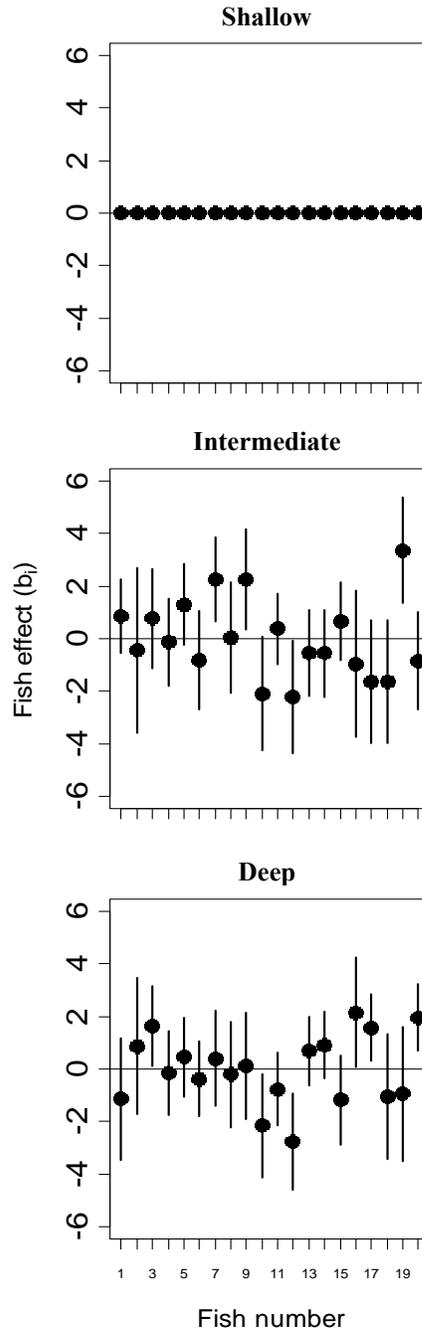
**Figure 6.** Stream flow stage index in Cherry Run in Clinton County, PA from 21 September 2010 (Day 1) to 24 January 2011 (Day 126). High flow events of 30 September and 1 December are indicated.



**Figure 7.** Three-dimensional plot of the interaction between fish size (expressed as weight in grams) and time on movement for 36 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed in Clinton County, PA. Middle surface is predicted effect, upper and lower surfaces represent  $\pm 2$  standard errors. Weight is the natural log of the weight (g) of the individual brook trout, time is the grand-mean centered day of the study, and movement is the distance in meters between locations for each individual brook trout.

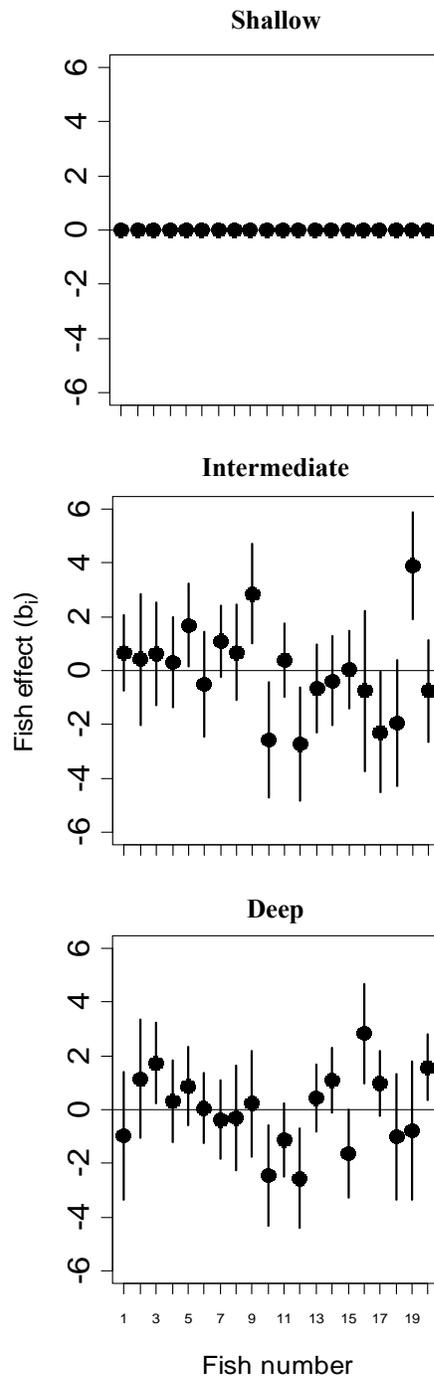


**Figure 8.** Three-dimensional plot of the interaction between flow and time on movement for 36 wild brook trout radio-tracked between 20 September 2001 and 24 January 2011 in the Fishing Creek watershed in Clinton County, PA. Middle surface is predicted effect, upper and lower surfaces represent  $\pm 2$  standard errors. Flow is the change in the stream stage flow index, time is the grand-mean centered day of the study, and movement is the distance in meters between locations for each individual brook trout.



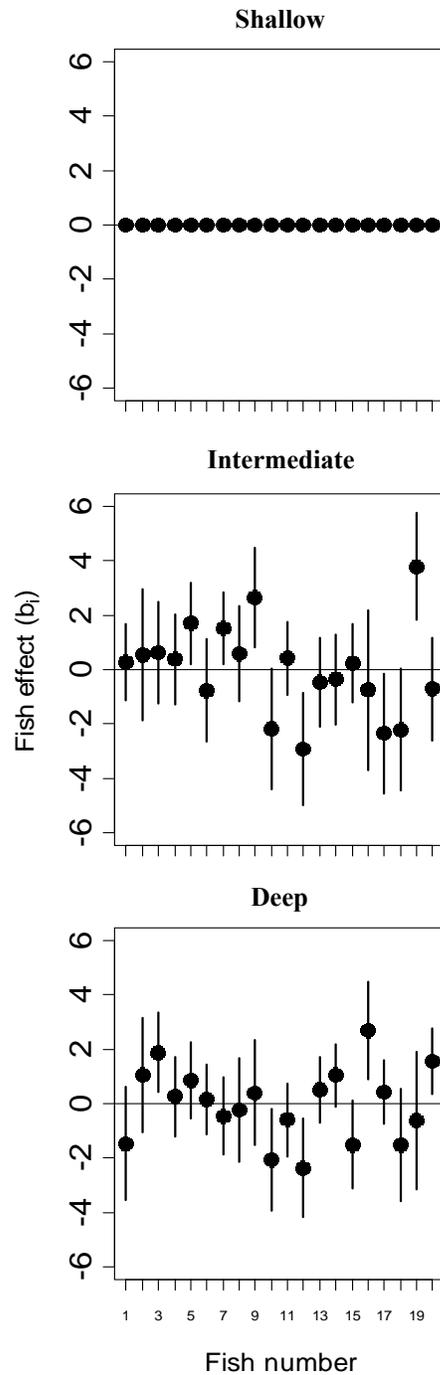
**Figure 9.** Graphs of Best Linear Unbiased Predictors (BLUPs) for individual fish illustrating individual heterogeneity at the 250 m scale in the use of each pool habitat classified by maximum residual depth for 20 wild brook trout radio-tracked between 20 September 2010 and

24 January 2011 in Cherry Run in Clinton County, PA. The tick marks on the  $x$ -axis are the individual fish and the  $y$ -axis is the value of the BLUP. Circles are means and vertical bars are 95% confidence intervals. A BLUP value above zero indicates that an individual fish used a habitat type more than the population average and a BLUP value below zero indicates that an individual fish used a habitat type less than the population average.



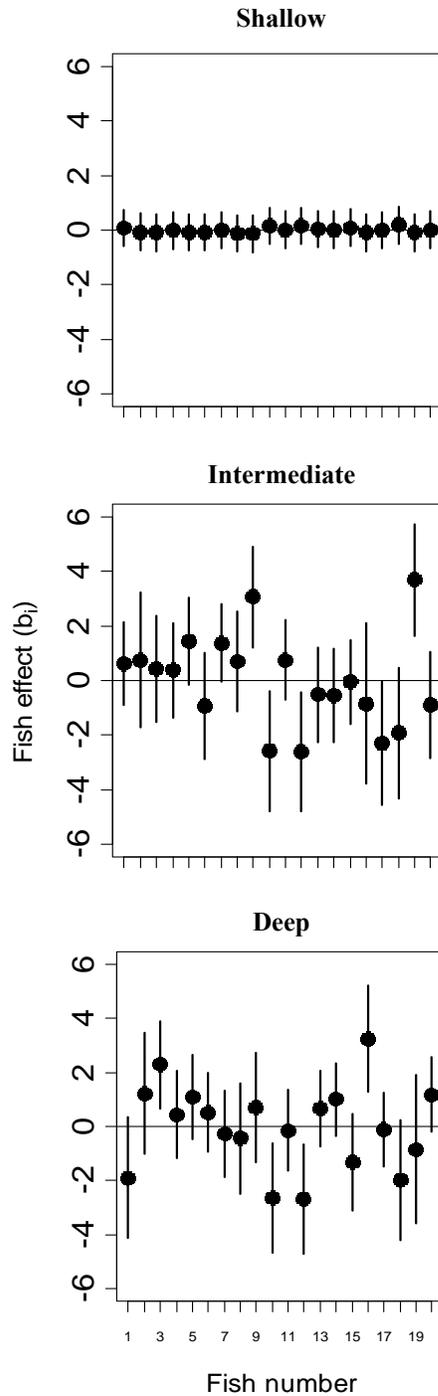
**Figure 10.** Graphs of Best Linear Unbiased Predictors (BLUPs) for individual fish illustrating individual heterogeneity at the 500 m scale in the use of each pool habitat classified by maximum residual depth for 20 wild brook trout radio-tracked between 20 September 2010 and

24 January 2011 in Cherry Run in Clinton County, PA. The tick marks on the  $x$ -axis are the individual fish and the  $y$ -axis is the value of the BLUP. Circles are means and vertical bars are 95% confidence intervals. Solid horizontal line at zero was added to aid interpretation. A BLUP value above zero indicates that an individual fish used a habitat type more than the population average and a BLUP value below zero indicates that an individual fish used a habitat type less than the population average.



**Figure 11.** Graphs of Best Linear Unbiased Predictors (BLUPs) for individual fish illustrating individual heterogeneity at the 1,000 m scale in the use of each pool habitat classified by maximum residual depth for 20 wild brook trout radio-tracked between 20 September 2010 and

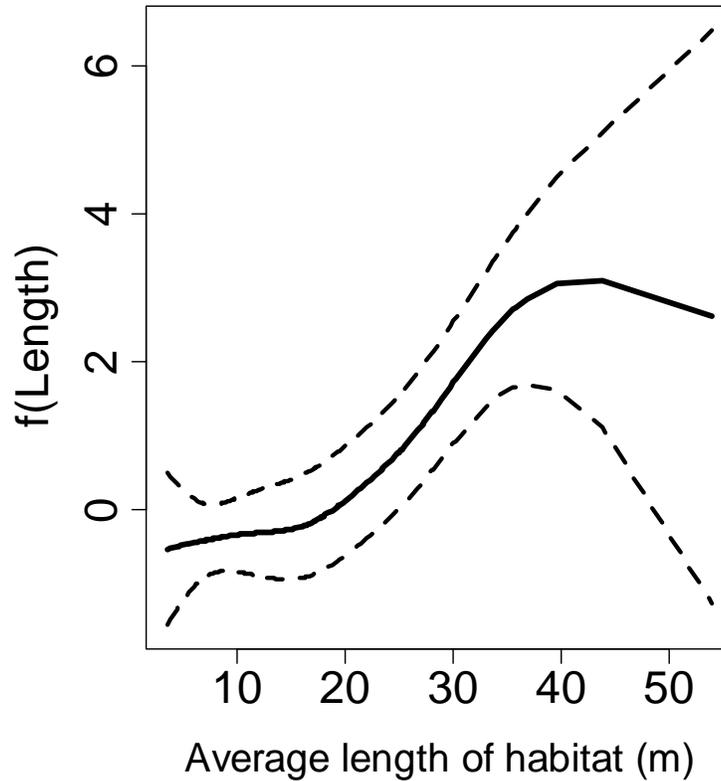
24 January 2011 in Cherry Run in Clinton County, PA. The tick marks on the  $x$ -axis are the individual fish and the  $y$ -axis is the value of the BLUP. Circles are means and vertical bars are 95% confidence intervals. Solid horizontal line at zero was added to aid interpretation. A BLUP value above zero indicates that an individual fish used a habitat type more than the population average and a BLUP value below zero indicates that an individual fish used a habitat type less than the population average.



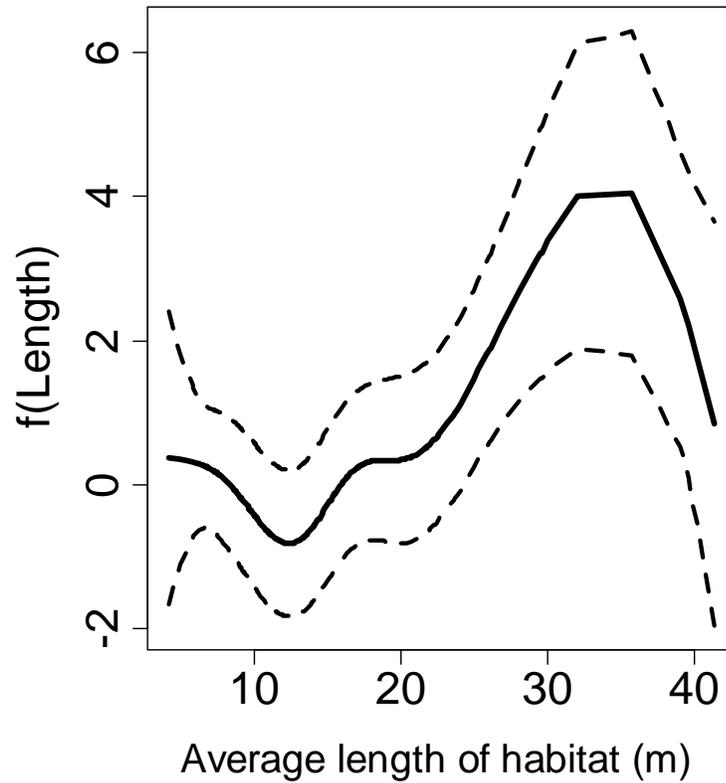
**Figure 12.** Graphs of Best Linear Unbiased Predictors (BLUPs) for individual fish illustrating individual heterogeneity at the landscape scale in the use of each pool habitat classified by maximum residual depth for 20 wild brook trout radio-tracked between 20 September 2010 and

24 January 2011 in Cherry Run in Clinton County, PA. The tick marks on the  $x$ -axis are the individual fish and the  $y$ -axis is the value of the BLUP. Circles are means and vertical bars are 95% confidence intervals. Solid horizontal line at zero was added to aid interpretation.

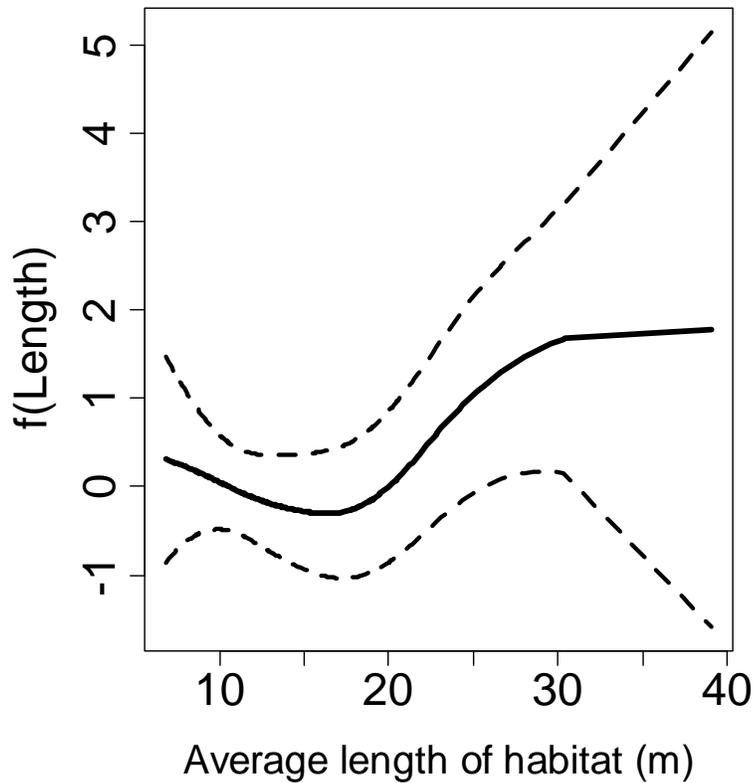
A BLUP value above zero indicates that an individual fish used a habitat type more than the population average and a BLUP value below zero indicates that an individual fish used a habitat type less than the population average.



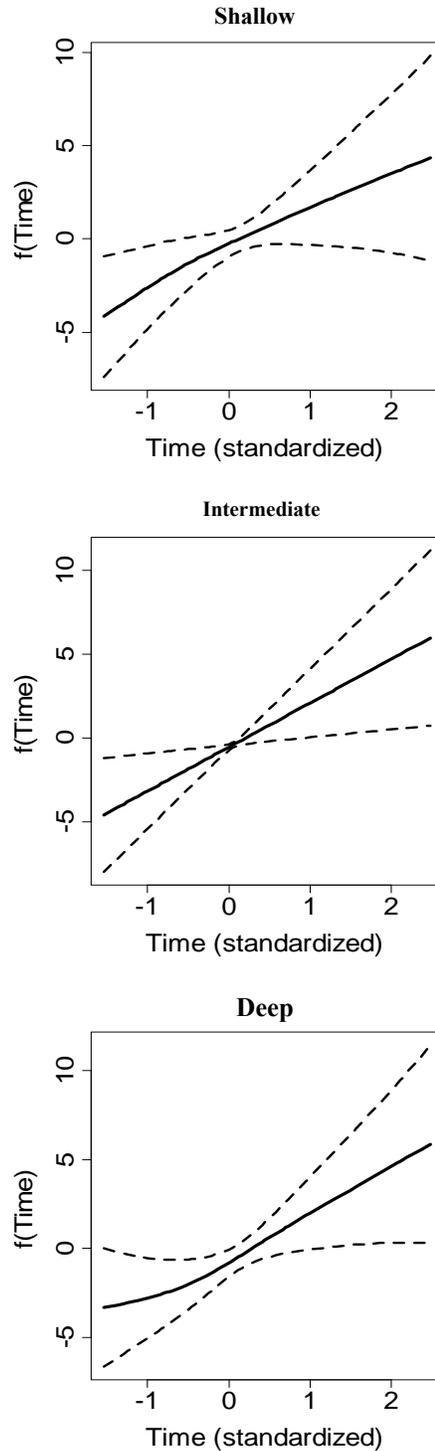
**Figure 13.** Estimated nonparametric effect of habitat patch length on habitat selection at the 250 m scale, for model HM4 (see Methods for details), for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The effect is habitat-specific and defined globally. The  $x$ -axis is the average length of the habitat patches in meters in the choice sets and the  $y$ -axis shows the effect of the length of a habitat patch on brook trout habitat selection.



**Figure 14.** Estimated nonparametric effect of habitat patch length on habitat selection at the 500 m scale, for model HM5 (see Methods for details), for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The effect is habitat-specific and defined globally. The  $x$ -axis is the average length of the habitat patches in meters in the choice sets and the  $y$ -axis shows the effect of the length of a habitat patch on brook trout habitat selection.

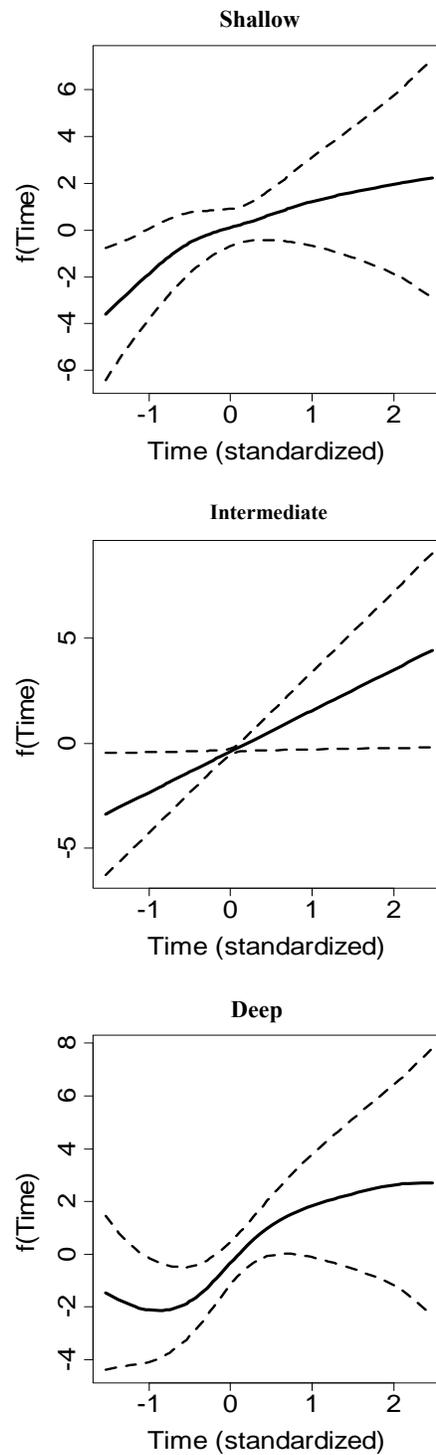


**Figure 15.** Estimated nonparametric effect of habitat patch length on habitat selection at the 1,000 m scale, for model HM4 (see Methods for details), for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The effect is habitat-specific and defined globally. The  $x$ -axis is the average length of the habitat patches in meters in the choice sets and the  $y$ -axis shows the effect of the length of a habitat patch on brook trout habitat selection.



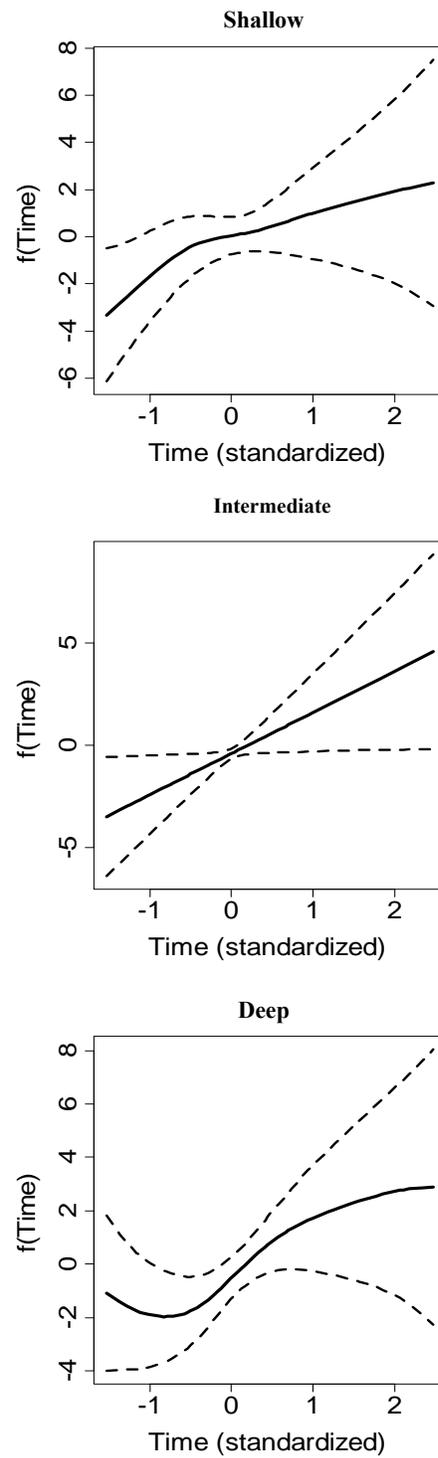
**Figure 16.** Estimated nonparametric effect of time on habitat selection at the 250 m scale for each pool habitat classified by maximum residual depth for model HM4 (see Methods for

details) for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The *x*-axis is time (standardized, see Methods for details) and the *y*-axis shows the effect of time on brook trout habitat selection.



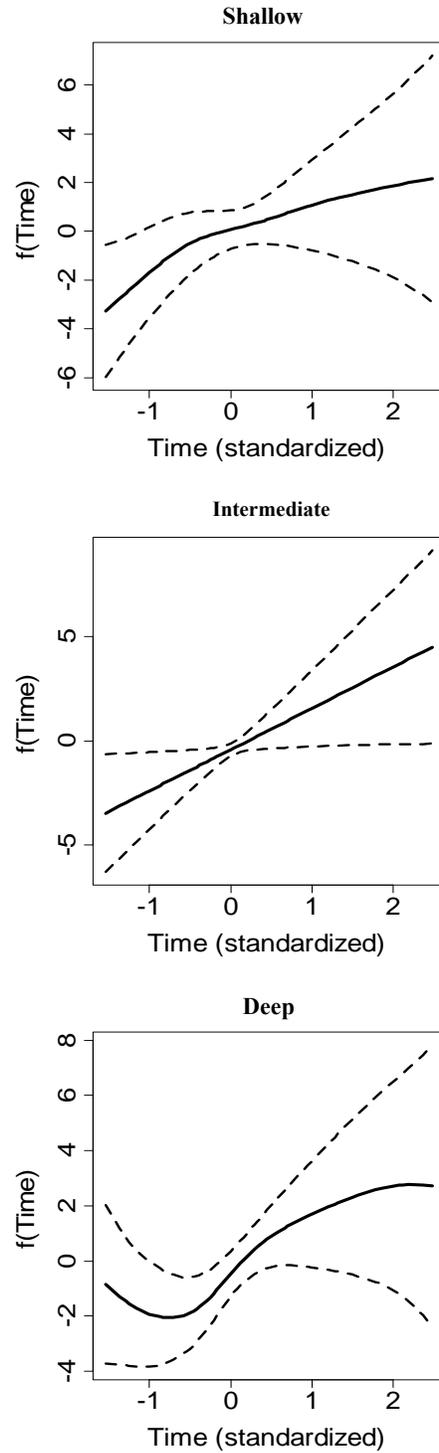
**Figure 17.** Estimated nonparametric effect of time on habitat selection at the 500 m scale for each pool habitat classified by maximum residual depth for model HM5 (see Methods for

details) for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The *x*-axis is time (standardized, see Methods for details) and the *y*-axis shows the effect of time on brook trout habitat selection.



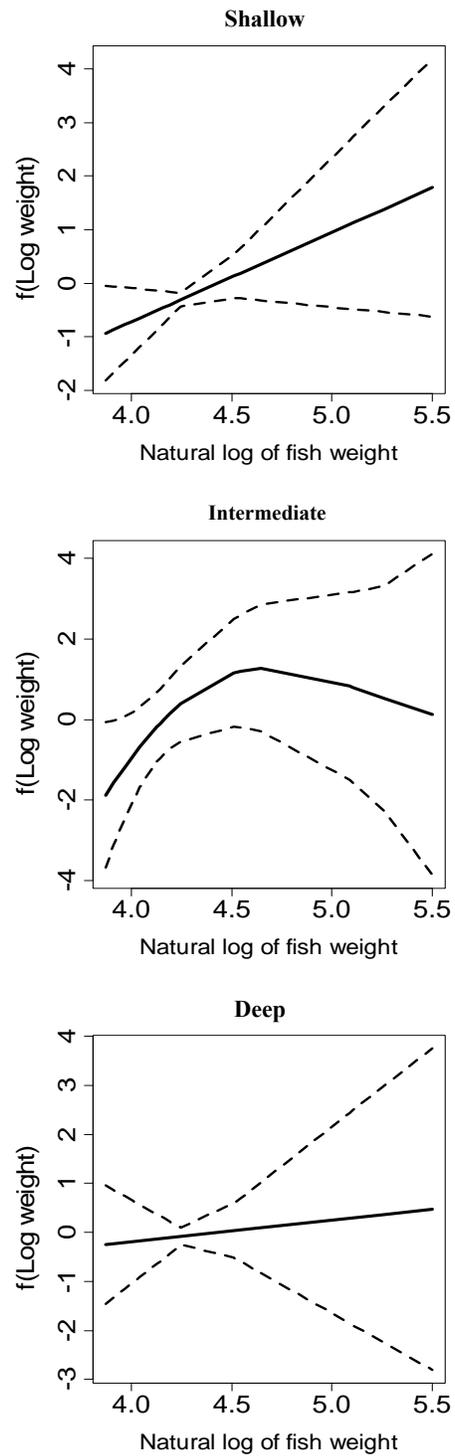
**Figure 18.** Estimated nonparametric effect of time on habitat selection at the 1,00 m scale for each pool habitat classified by maximum residual depth for model HM4 (see Methods for

details) for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The  $x$ -axis is time (standardized, see Methods for details) and the  $y$ -axis shows the effect of time on brook trout habitat selection.



**Figure 19.** Estimated nonparametric effect of time on habitat selection at the landscape scale for each pool habitat classified by maximum residual depth for model LHM2 (see Methods for

details) for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The *x*-axis is time (standardized, see Methods for details) and the *y*-axis shows the effect of time on brook trout habitat selection.



**Figure 20.** Estimated nonparametric effect of the natural log of fish weight (g) on habitat selection at the 500 m scale for each pool habitat classified by maximum residual depth for

model HM5 (see Methods for details) for 20 wild brook trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run in Clinton County, PA. Solid line is predicted mean and dashed lines are 95% confidence intervals. The  $x$ -axis is the natural log of fish weight in grams and the  $y$ -axis shows the effect of the natural log of fish weight on brook trout habitat selection.

## Chapter 5

### DISCUSSION

*Brook trout movement.* – Seasonal movement was observed in 36 wild brook trout that were radio-tracked in central Pennsylvania between 20 September 2010 and 24 January 2011. As expected, there was increased activity during spawning season in October and November. This coincided with the time of year when water temperatures were between 8-16 °C. In addition to increased activity in most of the fish, several of the brook trout exhibited long-distance movements (> 1 km) during this period. These patterns are consistent with other biotelemetry studies evaluating seasonal movement in salmonids. For example, long distance movements and increased activity of brown trout during the fall (also spawning season for brown trout) have been observed (Meyers et al. 1992; Burrell et al. 2000). For brook trout, studies have identified increases in the frequency and distance of movements just prior to and during spawning season (Curry et al. 2002; Hansbarger et al. 2010). Sampling methods using electrofishing and weirs also have reported comparable seasonal activity for brook trout during the fall (Gowan and Fausch 1996; Peterson and Fausch 2003; Petty et al. 2005).

Although there was a general increase in movement throughout the fall, there were two specific periods of notably higher activity. The first one occurred during late September and the second during mid-November. These times of year coincide with the beginning and end of spawning season for wild brook trout in central Pennsylvania. Mid-November also corresponded to the time of year when stream temperatures began to decline towards winter conditions (i.e., average daily water temperature < 7°C). Though it was during this second period of increased activity that five brook trout moved downstream from lower Cherry Run into Fishing Creek and another brook trout moved 6.9 km downstream in Fishing Creek, it is uncertain whether this

movement was related to spawning or to decreasing water temperatures. Brown and Mackay (1995) observed a similar trend during a biotelemetry study on cutthroat trout, with a period of increased movement at the onset of the spawning season followed by a subsequent period of increased activity just prior to winter.

While there was an influence of time of year on brook trout movement, it is important to emphasize the variability among individual fish, with some fish consistently more active throughout the tracking period, while others moved very little. Even though main-stem brook trout were generally more mobile than those in the tributaries, this among-fish variability was observed across the study area. For instance, 14 of the fish, including two Fishing Creek brook trout never moved more than approximately 200 m from their release point. However, ten fish moved > 1 km from their release point, including three lower Cherry Run brook trout. Two Fishing Creek brook trout moved > 5 km from their release point (5.4 km and 6.9 km). Roghair and Dolloff (2005) observed a similar trend in wild eastern brook trout, with seasonal movements of < 100 m being observed for most of the fish, while the rest moved > 800 m. This variability in movement tendencies appears to be typical in other stream salmonids as well. In a recent study that used biotelemetry to track brown trout and rainbow trout, individual fish from both species exhibited variability in movement tendencies, with net movement ranging from < 200 m to > 3 km (Quinn and Kwak 2011). Burrell (2000) observed movements of brown trout during spawning season that ranged from 206 m – 7,650 m. In a study examining spatial dynamics of spawning in cutthroat trout, rainbow trout, and hybrids in the Yellowstone River, movements of individual fish of < 500 m to > 40 km were reported for all three species (DeRito et al. 2010).

Across all brook trout, activity declined in December in relation to declining stream temperatures and eventually ceased all-together in January. This trend of decreased activity as stream temperatures dropped below 7 °C has been reported for bull trout *Salvelinus confluentus* (Jakober et al. 1998), and cutthroat trout (Jakober et al. 1998; Hilderbrand and Kershner 2000), as well as brook trout (Curry et al. 2002; Lindstrom and Hubert 2004). Chisholm et al. (1987) did observe some brook trout that remained active throughout the winter in a Wyoming alpine stream system, with the movements associated with decreased instream ice formation at higher elevations. Periods of increased activity during the winter months also have been documented for brown trout, possibly due to increased nocturnal movements as a result of decreased daylight (Bunnell et al. 1998; Burrell et al. 2000). Heggenes et al. (1993) documented similar movement trends in brown trout, with nocturnal activity and feeding observed throughout the winter. I did observe a single brook trout in lower Cherry Run move downstream ~2.5 km during December into the confluence of Cherry Run and Fishing Creek. This area remained around 2 °C during January, whereas lower Cherry Run was typically around 0 °C. Although confluences have been shown to be important areas of thermal refuge during the summer for eastern brook trout (Baird and Krueger 2003), this observed winter movement may have been due to the decreased ice formation I observed in this area, rather than being directly related to thermal preferences. A lack of anchor ice (submerged ice formation) is an important habitat characteristic associated with overwintering survival in salmonids (Brown and Mackay 1995; Cunjak 1996; Jakober et al. 1998). However, considering the relatively small number of fish that were tracked during late December and January, it is difficult to explain this movement by a single brook trout or to ascertain the importance of this area of confluence as overwintering habitat for Cherry Run brook trout.

Also notable in terms of general movement characteristics of the brook trout, was the tendency of fish to return to the site where they were captured after being surgically-implanted. A preference for specific stream areas also has been documented for brown trout (Bachman 1984; Young 1994; Burrell et al. 2000). Conversely, Bélanger and Rodríguez (2001) did not observe site preference in stream-dwelling brook trout as fish released less than 900 m from their capture point did not return to this stream area. Scruton et al. (2003) also did not observe site preferences in juvenile brook trout; however, most movements were observed at night. Because I did not monitor diurnal movements and was unable to track at night (due to the 12 h off period of the transmitters), it was not possible to estimate how far a brook trout would move during a 24 h period. Also, some fish were typically found in the same stream area for multiple locations, sometimes up to several weeks, followed by a brief period of activity. After these movements, the brook trout would then typically return to a propensity of being located in particular stream area. Brown and Mackay (1995) observed a similar trend in cutthroat trout, with fish that appeared immobile demonstrating a short period of movements before returning to sedentary behavior.

Fish size also was related to movement. The larger Fishing Creek brook trout, in general, moved longer distances than brook trout in the tributaries, especially during spawning season. This was not surprising as a trend of larger fish moving more often and at greater distances has been reported for many species, including stream-dwelling brook trout (Riley et al. 1992) and brown trout (Bunnell et al. 1998; Quinn and Kwak 2010). However, by utilizing GAMMs, I was able to explore the magnitude of both linear and nonlinear relationships of fish size on brook trout movement over time. The results of the movement models suggest that the relationship between fish size and wild brook trout movement is largely a function of the time of year. This

was interpreted as larger brook trout displaying more movement during the fall, but the size of a fish having less influence on movement as winter approaches. It must be noted, however, that because all of the larger fish were located in Fishing Creek, it is difficult to separate out a true “fish size effect” from a “stream effect” in this analysis. The movement models indicated a similar temporal trend with stream flow, as the relationship of an increase in flow stage on brook trout movement decreased over time. Large scale movements and increased activity were recorded during a high flow event in September, followed by little activity during a subsequent high flow event in December. These results can be interpreted that increased flows, combined with the time of year, may have triggered a mechanism in the brook trout that increased activity. Some of the movement could have been a result of being dislodged from specific habitats, or due to fish seeking refuge from harsh environmental conditions due to the high flow. However, movement was primarily upstream during this period (including the larger-scale movements of > 1 km). This suggested that brook trout movement was primarily due to elevated activity, rather than forced movement as a result of high flows. Other studies consistently correlate high flows with increased activity in brook trout (e.g. Gowan and Fausch 1996; Scruton et al. 2003; Murchie and Smokorowski 2004), although typically during the summer or early fall.

Overall, the movement models indicated that trends in wild brook trout movement were mostly related to temporal effects and suggest that, although other factors may drive movement, in this particular system it is largely associated with spawning activity. This may not be the case for all brook trout populations, as the spatial distribution of habitats required for spawning, overwintering, and foraging may all influence the timing and magnitude of stream-dwelling fish movements (Schoby and Keeley 2011).

Although there were apparent differences in average movement between the streams (i.e., Fishing Creek and lower Cherry Run fish were more active and moved longer distances than the upper Cherry Run and UNT brook trout), a failure to detect any differences in movement over time between the streams may have been a result of increased activity across all streams during spawning season, even though total movement, on average, varied. In addition, the high individual variability in movement tendencies and relatively small sample sizes also likely reduced my ability to detect stream-specific temporal trends, if present. Although there was little evidence to suggest that trends among streams differed, there was an apparent relationship between average movement and stream gradient, with brook trout, on average, moving less in higher gradient reaches/tributaries when compared to fish in the lower gradient stream reaches. This study was not design to address the effects of stream gradient, but additional research could be performed to further elucidate the effects of stream gradient on fish movement.

*Brook trout habitat use.* - The use of discrete choice modeling allowed me to evaluate the seasonal use of the physical stream habitat in Cherry Run by 20 wild brook trout. Of particular importance was (1) being able to evaluate habitat selection based on both what was used by the fish and what was available, (2) the ability to examine both linear and nonparametric effects in the models and (3) being able to model habitat use at different spatial scales.

The fact that discrete choice models with random effects have, to the best of my knowledge, not been used to study habitat selection in fishes is perhaps due to logistical issues (i.e., access to streams) and time constraints in needing to quantify an entire observation area in an aquatic system (i.e., GIS layers of the physical habitat typically do not exist as in terrestrial systems). However, as I have demonstrated, creating a customized GIS layer by surveying

thalweg profiles and mapping residual pool habitat is possible over relatively large spatial scales. Combining such habitat maps with the flexibility of discrete choice modeling provides a new tool for elucidating fish/ habitat associations at multiple spatial scales.

Overall, selection by the brook trout was similar for the shallow, intermediate, and deep residual pools in relation to non-pool habitats; however, a seasonal trend in habitat selection was captured by the models at all spatial scales. Seasonal variations in habitat use have been documented in salmonids, with the relationship attributed to temperature (Heggenes and Saltveit 1990; Orsi et al. 2000; Heggenes and Dokk 2001; Bramblett et al. 2002), spawning (Swanberg 1997; Geist and Dauble 1998; Amelio et al. 2008), and food availability (Nislow et al. 1999; Bremset 2000; Orsi et al. 2000). Similar to movement, habitat use in brook trout was largely related to the time of year, with the models indicating the selection of shallow residuals pools during October and November 2010 (especially during spawning season). The selection of this habitat may not necessarily have been directly related to the residual depth, but perhaps a function of other physical characteristics of this habitat type that were important for spawning. For example, substrate size has been related to redd-site selection in brook trout, particularly coarser substrate typically found in shallower stream areas (Witzel and MacCrimmon 1983; Snucins et al. 1992; Bernier-Bourgault and Magnan 2002). However, this relationship may be more complex. The preference of a particular substrate by spawning brook trout may be related to sorting, as well as size (Witzel and MacCrimmon 1983). Also, water velocity may have played a role in spawning habitat selection. Areas of groundwater upwelling, which is commonly associated with brook trout-redd site selection (see drivers of brook trout movement and habitat use), is more likely to occur in lower velocity areas common in deeper water habitats in streams (Essington et al. 1998). However, in the absence of upwelling, brook may select for areas of

higher water velocity, possibly in shallower habitats (Essington et al. 1998; Bernier-Bourgault and Magnan 2002). In any event, since I did not characterize differences in substrate or water velocity between the residual pool categories, no inferences can be made as to their roles in brook habitat selection in Cherry Run. And although the lack of a limestone influence in the underlying geology would suggest the absence of upwelling in Cherry Run, I cannot completely eliminate the possibility that areas of groundwater discharge were present. Increased selection of deep residual pools was identified in the models during December 2010. In addition to brook trout (Chisholm et al. 1987; Lindstrom and Hubert 2004), coho salmon *Oncorhynchus kisutch* (Nickelson et al. 1992), bull trout (Jakober et al. 1998) and cutthroat trout (Jakober et al. 1998; Lindstrom and Hubert 2004) have all been reported to occupy deep pools in the winter. Maki-Petäys et al. (1997) did observe movement into shallower pools by brown trout during the winter, but this was thought to be a product of seasonal habitat availability. Deeper water habitats are considered favorable to overwintering salmonids due to overhead ice cover, lack of anchor ice, and stable water temperatures (Chisholm et al. 1987; Brown and Mackay 1995; Jakober et al. 1998). Groundwater upwelling also may play a role in winter habitat selection in salmonids (Cunjak and Power 1986; Brown and Mackay 1995), but this was likely not a factor in habitat selection by brook trout in Cherry Run (see above).

The random effects in the models indicated there was little variability in how shallow residual pools were used by individual brook trout and relatively high variability among individual fish in the use of intermediate and deep residual pools. These results suggest that spawning behavior was a strong influence on all the brook trout tracked in this study, resulting in increased use of shallow residual pool habitats and little variation among fish. Whereas, habitat selection for deeper pools was related to factors acting on each brook trout differently, such as

thermal preferences and food availability, resulting in a large amount of variation among fish in habitat use (Jakober et al 2000). Also, interspecific and intraspecific social interactions could potentially be a factor related to habitat use, especially given the presence of brown trout in Cherry Run.

For example, brown trout have been shown to influence the available winter habitat of brook trout in sympatric populations (Cunjak and Power 1986). In addition, brown trout tend to grow larger than brook trout and are known to have high predation rates on other fish species (Johnson 1981; Waters 1983) and a competitive advantage over brook trout in feeding positions has been observed (Fausch and White 1981). Also, the spawning season of brown trout occurs later in the year, but it does overlap with brook trout spawning and brown trout have been observed utilizing similar habitats and superimposing brook trout redds (Witzel and MacCrimmon 1983). All of these interactions could potentially influence individual habitat use and contribute to the observed variability in the use of intermediate and deep pools. However, during the sampling in September 2010, the abundance of both brook trout and brown trout was low in Cherry Run (population estimate data was not collected). In addition, the thalweg profile of Cherry Run indicated a relatively high degree of residual pool availability. Thus, both interspecific and intraspecific competition for specific habitat types was thought to be low.

The habitat use models also indicated an influence of habitat patch length on brook trout habitat selection. By using discrete choice modeling, I was able to estimate the effect of the length of a habitat patch on habitat selection by the wild brook trout, independent of residual depth. The models indicated a threshold relationship, with increased selection for habitat patches up to a length of approximately 25 – 35 m, and a decreased selection of habitat patches of greater lengths. This relationship was not simply an artifact of little habitat patches of greater than 35 m

being present in Cherry Run, as residual pool habitat of greater than 35 m in length comprised ~8 % of the residual pools .

The size of a brook trout also was related to habitat selection. A relationship of body size on the habitat preferences of stream fishes has been documented, with larger fish tending to select for habitats of greater depth (Schlosser 1987; Heggenes et al. 1991), possibly due to increased predation risk by terrestrial animals in shallower habitats (Harvey and Stewart 1991). In this study, the opposite was observed, with an increased selection of shallow residual pool habitat by larger brook trout. This result was most evident at the 500 m scale, where fish size based on weight was included in the top-ranked model. Although difficult to interpret, especially considering the relatively small sample size of brook trout, this relationship was likely related to larger Fishing Creek brook trout using shallow residual pool habitat in Cherry Run during spawning season.

The transient use of the shallow residual pools in Cherry Run by Fishing Creek brook trout, presumably for spawning habitat, may have been in part related to differences in the underlying geology between the streams. The more stable stream environment in streams with a limestone influence and groundwater inputs (see Study area) leads to increased productivity and larger, more diverse aquatic invertebrate populations (Smith and Wood 2002; Wood et al. 2005). Fishing Creek would likely present more optimal foraging opportunities than Cherry Run for brook trout. The increased productivity in Fishing Creek as compared to the tributaries also may partially account for the larger fish size and more abundant trout populations.

Overall, trends in the habitat use models were similar across all four spatial scales. For instance, the influence of time on residual pool selection was comparable at all of the scales, in which shallow residual pools were selected by the brook trout during spawning season, followed

by an increased selection of deep residual pools in late fall winter. In addition, the magnitude of habitat-specific heterogeneity in use among individual fish was consistent across spatial scales. A failure to detect differing patterns in habitat use at varying scales suggests either that (1) in this system scale was not important because the distribution of residual pool habitat was relatively homogenous throughout Cherry Run, resulting in similar choice sets at each spatial scale, or (2) that the scales chosen for this analysis prevented the elucidation of scale-dependent relationships. For instance, if home range data were available for brook trout in this system, a hierarchical approach for assigning available habitat at different scales could have been used (Johnson 1980). This approach to determining biologically meaningful scales for assessing habitat use may increase the ability to detect scale-dependent patterns. A hierarchical approach would also facilitate the identification and use of scale-dependent habitat covariates, because different habitat characteristics may be important depending on the processes driving habitat use at a given scale (Johnson 1980). Also, the residual pool depth categories I used in the models lacked *a priori* justification. Although there were natural breaks in the data that allowed me to divide the residual pools into the three categories, I acknowledge that these categories are based on statistics, rather than of ecological importance. However, pool habitat is important for stream-dwelling salmonids (see Quantifying stream habitat), so quantifying residual pool habitat as a metric of interest (regardless of how it is categorized) does have ecological and biological significance.

In addition to GPS error (estimated at 5 m) and my potential error in estimating the fish's location (2 m), there was some degree of inaccuracy in matching the fish location with a data point in the thalweg profile. Some of the inaccuracy was also due to the fact that the latitude and longitude of the data points in the profile that did not correspond with a GPS waypoint were

estimated (see quantifying stream habitat). Also, since thalweg measurements were taken approximately every 5 m, the fish location did not always correspond with a location in the profile. Given these potential sources of measurement error, however, there was evidence that suggested that this error was minimal and that the fish locations and the thalweg profile correspond spatially. For example, the distance between data points that occurred on both sides of a bridge across Cherry Run corresponded with the actual length of the bridge by  $< 2$  m. Also, field observations estimating relatively small distances between fish locations agreed with the movement calculations in both distance and direction. For example, if I estimated in the field that a brook trout moved 20 m upstream between locations, this methodology would indeed place the fish upstream at a comparable distance. Considering potential spatial error in identifying the exact location of the fish, I estimate that the fish location is within 10 m of its actual location. In most cases, changing the fish location by 10 m upstream or downstream would not have changed the used habitat classification. Further, although the proximity tool in ArcMap was the primary method in classifying each fish location, field notes recorded at the time of the location were also used to increase accuracy and to verify or change the classification as deemed necessary. For example, if this methodology placed a brook trout in non-pool habitat and field notes clearly suggested otherwise, the fish was moved to nearest residual pool in the thalweg profile.

*Future research.*- Surveying thalweg profiles of the study area was an effective way to quantify the physical stream habitat and to evaluate wild brook trout habitat selection using discrete choice modeling. Yet, there were some limitations to this approach related to the methods used in developing the residual pool depth categories. Each residual pool was classified based the maximum residual depth within the habitat. This resulted in a single measurement being applied

to the entire residual pool and ignored heterogeneity in residual depth within a pool. Although more time consuming, additional measurements within a residual could help to better characterize stream habitat. For example, it could be beneficial to incorporate the width of the stream channel (wetted and bankfull width are both common geomorphic measurements taken in streams) into the models. By using discrete choice modeling, the influence of width in brook trout habitat selection could be evaluated independent of other habitat variables, since this metric may be important when managing stream salmonid populations. For example, bankfull width has been shown to be related to the abundance of cutthroat trout and is often included in the metrics used to evaluate habitat when establishing populations that have been moved from impaired stream areas (Rosenfeld et al. 2000; Harig and Fausch 2002; Young et al. 2005).

While the modeling results did not suggest that a change in water temperature was a factor in brook trout movement, it does not mean such a relationship did not exist. Although I used consistent criteria in assigning the greatest increase or decrease in water temperature between fish locations, not having fish locations each day likely generated some error in matching up when a fish moved with when the temperature changed. A brook trout study focused on examining daily and/or diurnal movements may detect a relationship of fluctuating water temperatures on movement. Nevertheless, if fluctuating water temperature was strongly associated with seasonal movement of the brook trout in this study, I would have likely detected its influence. Also, the placement of the water temperature loggers did not provide any sort of temperature profile of the streams. Microhabitats of water temperature may have influenced both the movement and the habitat use of the brook trout (Cunjak and Power 1986; Baird and Krueger 2003).

Lastly, it would be valuable to conduct a movement and habitat use study with allopatric wild brook trout populations and employ methods similar to those described here. This would eliminate the potential influence of brown trout on movement and habitat use. However, the possibility of intraspecific competition between brook trout would still exist. It would also be beneficial, if possible, to identify the sex of the individual brook trout. Differences in movement and habitat use trends may exist between male and females in this study, but I was unable to account for them due to the difficulty in confidently sexing brook trout in the field.

*Brook trout conservation and management.* - This research adds to the existing knowledge of stream-dwelling brook trout ecology and provides important information pertaining to the life history of eastern wild brook trout. The observed large-scale fish movements, heterogeneity among streams and individual fish in movements, and heterogeneity among individual fish in habitat use are particularly relevant to fisheries management and stream restoration efforts. In addition in aiding to provide a better understanding of seasonal movement trends, this study provides insight into how wild brook trout utilize the physical stream habitat. In particular, a nonlinear relationship was observed with respect to the length of residual pools, as the discrete choice models identified a threshold effect in the selection of habitat by the brook trout. Without considering nonlinear relationships, an incorrect positive linear association could have been made between brook trout habitat selection and residual pool length. Incorrect or incomplete analyses related to ecological data could lead to erroneous, and potentially costly, management decisions. The discrete choice models also suggest habitat heterogeneity is important in conserving brook trout populations. Habitat selection varied among individual fish and changed

seasonally. Both of these metrics, residual depth and pool length are stream habitat characteristics that can be manipulated when managing and restoring brook trout habitat.

Some brook trout were observed moving between the main-stem, Fishing Creek, and lower Cherry Run during spawning season. However, Fishing Creek brook trout were not located in UNT, upper Cherry Run, or Bear Run despite these stream reaches being nearby and accessible. Although brook trout were not tagged in Bear Run, due to the close proximity of Bear Run with the study streams (less than 1 km from both UNT and Cherry Run) a signal would have been detected during routine tracking if fish utilized this tributary. Also, the length of Bear Run was walked periodically in an attempt to locate fish in which contact had been lost. There also was no interaction identified between lower Cherry Run and upper Cherry Run brook trout, despite any physical barriers preventing movement. These observations may have been related to increased gradient in these stream reaches or the decreased residual pool availability apparent in the thalweg profile of UNT (although residual pool habitat was similar between upper and lower Cherry Run). However, more intensive stream surveys are necessary to identify differences (e.g., flow velocity and substrate) between the stream reaches in terms of providing spawning habitat.

The trends described above underscore the value of understanding the movement dynamics of a fish species when managing for self-sustaining populations. In particular, there are two important points relative to the successful management of wild brook trout populations. First, it is important to maintain stream connectivity, since tributaries adjacent to the main-stem of a system may provide important spawning or other critical habitat. Hansbarger et al. (2010) also documented the use of smaller tributaries by main-stem brook trout in a study in a high-elevation watershed in West Virginia. To help maintain this connectivity, physical and environmental barriers (e.g., degraded habitat) should be minimized. Second, it is important to

realize that not all streams may be contributing equally, in terms of reproductive potential, to brook trout populations within a stream system, as demonstrated by main-stem Fishing Creek brook trout only using lower Cherry Run for spawning despite the availability of other tributaries. Consequently, some tributaries or areas of tributaries could be expected to be recolonized at different rates from main-stem and/or adjacent tributaries if local extinctions were to occur. An approach that can help to address wild brook trout management and conservation across a stream system is to employ a watershed perspective. As opposed to managing in discrete stream reaches, a watershed approach can help managers address and maintain stream connectivity and understand recolonization potential throughout an entire system (Wesche and Isaak 1999; Roghair and Dolloff 2005; Letcher et al. 2007; Hansbarger et al 2010). With the threat of increased degradation of headwater stream systems, due to the continued expansion of anthropogenic activities such as natural gas exploration and extraction, a watershed approach is particularly relevant to much of the remaining eastern wild brook trout habitat, especially considering that many populations are already isolated and/or fragmented.

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