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FLUVIAL AND ADFLUVIAL BROOK TROUT
(SALVELINUS FONTINALIS) MOVEMENT
PATTERNS WITHIN SEVENMILE CREEK
AND MOSQUITO RIVER, PICTURED
ROCKS NATIONAL LAKESHORE,
MICHIGAN

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FLUVIAL AND ADFLUVIAL BROOK TROUT (*SALVELINUS FONTINALIS*) MOVEMENT
PATTERNS WITHIN SEVENMILE CREEK AND MOSQUITO RIVER, PICTURED ROCKS
NATIONAL LAKESHORE, MICHIGAN

By

Robert L. Cross

THESIS

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ABSTRACT

FLUVIAL AND ADFLUVIAL BROOK TROUT (*SALVELINUS FONTINALIS*) MOVEMENT PATTERNS WITHIN SEVENMILE CREEK AND MOSQUITO RIVER, PICTURED ROCKS NATIONAL LAKESHORE, MICHIGAN

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Robert L. Cross

Pictured Rocks National Lakeshore (PIRO) is home to several partially migrating populations of brook trout (*Salvelinus fontinalis*). The presence of fluvial and adfluvial movement patterns led to a large scale study of their movement behavior and morphological characteristics. The study involved measuring and implanting brook trout with passive integrated transponder (PIT) tags beginning in 2004 within Sevenmile Creek and Mosquito River. The project used radio frequency identification (RFID) antennas at the mouth of each river to detect PIT tagged brook trout moving in and out of the streams. Electroshocking within the rivers was used to track within stream movements of brook trout. A subset of fluvial individuals in both systems was found to move the entire sampled length of each stream. A combined 53% of all fluvial brook trout were found more than 150 m from their original capture location (OCL). Brook trout density was significantly correlated to fluvial movement within Mosquito River, suggesting that density could be a stimulus for fluvial movements. Also within Sevenmile Creek 62% of individuals were correctly assigned as fluvial or adfluvial using their OCL. Overall the lack of distinguishing characteristics between fluvial and adfluvial brook trout suggests

that these life history tactics are varying degrees on a movement continuum within brook trout populations.

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Robert L. Cross

2013

DEDICATION

This thesis is dedicated to my wife, Jennifer Cross, and to my parents, Daniel and Laurie Cross.

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LIST OF ABBREVIATIONS

| | | |
|-------------|-------|---|
| ANCOVA | | Analysis of Covariance |
| ANOVA | | Analysis of Variance |
| CPUE | | Catch Per Unit Effort |
| D_{avg} | | Average distance moved between capture events |
| D_{max} | | Maximum distance from original capture location |
| D_{total} | | Total recorded distance moved |
| IACUC | | Institutional Animal Care and Use Committee |
| K | | Fulton's Condition Factor |
| OCL | | Original Capture Location |
| PIT | | Passive Integrated Transponder |
| PIRO | | Pictured Rocks National Lakeshore |
| RFID | | Radio Frequency Identification |
| RMP | | Restricted Movement Paradigm |
| TL | | Total Length (mm) |
| W_r | | Relative Weight (g) |

CHAPTER 1: INTRODUCTION

Brook trout (*Salvelinus fontinalis*) are a slender bodied charr found throughout North America (Becker 1983). Regionally specific common names include brook charr, specks, speckled trout, aurora trout, brookie, and squaretail. The brook trout is a highly sought after cold-water game species identified by well-defined, vermiculated base coloration and bright multicolored spots. Sexual dimorphism is only present in breeding individuals. During breeding season, sexually mature males become brightly colored and develop a hooked jaw, called a kype (Becker 1983). Sexual dimorphism is not present throughout the rest of the year. Mean length for stream-dwelling brook trout ranges from 152 to 203 mm (Becker 1983). The largest brook trout on record weighed 6.6 kg and was caught in the Nipigon River, Ontario. Their extreme adaptability and plasticity has allowed them to exist in many forms throughout their native range.

Native brook trout populations span from the eastern seaboard as far west as the Great Lakes region and Manitoba (Becker 1983; MacCrimmon 1969). Populations of brook trout occur northward to the Arctic Circle and as far south as the southern Appalachian Mountains (Habera and Moore 2005; MacCrimmon 1969). Although brook trout are only native to northeastern North America, European settlement drastically altered the distribution of brook trout throughout the United States. Presently, the species has been spread across North America and introduced into every continent except for Africa and Antarctica. Stocking of brook trout in the western United States

began in the early to mid-1900's (Bahls 1992) and has since been associated with declines in native salmonid populations (Dunham et al. 2002; Peterson et al. 2004). The successful introduction of brook trout as a non-native species is in part due to its adaptability. Dunham et al. (2002) reviewed the literature on brook trout invasion and concluded that extreme plasticity in age of maturation is a causative factor in their successful introduction. Brook trout are often considered the most tolerant of the char (*Salvelinus* spp.) due to their survival in a wide range of conditions.

Although brook trout are found in many habitat types and conditions, they are most commonly found in cool (13.9-15.6 °C), clear, spring fed streams and headwater ponds (Becker 1983). Within fluvial systems brook trout are generally associated with deep, slow-moving pools and coarse woody debris, although the degree of association with these conditions changes on a seasonal and ontogenetic basis (Johnson 2008). A high tolerance in brook trout for variable conditions has allowed them to adapt to multiple habitat types throughout their native and introduced range such as the high elevation streams of Colorado (Gowan and Fausch 1996) and acidic lakes of Quebec (Frenette et al. 1986).

Brook trout have the capacity to use a continuum of habitats from small headwater tributaries to large freshwater lakes and even salt water (Huckins and Baker 2008; Ridgway 2008; Thériault and Dodson 2003). In some populations multiple ecotypes are present. Some ecotypes are known to undergo drastic ontogenetic niche shifts (D'Amelio and Wilson 2008; Huckins and Baker 2008; Mucha and Mackereth 2008; Thériault and Dodson 2003). In northeastern Canada, anadromous brook trout

termed “salters” migrate from freshwater tributaries into the Atlantic Ocean within their first two years of life (Theriault and Dodson, 2003). Lacustrine, or lake dwelling, brook trout are found in the well-oxygenated lakes of Ontario and Quebec as well as Lake Superior (Fraser and Bernatchez 2008; Ridgway 2008). A potadromous ecotype analogous to anadromous brook trout is also endemic to the Lake Superior watershed (Huckins et al. 2008; Mucha and Mackereth 2008; Ridgway 2008).

Within the Lake Superior watershed, brook trout have the ability to use habitats outside of their natal stream. Any brook trout found within Lake Superior is given the name “coaster”. The term coaster is derived from this ecotype’s proclivity for shoreline habitat during their adult life (Becker 1983). These fish can either be derived from stream dwelling (fluvial) populations or be entirely lake dwelling (lacustrine). Adfluvial coasters are individuals that are derived from a fluvial population and migrate into Lake Superior as juveniles. Adult adfluvial coasters then return to their natal stream in autumn to spawn and then return to Lake Superior. Unlike semelparous Pacific salmonids, adfluvial brook trout are iteroparous, spawning multiple times throughout their lifetime. Declining numbers of coaster populations within the Lake Superior watershed have led to growing interest in restoration efforts (Huckins et al. 2008; Kusnierz et al. 2009; Ridgway 2008; Sloss et al. 2008). However, little is known about the ultimate and proximate factors responsible for the development of these alternate life history tactics. Without understanding these factors, restoration efforts may continue to be limited to stocking.

Historically, large schools of adfluvial brook trout could be found along Lake Superior's shoreline (Roosevelt 1884). These adfluvial brook trout spawned in at least 106 tributaries throughout the watershed (Scott and Crossman 1973). At present, only a few remnant populations of brook trout within Lake Superior are known to use habitat outside of their natal stream (Isle Royale, Lake Nipigon and Nipigon Bay, Salmon Trout River, and Pictured Rocks National Lakeshore); some of these populations are completely lacustrine while others are believed to be adfluvial. In addition to overexploitation, poor land use (e.g. logging and farming), barriers to migration (e.g. dams), and pollution have led to the decline of adfluvial populations (Schreiner et al. 2008). Declining numbers of adfluvial brook trout in Lake Superior have called attention to the need for further adfluvial coaster research.

In sympatric systems, emphasis has been put on distinguishing adfluvial coasters from fluvial brook trout. Classified as a dichotomy of behaviors, these purported ecotypes have typically been treated as mutually exclusive. Difficulty in defining brook trout activity as migration, movement, or dispersal is partially the result of sampling techniques. If sampling takes place on a population or subpopulation level and not an individual level, nomadic movement may be mistaken for migration. Migration is a term often, though not exclusively, used for annual migration in fish. Annual migration is movement, generally to or from breeding habitat, which is driven by seasonal cycles (Dingle and Drake 2007). Fluvial brook trout movement within or between streams may be postnatal dispersal or, more likely, nomadism. Nomadism as described by Dingle and Drake (2007) is an irregular pattern of movement whose focal points are temporary

breeding sites. Postnatal dispersal is described as leaving ones place of birth in order to breed in an alternate location (Dingle and Drake 2007). More attention needs to be paid to the movement patterns displayed, their cause, and their ecological and evolutionary significance.

Reproductive isolation and genetic distinction between adfluvial and fluvial brook trout within partially migrating populations remained unknown throughout the beginning stages of coaster rehabilitation. Without knowing the degree of isolation within these populations, managers attempting to restore adfluvial populations stocked what was known as “coaster strain” brook trout in locations that were believed to be historical adfluvial coaster habitat (Leonard et al. 2013). However, despite the large variation in behavior between fluvial and adfluvial brook trout it has been shown that they are alternate life history variants derived from populations of fluvial brook trout (D’Amelio and Wilson 2008). Therefore, fluvial populations can potentially produce migratory individuals under a particular set of environmental conditions (Scribner et al. 2012).

Gross (1996) determined that alternative tactics may be the result of phenotypic plasticity derived from the same genetic strategy (see also Gross and Repka 1998). This hypothesis, termed the “Conditional Strategy”, states that tactics are “chosen” at the individual level based on the fish’s conditions (Gross 1996). This selection allows an individual to realize its greatest potential fitness based on its conditions. According to this hypothesis, individuals compete based on their life history tactics, but their tactics do not compete evolutionarily because they both produce and are produced by the

same genetically linked conditional strategy. Wysujack et al. (2009) found that migration in brown trout (*Salmo trutta*) is a conditional strategy at least partially driven by nutrient availability. Thériault and Dodson (2003) found that salter brook trout in Quebec may have a minimum size threshold that restricts migration, suggesting that brook trout anadromy is conditional. These findings are consistent with Curry et al. (2002) who found that brook trout migration is not set at the population level. Conditional strategies may explain the lack of genetic or reliable discernible morphological divergence between ecotypes in Lake Superior.

Based on the findings of Gerking (1959) and Bachman (1984), stream dwelling salmonids were thought to have small home ranges (<50m). Thus, compartmentalizing partially migrating populations of trout into “migrants” and “residents” would be sufficient. However, recent studies have questioned the dogma of non-anadromous trout movement within streams, later termed the “restricted movement paradigm” (RMP) (Gowan et al. 1994; Gowan and Fausch 1996, 2002). Gowan and Fausch (1996) found that the long held concept of restricted movement in fluvial trout may be flawed, and based on biased sampling methods. Gowan et al. (1994) found that movement studies primarily focused on the percentage of fish recaptured that were found within their home range. When the study was expanded to look at the percentage of total marked fish found within their home range, over half of the fish had migrated >50m with some migrating over 3000m. Clapp et al. (1990) found that large brown trout (>400mm) in Michigan’s Au Sable River migrated roughly 10 km from their summer habitat to slower and deeper overwintering habitat. In Alberta, Canada, cutthroat trout

(*Oncorhynchus clarkii*) moved up to 7.6km seasonally in search of suitable habitat (Brown and Mackay 1995). In a later study, Gowan and Fausch (2002) determined that brook trout moved during the summer months in search of favorable territory. They suggested that these movements allowed dominant fish to identify the highest quality habitat throughout changing conditions. Fluvial brook trout have also been found to migrate upstream in response to non-native salmonid spawning migrations (Janetski et al. 2011). These changes in habitat use within streams may be driven by the same environmental factors as larger niche shifts. Therefore, it is critical to examine brook trout movements using an individualistic approach. This fine scale approach will aid in the identification of environmental cues responsible for movement within and among aquatic systems and help clarify our understanding of sympatric fluvial and adfluvial brook trout.

Movements have historically been classified as a strategy “chosen” by an individual at a critical life stage. However, it is possible that plasticity at a larger resolution, such as the ontogenetic level, may in fact be the result of changes at a much finer scale. Movements within and among systems may be the result of daily or seasonal interactions of an individual with its environment. Gowan and Fausch (2002) found that food availability at a reach scale may be a driving factor for brook trout movements within streams. An individualistic approach to studying riverine fish as discussed by Juanes and Letcher (2000) allows for the determination of characteristics normally lost at the population level. Such characteristics include both short and long term movements as well as individual growth patterns in response to the adoption of

alternate life history tactics. This information can then be correlated to an individual's migration history to isolate the mechanisms responsible for inter- and intra-system movements.

In 2000, the stocking of Tobin Harbor strain brook trout began in a coordinated effort to rehabilitate coaster brook trout in Pictured Rocks National Lakeshore (PIRO). From the years 2000 through 2005, about 211,000 brook trout were stocked into three Lake Superior tributaries within PIRO (Mosquito River, Sevenmile Creek, Hurricane River). In conjunction with the stocking effort, researchers from Northern Michigan University began a long term brook trout monitoring study. Hatchery fish were marked with a fin clip distinct to the batch year and stocking location prior to release. This allowed for the differentiation of hatchery and wild fish. Beginning in 2003, both wild and hatchery fish were tagged with passive integrated transponder (PIT) tags to further identify the fish within study streams. These tags allow for the identification of individual fish as well as the site of their original capture. Coupled with radio frequency identification (RFID) antennas at the mouths of the streams, PIT tags allowed researchers to monitor movements of tagged brook trout between systems.

Stimmell (2006) was able to monitor the population level movements of both hatchery and wild brook trout within PIRO. When comparing the condition of wild and hatchery brook trout, he found that wild brook trout had greater condition than the Tobin Harbor (hatchery) strain. He also found that movement of brook trout within and among the study streams from May 2003 to Nov 2004 was most prevalent in the spring and fall and strongly correlated to photoperiod. Both wild and hatchery fish migrated

into Lake Superior from the Hurricane River. Later, Kusnierz et al. (2009) found the greatest movement within these streams during autumn with the next greatest period of movement in the summer. The main focus of the study by Kusnierz et al. (2009) was to determine the age structure of brook trout within PIRO and to summarize the movement of brook trout between systems. There was no significant difference between length, or age, of fish between streams or life history variants (fluvial, adfluvial). However, the two life histories varied in condition at specific size classes. Fish were found moving between streams using Lake Superior as a corridor.

These studies have exposed information regarding population level movements of adfluvial brook trout. However, individual level information is needed in order to determine individual growth patterns and movement histories. Also, no studies have been conducted on the individual and population level movements of fluvial brook trout within these systems. My research took place at this resolution in order to test the following hypotheses:

- 1) The majority of tagged, fluvial brook trout move more than 150m from their original capture location
- 2) Inter and intra-stream fish movement is related to body condition
- 3) Proportion of individuals leaving the stream is related to fish size.
- 4) Movement patterns are related to the relative density of brook trout, rainbow trout, and coho salmon.

The goal of this study was to expand upon the previous studies conducted within PIRO (Kusnierz et al. 2009; Stimmell 2006) by using individual-level data and expanding

the study area. My objective was to use individualized data in order to: 1) describe the movement patterns of fluvial brook trout and 2) determine what factors or combination of factors lead to changes in individual movement patterns. Previous studies conducted within PIRO evaluated population level patterns in brook trout movement. These studies were also concerned primarily with inter-system movement while ignoring valuable perspective offered by including intra-system movements. I used both passive PIT tag data collected from the antennas and electrofishing data on tagged fish collected throughout the brook trout monitoring study within PIRO from 2004 to 2011. Radio frequency identification antenna data aided in the identification of inter-system movements (adfluvial) while electrofishing mark recapture offered physical measurements as well as intra-system movement patterns (fluvial) and life history parameters. This allowed for the identification of individual morphological and movement histories leading to the adoption of alternate life history traits. Movements were evaluated in respect to condition, relative weight, length, and original capture location.

CHAPTER 2: A COMPARISON OF ADFLUVIAL AND FLUVIAL BROOK TROUT (*SALVELINUS FONTINALIS*) WITHIN PICTURED ROCKS NATIONAL LAKESHORE, MICHIGAN

CHAPTER SUMMARY

Brook trout within the Lake Superior watershed are known to express multiple life history variations. Both adfluvial and fluvial brook trout have been identified within Pictured Rocks National Lakeshore, Michigan. A four year study was conducted from May 2008 through November 2011 in order to examine differences in length, condition, and original capture location between adfluvial and fluvial brook trout. Salmonid density was also examined as a possible stimulus for the expression of adfluvial behavior within the Lakeshore. Brook trout were collected from two streams (Sevenmile Creek and Mosquito River) and implanted with passive integrated transponders (PIT) during electrofishing surveys. Fish were subsequently detected leaving the mouth of the river with a double radio frequency identification (RFID) antenna array. Tag detections at the antenna were most common in the spring and fall, most likely in association with temperature or seasonal change. Movement pattern was not significantly related to total length of fish in either system. Condition was not significantly different between the individuals of the two movement patterns in either stream. Within Sevenmile Creek, adfluvial individuals were found significantly closer to the mouth. In Mosquito River, the density of brook trout was positively related to the number of adfluvial individuals originally tagged in each reach. Brook trout within these streams appear to be responding to biotic and abiotic environmental stimuli in their expression of adfluvial behavior.

INTRODUCTION

Brook trout (*Salvelinus fontinalis*) in the Lake Superior watershed have the ability to inhabit a continuum of habitats, from first order streams to the pelagic and coastal zones of the lake (Huckins and Baker 2008; Huckins et al. 2008; Mucha and Mackereth 2008; Ridgeway, 2008). Individuals that spend their entire life within their natal stream are termed resident or fluvial. Any brook trout that uses habitat outside of a stream is given the name “coaster” (Becker 1983). Coasters within the Lake Superior watershed may either be lacustrine (entirely lake-dwelling) or adfluvial (potadromous migrants). Adfluvial brook trout generally exit their natal stream in the spring and return as adults to spawn.

Historically, coasters were said to inhabit many of Lake Superior’s tributaries (Newman 2003). It has been hypothesized that poor land use practices, logging, overharvest, and non-native species introductions were the largest contributors to the collapse of the fishery (Schreiner et al. 2008). At present, documented remnant coaster populations only exist in the Salmon Trout River (adfluvial), Pictured Rocks National Lakeshore (PIRO) (adfluvial), Isle Royale, MI (adfluvial and lacustrine), and Lake Nipigon and Nipigon Bay, ON (lacustrine and adfluvial). Adfluvial brook trout within Lake Superior’s remnant populations are likely derived from sympatric populations of fluvial and adfluvial individuals (D’Amelio and Wilson 2008; Scribner et al. 2012) and represent partially migrant populations.

Partially migrating populations are common among salmonid species. Such populations have been documented in coastal cutthroat trout (*Oncorhynchus clarkii*

clarkii) (Zydlewski et al. 2009), brown trout (*Salmo trutta*) (Hendry et al. 2004; Wysujack et al. 2009), Atlantic salmon (*Salmo salar*) (Klemetsen et al. 2003; Metcalfe et al. 1989) and Arctic charr (*Salvelinus alpinus*) (Klemetsen et al. 2003). Migration between aquatic systems often results in ecotypes that are larger and more fecund than their fluvial conspecifics (Jonsson and Jonsson 1993). Larger body size has been documented in coasters from Lake Nipigon, Nipigon Bay, Isle Royale, and Salmon Trout River, with the greatest body size in coasters inhabiting the northern shoreline of the lake (Huckins et al. 2008).

Despite the large variation in behavior between fish with adfluvial and fluvial life histories, they are likely ecotypes derived from populations of fluvial brook trout (D'Amelio and Wilson 2008; Scribner et al. 2012). Therefore, fluvial populations may potentially produce migratory individuals under a particular set of environmental conditions (Scribner et al. 2012). Gross (1996) determined that alternative tactics may be the result of phenotypic plasticity derived from the same genetic strategy (see also Gross and Repka 1998). This hypothesis, termed the "Conditional Strategy", states that tactics are based on individual conditions (Gross 1996). According to this hypothesis, individuals compete based on their life history tactics, but their tactics do not compete evolutionarily because they both produce and are produced by the same genetically-linked conditional strategy. Wysujack et al. (2009) found that migration in brown trout is a conditional strategy and is at least partially driven by nutrient availability. Thériault and Dodson (2003) found that salter brook trout in Quebec (an anadromous form) may have a minimum size threshold that restricts migration. These findings are consistent

with a study by Curry et al. (2002) who found that brook trout migration is not determined at the population level. Conditional strategies may thus explain the lack of genetic or reliable discernible morphological divergence between ecotypes.

Furthermore, if brook trout movement is based on a set of environmental or physical conditions, then it may be possible to identify these conditions and predict individual movement patterns, perhaps even managing for a particular ecotype.

Without any known genetic or morphological differences, it has proven difficult to study or specifically manage adfluvial brook trout during their in-stream life stages. A long-term study took place within PIRO from 2003 to 2011 to track the in-stream movements of individual brook trout within three Lake Superior tributaries (Hurricane River, Mosquito River, and Sevenmile Creek). The intent of this project was to identify differences between adfluvial and fluvial brook trout through the use of passive integrated transponder (PIT) telemetry. The stocking of Tobin Harbor strain brook trout took place from 2000 to 2005 and more than 211,000 individuals were released. Stimmell (2006) showed that both wild and hatchery strain individuals were moving out of the river. He also showed that body condition did not vary significantly between wild or stocked adfluvial and fluvial fish. A later study of the Hurricane River by Kusnierz et al. (2009) revealed no difference in the length of wild adfluvial and wild fluvial brook trout either during or after the stocking program. However, there was a significant difference in Fulton's condition factor between fish with the two movement patterns.

I also focused on differentiating between adfluvial and fluvial brook trout from PIRO streams (Sevenmile Creek and Mosquito River). However, my study began three

years after the coaster stocking program ended. The objective of my study was to identify any differences in length, body condition, or original capture location (OCL) between adfluvial and fluvial brook trout within and between the two streams. One goal of this study was to evaluate the relationship between Fulton's condition factor (K) and movement patterns of the brook trout of PIRO. The final goal of the study was to use significant variables as predictors for brook trout movement patterns. If brook trout migration is a conditional strategy, then differences in condition, length, or OCL could explain movement patterns of this partially migrating population of brook trout.

MATERIALS AND METHODS

STUDY SITES

Sevenmile Creek (46° 37' 16.28" N, 86° 15' 25.75" W) and Mosquito River (46° 31' 33.86" N, 86° 29' 37.2" W) are located within Pictured Rocks National Lakeshore on the northern coast of Michigan's Upper Peninsula (Figure 2.1). Since the Lakeshore's establishment in 1966, it has been protected from development and logging. The streams within the Lakeshore are, however, subject to moderate fishing pressure. Sevenmile Creek runs through the middle of the Lakeshore and Mosquito River is located on the western end. The entire sampled length of both streams runs through mixed coniferous deciduous forests. Both streams are inhabited by native brook trout, central mudminnow (*Umbra limi*), sculpin (*Cottus* spp.), dace (*Rhinichthys* spp.), and suckers (*Catostomus* spp.). Non-native species include coho salmon (*Oncorhynchus kisutch*), pink salmon (*O. gorbuscha*), and rainbow trout (*O. mykiss*). Fluvial populations

of fish within these streams are potentially impacted by annual potadromous migrations of Pacific salmon, rainbow trout, and suckers.

Sevenmile Creek is a second order stream running from Sevenmile Lake into Lake Superior. The headwaters of the river are composed of beaver ponds with slow water velocity and silt accumulation. Downstream of the beaver ponds, the substrate consists of sand and gravel. The river flows through a sandy beach before emptying into Lake Superior.

Mosquito River is a third order stream that is greatly influenced by surface runoff due to the presence of bedrock and sandstone sheets at or near the soil surface. The sampled area within Mosquito River is defined by the mouth of the river emptying into Lake Superior and impassable waterfalls 2.6 river kilometers upstream of the mouth. The mouth is characterized by shallow fast water running over exposed bedrock shelves and sandstone. Upstream of the mouth, substrate is primarily sand and gravel.

ACTIVE SAMPLING

Active sampling took place with a single probe electrofishing backpack (model: AbP-3TM pulsed DC, ETS Electrofishing, Verona, WI) on a monthly basis from May to November from 2008 to 2011. The streams were broken up into 150m reaches starting with reach 0 at the mouth of the river. The river was also divided into three sections (upper, middle, lower). The entire stream was sampled on a by-reach basis every May, August, and November; these sampling events were termed sweeps. A subset of two reaches per section was sampled during iceless, non-sweeps months. During sampling events all brook trout $\geq 100\text{mm}$ were scanned with a portable PIT tag reader. If the fish

had previously been tagged, then location, total length (mm), and weight (g) were recorded and the fish was released at its approximate capture location. Untagged fish were measured for total length (mm) and weight (g), and then PIT tagged with an identification number corresponding to the river and individual.

PASSIVE SAMPLING

Passive sampling was completed using a double RFID antenna array at the mouth of each river. The antennas were solar powered double loop half duplex RFID antennas with multi-antenna HDX RFID readers (Texas Instruments, Dallas, TX) on a 30ms cycle. The addition of the second antenna within 10m of the first antenna allowed for determination of direction of fish movement (up or downstream). The antenna data for this study came from antennas installed in the rivers in 2003. The addition of the second antenna to the established array occurred in the spring of 2008. Antennas were powered by solar panels located in close proximity to the array. The antennas ran continuously throughout the summer, but lapsed occasionally due to exposure to snow and decreased photoperiod during the late fall, winter, and early spring. Intermittent data was collected during those months.

TAGGING

PIT tags were used for the individual identification of brook trout ≥ 100 mm through the study. Brook trout were tagged with 23mm half-duplex PIT tags (Texas Instruments, Dallas, TX). Brook trout were tagged throughout the sampling season. Tags were implanted into the peritoneal cavity of the fish, anteriodorsal to the pelvic fin. Tag retention in brook trout was high during the sampling season with the

exception of spawning season when tag losses may have occurred due to gamete release. Captured brook trout with tagging scars and fin clips, but no detectable PIT tag, were noted as such on the data sheet and retagged.

DATA ANALYSIS

Individual capture histories were used to determine movement type. Fluvial individuals are those that were captured, tagged and recaptured a minimum of one time within the stream. Adfluvial brook trout were those that were captured, tagged and detected leaving their natal stream or entering another stream. The upstream antenna was labeled A2 and the downstream antenna was labeled A1. For this study, adfluvial individuals had an antenna detection history of A2→A1, A1→A1, or A1→A2. An antenna history of A2→A2 was considered to be an individual that never exited the stream. Capture histories were also used to determine parameters such as original capture location (OCL) and multiple measures of movement distances.

The parameter OCL was the reach in which an individual was tagged and represents the first entry in each capture history. Original capture location was used as a surrogate point of origin for individuals as well as proximity to the mouth of the river. Maximum distance from original capture location (D_{\max}) is the maximum distance that an individual was found from its OCL. D_{\max} was used as an index of mobility which allowed individuals to be ranked based on the furthest distance they were found from their OCL. Total recorded movement (D_{total}) was the sum of an individual's movements both upstream and downstream. This differs from D_{\max} since it accounts for all recorded movements, not just the greatest distance between relocations. The D_{total} of

these individuals was divided by $(1 - n)$ with n representing the number of capture events for a given individual. This yielded the average distance (D_{avg}) between capture events. This measurement removes inherent bias towards greater D_{total} among fish with more capture events and allows for the interpretation of the movement distances without including the number of events as a variable. It is important to note that these values were treated as an index of movement, not a complete record of actual total movement. Gear and sampling restrictions prevent the recording of continuous movement.

Fulton's Condition Factor (K) was determined for each tagged individual at the time of first capture as: $K = W/(L^3) \times 100$ (Nielson and Johnson 1983) where W is the weight (g) and L is total length (cm). Month of capture was used as a covariate for condition in the analysis of variance (ANOVA) in order to mitigate seasonal bias. Linear regression was used to test the relationship between adfluvial brook trout frequency and the catch per unit effort (CPUE) of brook trout, rainbow trout, and coho salmon, with OCL as a case term. ANOVA was used for both rivers in order to detect differences in mean total length between movement types. Logistic regression was used to predict movement pattern based on the OCL parameter. The frequency of adfluvial brook trout in each OCL was correlated with catch per unit effort (CPUE; individuals/m²) of brook trout, coho salmon, and rainbow trout using linear regression. All statistical analyses were run in SPSS (version 19.0) and I used $\alpha=0.05$ for all hypothesis tests.

RESULTS

In Sevenmile Creek, 249 brook trout were tagged and subsequently recaptured using passive and active sampling techniques from 2008 to 2011. Of these individuals, 140 (56%) were only captured within the stream while electrofishing and were labeled as fluvial. The other 109 (44%) individuals were detected leaving the river by the antenna array, in addition to being captured during sampling, and were termed adfluvial. In Mosquito River, 401 brook trout were tagged and recaptured. Of these 401 fish, 366 (91%) were captured again within the river, and 35(9%) were detected leaving the river. The greatest detection rates were observed in the spring and fall. In Sevenmile Creek these periods occurred during May and August (Figure 2.2, 2.3), while in Mosquito they occurred during April and September (Figure 2.2, 2.4).

Adfluvial brook trout within Sevenmile Creek had OCL as far as 1950m (13 reaches) upstream from Lake Superior. The average D_{\max} was 1000.5m (6.6 reaches ± 0.3) for adfluvial and 309.5m (2.0 reaches ± 0.1) for fluvial brook trout. The mean D_{total} for adfluvial brook trout was 1177.9m (7.8 reaches ± 0.5). The mean fluvial D_{avg} was 268.2m (1.7 reaches ± 0.1) and 817.9m (5.4 reaches ± 0.3) for adfluvial individuals. Logistic regression correctly predicted 45-77.3% (62.3% overall) of fluvial and adfluvial brook trout based on the individual's OCL. The mean OCL for adfluvial fish (6.6 reaches ± 0.3) was lower than that of fluvial individuals (8.6 reaches ± 0.3) (Figure 2.5). The modal OCL for both adfluvial and fluvial movement types was reach 10 (19% and 17%, respectively).

In Sevenmile Creek mean total length of adfluvial brook trout (147 ± 3 mm) did not vary significantly from that of fluvial fish ($144\text{mm} \pm 2$) ($F = 0.888$, $df = 1$, $P = 0.347$). Condition also did not vary between adfluvial and fluvial individuals ($F = 0.449$, $df = 1$, $P = 0.503$). The frequency of adfluvial brook trout originally captured in each reach was not significantly related to brook trout, rainbow trout, or coho salmon relative density ($R^2 = >0.001$, 0.032 , 0.084 , respectively). The CPUE of brook trout in each OCL was not significantly related to the frequency of adfluvial brook trout (Figure 2.6).

Adfluvial brook trout within Mosquito River had an OCL as great as 2550m (17 reaches, the river maximum) upstream from Lake Superior. The average D_{\max} was 1650m ($11.1\text{reaches} \pm 0.9$) for adfluvial and 360m ($2.4\text{ reaches} \pm 0.1$) for fluvial brook trout. The mean D_{total} for adfluvial brook trout was 1718.5m ($11.4\text{ reaches} \pm 0.8$). The mean adfluvial D_{avg} was 817.9m ($5.4\text{ reaches} \pm 0.3$) and 272.9m ($1.8\text{ reaches} \pm 0.1$) for fluvial individuals. Logistic regression poorly predicted adfluvial brook trout behavior based on the individual's OCL (7.8%). The mean OCL for adfluvial fish (11 ± 0.9) was lower than that of fluvial individuals (12.0 ± 0.2) (Figure 2.7). In Mosquito River the modal OCL for adfluvial fish was reach 18 (23%) and for fluvial fish was reach 17 (15%); these reaches are the farthest upstream reaches in our study area (they are branches of the main stem and a tributary that are both bounded by waterfalls upstream and meet at a confluence at the lower end of these reaches).

In Mosquito River mean total length of adfluvial brook trout ($143\text{ mm} \pm 4$) did not vary significantly from that of fluvial fish ($142\text{mm} \pm 2$) ($F = 0.152$, $df = 1$, $P = 0.697$). Condition with the covariate month, did not vary significantly between ecotypes ($F =$

0.590, $df = 1$, $P = 0.443$). The abundance of adfluvial brook trout originally captured in each reach was positively related to brook trout CPUE ($R^2 = 0.58$; $P < 0.001$). The frequency of adfluvial brook trout was not significantly correlated to rainbow trout or coho salmon CPUE ($R^2 = 0.056, 0.084$, respectively). The frequency of adfluvial brook trout in each OCL was also significantly correlated to the overall CPUE of all salmonid species ($R^2 = 0.671$). This suggests that one factor in the expression of adfluvial behavior in this system is the density of conspecifics and possibly competition.

DISCUSSION

Brook trout in Lake Superior tributaries have both the ability to use a large variety of habitat types (D'Amelio and Wilson; Huckins and Baker 2008; Mucha and Mackereth 2008) and open access to many different habitat types. In these tributaries, a brook trout may move in search of favorable habitat or resources as Gowan and Fausch (1996) found in their Colorado streams. This habitat could include Lake Superior, depending on the individual's proximity to the mouth of the river.

Based on my results it does not appear that adfluvial brook trout have any distinguishing within-stream habitat requirements, as they were found in almost every reach of both streams. However, adfluvial individuals were found significantly closer to the mouth of Sevenmile Creek. This is noteworthy since brook trout in the Upper Peninsula of Michigan tend to be at lower densities closer to the mouths of rivers. In PIRO this pattern appears to be linked to the density of Pacific salmonids (J. Leonard, personal communication).

Mosquito River brook trout did not show the same relationship with OCL as in Sevenmile Creek. In this system the density of other brook trout within each reach was positively related to the number of adfluvial brook trout tagged in a reach. These patterns may indicate that intraspecific competition is influencing movement in brook trout. However, lack of consistency (between rivers) between patterns of brook trout CPUE and the frequency of adfluvial brook trout suggest that brook trout CPUE is not the only variable responsible for fluctuations in adfluvial frequency by reach (Figures 2.8). System-specific variables may be responsible for the expression of large movements in brook trout. Adfluvial behavior may be inherent in all fluvial brook trout with its expression dependent on the interaction of environmental and potentially genetic conditions. Alternatively, the expression of adfluvial behavior may simply be the most extreme case of searching behavior.

My findings parallel those of Cucherousset et al. (2005) who found that movement behavior in brown trout falls along a continuum with extremes ranging from ocean going migrants to stream dwelling residents. If both fish movement and the habitat that fish use are treated as a continuum, then much of the previous work done on fluvial salmonid movement is congruent with my study (Brown and Mackay 1995; Clapp et al. 1990; Gowan et al. 1994; Gowan and Fausch 2002).

Multiple studies have shown no detectable genetic divergence between fluvial and adfluvial brook trout within Lake Superior (D'Amelio and Wilson 2008; Scribner et al. 2012). I found no differences in body length and condition between fluvial brook trout adfluvial individuals before they left the stream. The lack of any known physical or

genetic differences between fish that exhibit the two movement types supports a conditional strategy. The adoption of alternate life history traits at the individual level as discussed by Gross (1996) suggests that variable life history tactics in partially migrating populations reflect phenotypic plasticity. Individuals “select” a life history tactic based on their environmental and resulting individual characteristics. Such characteristics could include body condition, growth, or competition, including behavioral interactions. The interaction of these characteristics and genetic and environmental conditions may make it difficult to clearly identify physical differences between the two patterns.

I was able to further evaluate the division between adfluvial and fluvial brook trout. However information about individual growth rates and metabolism may help us to further understand why two individuals of the same apparent length, condition, and proximity to Lake Superior may express different movement patterns. Understanding the mortality and fitness associated with each movement pattern will also help to determine the costs and benefits of alternate life history tactics. With the lack of genetic divergence between movement patterns in these populations, it is likely that physiological and environmental interactions are responsible; however, greater refinement of genetic techniques applied to the problem may also enhance our understanding. From this study, we now understand the similarities between fluvial residents and pre-migratory adfluvial individuals. I also demonstrated that physical differentiation is not a practical tool for the identification or management of fish in partially migrating populations. This study has also shown that the management of

brook trout in any Lake Superior tributary should recognize the continuum of habitat between systems, with the potential for adfluvial behavior.

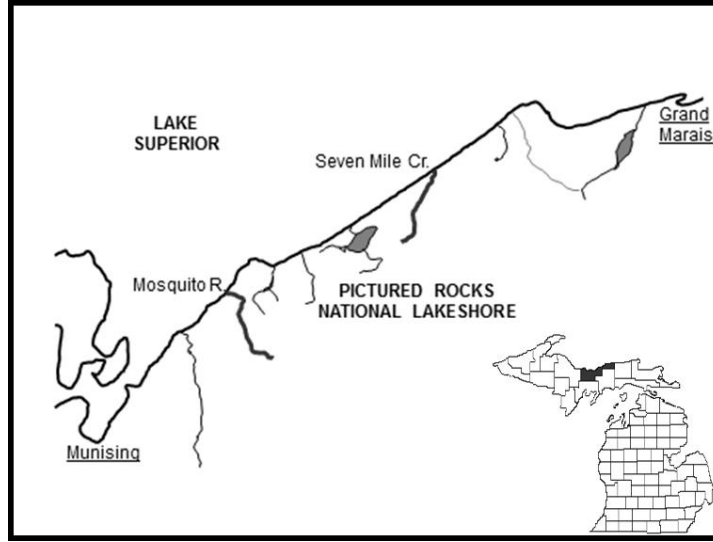


Figure 2.1 Sevenmile Creek and Mosquito River, Pictured Rocks National Lakeshore, Alger County, Michigan.

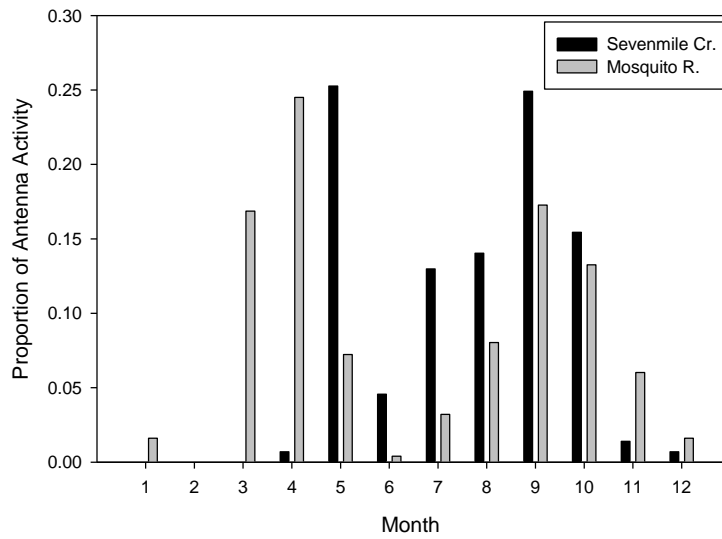


Figure 2.2 The proportion of monthly antenna activity for Sevenmile Creek and Mosquito River, Pictured Rocks National Lakeshore, MI.

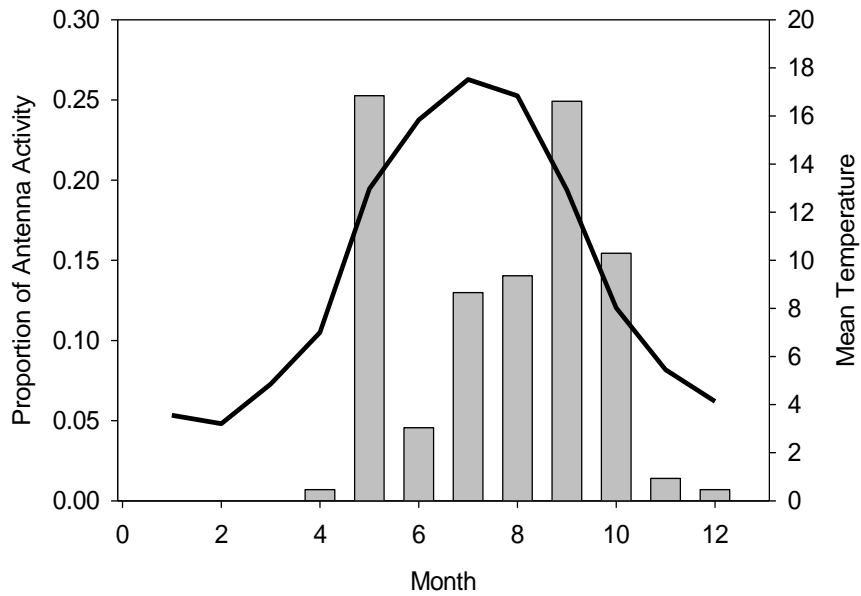


Figure 2.3 The proportion of monthly antenna activity and mean temperature in Sevenmile Creek, Pictured Rocks National Lakeshore, MI.

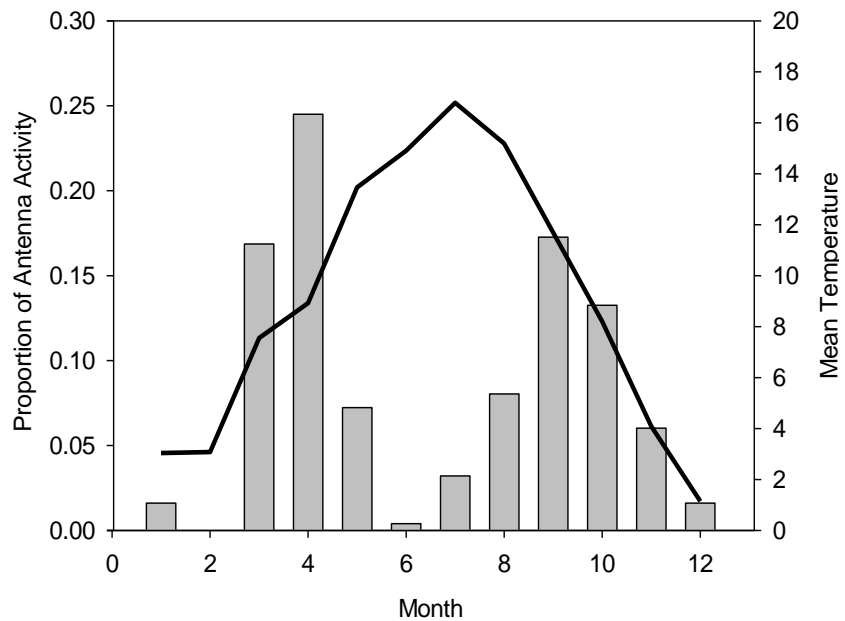


Figure 2.4 The proportion of monthly antenna activity and mean temperature in Mosquito River, Pictured Rocks National Lakeshore, MI.

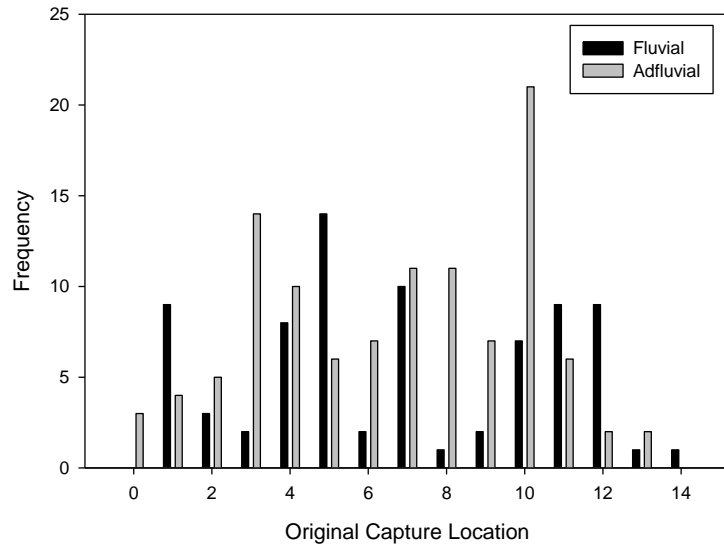


Figure 2.5 Frequency of adfluvial and fluvial brook trout in each original capture location of Sevenmile Creek, Pictured Rocks National Lakeshore, MI.

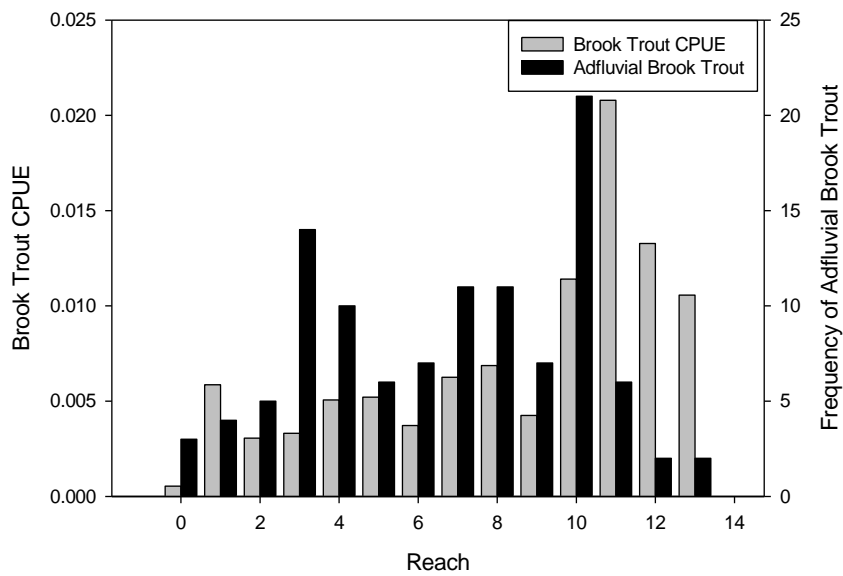


Figure 2.6 The frequency of adfluvial brook trout and brook trout CPUE in Sevenmile Creek, Pictured Rocks National Lakeshore, MI.

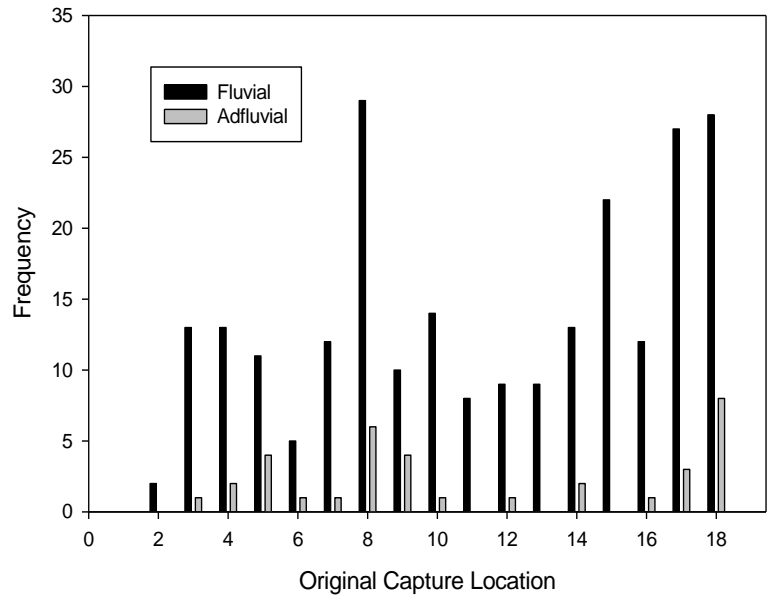


Figure 2.7 The frequency of adfluvial and fluvial brook trout in each original capture location of Mosquito River, Pictured Rocks National Lakeshore, MI.

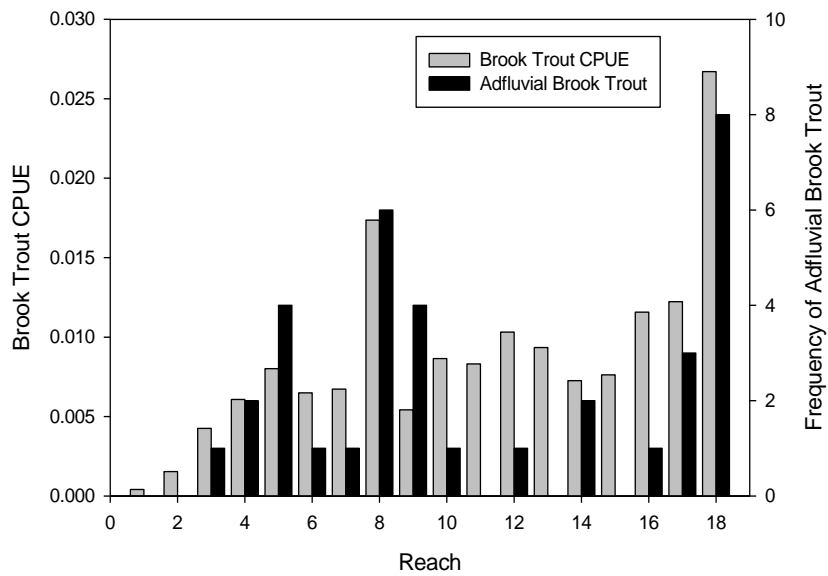


Figure 2.8 The frequency of adfluvial brook trout and brook trout CPUE in Mosquito River, Pictured Rocks National Lakeshore, MI.

CHAPTER 3: MOVEMENT PATTERNS OF FLUVIAL BROOK TROUT (*SALVELINUS FONTINALIS*) WITHIN THE LAKE SUPERIOR TRIBUTARIES OF PICTURED ROCKS NATIONAL LAKESHORE, MICHIGAN

CHAPTER SUMMARY

According to the Restricted Movement Paradigm (RMP), fluvial salmonids have very limited movement (<50m), with the exception of postnatal dispersal and reproductive migrations. I examined the individual movement histories of fluvial brook trout in order to determine the relevancy of the RMP in brook trout, and to classify fluvial brook trout movements in a partially migrating population. The study took place in two Lake Superior tributaries (Mosquito River and Sevenmile Creek) in Pictured Rocks National Lakeshore (PIRO), Michigan, using passive integrated transponder (PIT) tags. The fish were assigned to one of four movement patterns (stationed, downstream, upstream, nomadic) according to their capture history. I examined variation in condition (K), relative weight (W_r), total length (TL), and original capture location (OCL) between movement patterns. Both streams showed large proportions of fluvial brook trout with movements $\geq 150\text{m}$ from their OCL (48 and 59 %, respectively). On average fish moved 389.7 m (± 28.53 m) between capture events with some being detected as far as 2550m (17 reaches) from their OCL. Regression analysis revealed no relationship between movement pattern observed and K, W_r , or TL. However, the frequency of mobile brook trout was strongly related to brook trout relative abundance in Mosquito River, suggesting that competition may influence movement patterns. Four fluvial movement patterns were identified, ranging from stationary to highly mobile. These

findings when combined with the patterns of adfluvial brook trout, suggests that brook trout movement is a continuum rather than the two extremes currently described.

INTRODUCTION

Much of our knowledge of brook trout (*Salvelinus fontinalis*), as well as the way in which they are managed, is based on their movement patterns and population-specific life history characteristics. Understanding that fluvial brook trout have small home ranges (<50m) (Gerking 1959) allows them be managed on a by-river basis, or even managed in special management zones within the same river. Also, assuming that adfluvial brook trout are derived from a select few rivers encourages managers to focus efforts on those specific systems when conserving this type of fish. Any changes in the knowledge surrounding the movement patterns of brook trout may have wide ranging management implications and would alter our understanding of the ecological role of brook trout and their potential evolutionary responses to a changing environment.

Previous studies of Lake Superior watershed brook trout, as with many partially migrating populations, have categorized individuals as migratory (adfluvial) or non-migratory (fluvial). Migratory individuals have received substantial attention using genetic and telemetry techniques (Leonard et al. 2013). Genetic studies have collected samples from both fluvial and known adfluvial brook trout to examine genetic differences between these groups of fish within partially migrating populations (Scribner et al. 2012). While originally the two life history variants were thought to be genetically distinct, several studies have shown contradictory findings (D'Amelio and

Wilson 2008; Scribner et al. 2013). Researchers continue to try to understand the relationships among these behaviorally-determined groups of fish.

The absence of any genetic divergence between individuals displaying these two behaviors may be explained by phenotypic plasticity within the same genotype (Gross 1996). This hypothesis was termed “Conditional Strategy” and explains the presence of alternate life history strategies within one population at an individual level. According to Gross (1996), differences in the expression of an individual’s phenotype (body size, condition, physiology) dictate which life history trait an individual will express. In this hypothesis, the alternate life history traits are not competing with one another evolutionarily, and there is no set ratio of phenotypes. Rather, an individual expresses the life history trait that will maximize its success based on its phenotypic expression. Therefore, there is no presence of evolutionary divergence between fluvial and adfluvial brook trout under these conditions.

The high degree of movement observed in adfluvial brook trout as compared to the sedentary fluvial brook trout may suggest morphological or physiological differences between the two. However, it is possible that the variability in fluvial brook trout movement has been underestimated. Some of the earliest studies of fluvial salmonid movements produced very small estimates of home range (<50m) (Gerking 1959). These studies were then further supported by the work of Bachman (1984) with fluvial brown trout (*Salmo trutta*). The concept of small home ranges for fluvial salmonids was later termed the “restricted movement paradigm” (RMP) by Gowan et al. (1994) in a paper describing potential biases in single reach mark recapture studies. In

this ground breaking study, Gowan et al. (1994) found that through the use of radio telemetry fish could be recorded moving great distances within a stream. Rodriguez (2002) disputed the dismissal of the RMP, finding that high turnover rate did not always correlate to high movement, with the exception of brook trout. Rodriguez (2002) suggested that brook trout were “exceptionally mobile” compared to other less mobile salmonids. Gowan and Fausch (1996) found that over half of the fluvial brook trout tagged in their study had migrated more than 50m, with some migrating over 3000m. Clapp et al. (1990) found that large brown trout (>400mm) in Michigan’s Au Sable River migrate roughly 10 km from their summer habitat to slower and deeper overwintering habitat. In Alberta, Canada, cutthroat trout moved up to 7.6km seasonally in search of suitable habitat (Brown and Mackay 1995). The identification of such large migrations within fluvial populations of salmonids calls into question the delineation between what is considered a migratory versus a fluvial (resident) individual. Individuals within fluvial populations may exhibit different movement patterns in response to environmental factors and these differences in movement behaviors may have substantial influence on success at the individual level. These differences are, however, poorly documented or understood. The next step for researchers of these populations is to characterize these fluvial behaviors and determine what is driving the various degrees of movement within the same population.

Gowan and Fausch (2002) hypothesized that brook trout within their study sites migrate during summer months in search of seasonably favorable territory. This behavior would allow dominant fish to identify the highest quality habitat during

changing conditions. Fluvial brook trout have also been found to migrate upstream in response to non-native salmonid spawning migrations (Janetski et al. 2011). These changes in habitat use within streams may be driven by the same environmental factors as larger niche shifts such as potadromy within brook trout populations. Therefore, it is critical to examine brook trout movements utilizing an individualistic approach. This fine scale approach allows for the identification of environmental cues responsible for movement within and among aquatic systems.

I used passive integrated transponder (PIT) tags in conjunction with radio frequency identification (RFID) antennas and electrofishing to monitor brook trout movement within two Lake Superior tributaries over the course of 7 years. The antenna and electrofishing sampling provided two specific types of data. Antenna sampling continuously detected movement of tagged fish into or out of the stream, while electrofishing provided within stream location data as well as individual parameters such as length and weight. When these data were paired they provided a movement profile for individual brook trout. Movement histories were used to determine factors responsible for variability between fluvial brook trout movement patterns.

MATERIALS AND METHODS

STUDY SITES

The sample sites consisted of Sevenmile Creek ($46^{\circ} 37' 16.28''$ N, $86^{\circ} 15' 25.75''$ W) and Mosquito River ($46^{\circ} 31' 33.86''$ N, $86^{\circ} 29' 37.2''$ W) and sampled monthly for 7 years (2004 to 2011) from May to November. Both streams are found within Pictured Rocks National Lakeshore centrally located on the northern coast of Michigan's Upper

Peninsula (Figure 3.1). The Lakeshore was established in 1966 and has since been closed to development or logging. Both streams are subject to low to moderate fishing pressure (J. Leonard, pers. comm.) The streams run through mixed coniferous and deciduous forests. Native species within both streams include brook trout, central mudminnow (*Umbra limi*), sculpin (*Cottus* spp.), dace (*Rhinichthys* spp.), and suckers (*Catostomus* spp.). Both streams also have populations of non-native coho salmon (*Oncorhynchus kisutch*), pink salmon (*O. gorbuscha*), and rainbow trout (*O. mykiss*). Fluvial populations of fish within these streams are thus exposed to annual migrations of Pacific salmon, rainbow trout, and suckers.

Sevenmile Creek is a second order stream running from Sevenmile Lake into Lake Superior. The mouth of Sevenmile Creek is highly variable in its route, meandering through the sand shoreline. Upstream of the mouth, the substrate is gravel and sand with an increasing presence of beaver dams and impoundments towards the headwaters accompanied by increased sediment deposition and presence of silt substrate in the upper reaches. The upper limit of sampling is determined by stream conditions that inhibit sampling (deep beaver ponds).

Mosquito River is a third order stream. The river is groundwater fed, but remains greatly influenced by surface runoff due to the presence of bedrock and sandstone sheets at or near the soil surface. The mouth of Mosquito River is characterized by exposed bedrock shelves and sandstone. Upstream of the mouth, the substrate is primarily sand and gravel. Waterfalls at river km 2.6 present an impassible barrier to fish migration and served as the upstream limit for sampling.

Sampling of brook trout occurred using both passive and active sampling. Passive sampling using RFID antennas placed within 100m of the mouth of each river allowed for the detection of PIT tags implanted in brook trout immigrating or emigrating within the system; area downstream of the antenna was river mouth and provided generally poor holding water for salmonids. Active sampling using electrofishing backpacks (model: AbP-3TM pulsed DC, ETS Electrofishing, Verona, WI) detected the movement of brook trout within each stream and allowed for the collection of individual morphological parameters. Streams were split into three sections (upper, middle, lower), which were then divided into contiguous 150m reaches. Each reach was further subdivided into segments every 15m by transects, although most data presented is at the reach resolution. Electrofishing occurred monthly from May to November with a full sweep of each river taking place in May, August, and November. Subsampling of two reaches per section occurred monthly between sweeps.

All captured brook trout >100mm were implanted with uniquely coded, 23mm half-duplex PIT tags (Texas Instruments, Dallas, TX). Tags were implanted into the peritoneal cavity of the fish anteriodorsal to the pelvic fin. Length and weight were recorded for all brook trout captured throughout the study. All brook trout over 100mm were also scanned for PIT tags with a portable RFID antenna. If a fish was identified as a recapture, the identification number, length, and weight were recorded subsequent to release. Untagged brook trout were assigned an identification number and implanted with the corresponding PIT tag in accordance with Northern Michigan University Institutional Animal Care and Use Committee (IACUC) protocol.

The stationary double RFID antenna arrays were solar powered, double loop, half duplex RFID antennas with multi-antenna HDX RFID readers (Texas Instruments, Dallas, TX) on a 30ms cycle. The second antenna in the series allowed for the characterization of movement direction. Fish found crossing the antenna array were classified as fluvial or adfluvial based on antenna sequence criteria (Table 3.1).

Antenna detections were filtered on a monthly basis so that the first and last detection from an individual were used to assign its fate. Individuals were identified as adfluvial when they crossed both antennas heading downstream ($A2 \rightarrow A1$) or were only recorded on the lower antenna ($A1 \rightarrow A1$). These fish were assumed to have relocated to Lake Superior. This assumption was considered justified due to the antennas' close proximity to Lake Superior as well as the lack of suitable habitat below the antenna array. Fish that were detected on the upstream antenna ($A2$) and not on the downstream antenna ($A1$) were considered to be located in reach 1 for that series of detections and were classified as fluvial unless they were detected leaving the river at another time. Individuals classified as adfluvial were removed from the analysis of the fluvial brook trout portion of the study.

ANALYSIS

Individual capture histories were used to determine several movement parameters. Original capture location (OCL) was the site where a fish was first captured and tagged. Maximum distance from OCL (D_{\max}) is the maximum distance that an individual was found from its OCL at any time during the study. D_{\max} allowed individuals to be ranked based on their greatest movement from their tagging location. Total

recorded movement (D_{total}) was the sum of an individual's movements (both upstream and downstream). This differs from D_{max} since it accounts for all recorded movements, not just the greatest distance between relocations. The D_{total} of these individuals was divided by $(1 - n)$ with n representing the number of capture events for a given individual. This yielded the average distance (D_{avg}) between capture events. This measurement removes inherent bias towards greater D_{total} among fish with more capture events. This allows for the interpretation of the movement distances without including the number of events as a variable. It is important to note that these values were treated as an index of movement, not a complete record of actual total movement. Gear and sampling restrictions prevent the recording of continuous movement.

Fulton's Condition Factor (K) was determined for each tagged individual at the time of first capture as: $K = W / (L^3) \times 100$ (Nielson and Johnson 1983) where W is the weight (g) and L is total length (cm). Month of first capture was used as a covariate for condition in a linear regression in order to mitigate seasonal bias. Relative weight (W_r) was calculated for all brook trout ≥ 120 mm as $W_r = (W / W_s) \times 100$ (Nielson and Johnson, 1983) where W is weight (g) and W_s is the North American standard weight for brook trout of equal length ($\log_{10} W_s = -5.186 + 3.103 \log_{10} TL$) (Hyatt and Hubert, 2001).

Individual movement patterns were assigned to fish with a minimum of three capture events. Individuals were categorized as an upstream or downstream mover, a nomadic mover, or a stationed fish (Table 3.1) (Figure 3.2). Upstream and downstream movers were defined as individuals whose overall movements were ≥ 450 m (3 reaches)

or more in one direction. Nomadic individuals were those fish making at least two movements of 450m or more in opposing directions, often resulting in no net movement. Stationed individuals are those fish whose movements are > 450m (3 reaches) from their OCL. Distances were set at the 150m resolution. Parameters such as D_{\max} were calculated to the nearest reach and meters were calculated by multiplying the number of reaches moved by 150. Therefore, a move from reach-1 to reach-2 would be presented as a movement of 150m. This resolution means potential variation of +/-149m. This was accounted for by setting a three reach minimum for movement patterns.

Simple linear regressions were performed for both rivers in order to determine what factors (K , W_r , and L) were most strongly related to movement pattern. Regressions were run in SPSS (version 19.0). Linear regressions were independent for each river system and parameter and required the coding of dummy variables for movement pattern and the covariate month. ANOVA's were used to test for differences in mean OCL between fluvial and adfluvial fish. Mobile fluvial brook trout (downstream, upstream, nomadic) frequencies were combined on a by-reach OCL scale. This provided the number of individuals categorized by a mobile movement pattern originally found in each reach, allowing for the identification of patterns in fluvial movement by OCL. These OCL frequencies were then examined for correlation to catch per unit effort (CPUE, individuals/m²) of brook trout, coho salmon, and rainbow trout.

Streams were compared to each other with a Chi-square test of independence to determine any variability between the frequencies of movement pattern. Two factor

ANOVA's were used to determine variability of condition, and total length between the two stream and four movement patterns. A t-test was used to compare the average D_{max} for the two rivers. I used $\alpha = 0.05$ for all hypothesis tests. Regressions with an $R^2 \geq 0.5$ were considered have a strong relationship.

RESULTS

In Sevenmile Creek, 2256 brook trout were tagged over the course of the project. Of these, 361 (16 %) were recaptured and included in the analysis as fluvial brook trout. The modal OCL was reach 11 with 57 individuals (15%) followed by reach 10 with 47 individuals (12%). Fluvial brook trout within Sevenmile Creek were found a mean D_{max} of 309m (2.06 reaches ± 0.17) from their OCL. One fluvial brook trout was detected as far as 1950m (13 reaches) from its OCL. Within the fluvial data set, 48% of individuals (175 fish) moved 150m or more, and 27% (48 fish) were found over 1000m from their OCL; 75% of fluvial fish in the data set were detected at least 150m away from OCL. This group of mobile fluvial brook trout ($D_{max} > 150m$) had an mean D_{max} of 642m (4.3 reaches ± 0.3). The mean D_{total} moved for all fluvial brook trout within Sevenmile Creek was 350.9m (2.2 reaches ± 0.2). The mean distance between capture events (D_{avg}) was 268.9m (1.8 reaches ± 0.2) and was 556.6m (3.7 reaches ± 0.2) for only mobile individuals ($D_{max} > 150m$).

Of the 361 fluvial Sevenmile Creek brook trout included in the study, 78 (22%) individuals had capture histories including three or more detections. The mean movement between capture events for these fish was 266.7m (1.8 reaches ± 0.3). Within this subgroup, 48 individuals (61%) were categorized as stationed, 14 (18%) as

downstream directed movers, 9 (12%) as upstream directed movers, and 7 (9%) were nomadic (Figure 3.3, 3.4). Movement pattern was not related to W_r , TL, or K. Movement pattern varied significantly between OCL ($F = 7.29$, $df = 3$, $P < 0.001$), but showed no clear trend. The distribution of mobile individuals (downstream, upstream, nomadic) was not significantly related to the CPUE of brook trout, coho salmon, or rainbow trout ($R^2 = 0.485$, $F = 3.46$, $P = 0.055$) when examined on a reach basis. The distribution of these individuals by OCL was not homogenous throughout the stream (Figure 3.5).

In Mosquito River, 2050 brook trout were tagged throughout the course of the project. A total of 653 (32%) individuals were recaptured and included in the analysis as fluvial brook trout. The modal OCL was reach 17 with 98 individuals (15%) followed by reach 18 with 67 individuals (10%). Combined, these two reaches accounted for the OCL of 25% of the total individuals. Within Mosquito River, fluvial brook trout moved a mean D_{max} of 355.5m (2.4 reaches ± 0.2) from their OCL. One individual was 2550m (17 reaches) downstream of its OCL. Of the 689 fluvial brook trout from this river used in this project, 58.5% (382 fish) moved 150m or more throughout the study, and 12% (78 fish) were found more than 1000m from their OCL. Within this group of mobile brook trout (i.e. $D_{max} \geq 150m$), the mean D_{max} was 616.5m (4.1 reaches ± 0.2). The mean D_{total} for fluvial brook trout within Mosquito River was 385.5m (2.6 reaches ± 0.2). The mean distance moved between capture events (D_{avg}) was 184.2m (1.2 reaches ± 0.1) for all fluvial brook trout and 458.0m (3.1 reaches ± 0.2) for the group of mobile individuals ($D_{max} > 150m$).

Of the 653 fluvial Mosquito River brook trout included in the study, 202 (30%) individuals had capture histories including three or more events. Among these individuals, the mean distance moved between capture events was 282m (1.9 reaches ± 0.2). Within this subgroup, 113 individuals (56%) were categorized as stationed, 44 (22%) as downstream directed movers, 31 (15%) as upstream directed movers, and 14 (7%) were found to be nomadic (Figure 3.3, 3.4). Movement pattern could not be explained by TL, OCL, W_r , or K. When mobile fluvial brook trout (downstream, upstream, nomadic) were combined within each OCL, their frequency was significantly related to mean by-reach brook trout and rainbow trout CPUE from 2004-2011 ($R^2 = 0.654$, $F = 13.24$, $P = 0.001$) ($y = 6.535b + 612.96 * BKT - 165.619 * RBT$; (Figure 3.6). Mobile brook trout frequency was positively related to brook trout CPUE and negatively related to rainbow trout CPUE. However, there was still a large amount of variation when mobile brook trout frequency was graphed along with brook trout CPUE (Figure 3.7).

The proportions of movement patterns observed did not vary significantly between Sevenmile Creek and Mosquito River ($\chi^2 = 1.59$; $P = 0.662$) (Figure 3.3, 3.4). There was no significant difference in D_{max} ($F = 0.115$, $df = 1$, $P = 0.735$), condition ($F = 0.703$, $df = 1$, $P = 0.402$), or total length ($F = 0.296$, $df = 1$, $P = 0.587$) between the two systems.

DISCUSSION

The restricted movement paradigm (RMP) suggested that fluvial salmonids have small home ranges (<50m) and that movement greater than 50m could be attributed to spawning or natal dispersal (Bachman 1984; Gerking 1959). My findings contradicted

the RMP and supported the conditional brook trout movement model (Gowan and Fausch 2002). Approximately half of the individuals in Sevenmile Creek and Mosquito River moved 150m or more throughout the course of the study. If the majority of movement was postnatal dispersal as assumed by Gross (1996), then mean total length should be reflected in a greater size in stationary fish that had settled into small home ranges. However, there were fish of each size class within each movement pattern group. It is likely that some of the large movements seen in this study were associated with spawning activity. However, movement was consistently found throughout the iceless months and not concentrated during spawning season (October), which may imply little site fidelity in general for highly mobile individuals.

The focus of previous brook trout studies within Pictured Rocks National Lakeshore has been on distinguishing adfluvial from fluvial brook trout, as well as identifying indicators of potential adfluvial behavior (Huckins et al. 2008; Kusnierz et al. 2009; Stimmel 2006). Such indicators included age, length, and Fulton's condition. However, no studies had been conducted to identify movement patterns within the fluvial population of these systems. The movement patterns within these systems were assumed to be dichotomous, categorized as either adfluvial or fluvial individuals; however, my data has revealed more variability within these populations with three additional movement patterns within fluvial brook trout. I am unable to clarify if these movement patterns are permanent life history patterns; however, there is a consistency across years and river systems that suggests some predictability in occurrence of movement patterns. These movement patterns could be expressed in response to

some seasonal (Gowan and Fausch 2002; Janetski 2011) or stochastic event, or they may be fixed patterns due to conditions at an individual level (Gross 1996; Wysujack 2009). Regardless of control factors, it seems clear that individuals within the fluvial populations studied here are expressing substantial variability in movement behavior and future research should address both control mechanisms and population-level ramifications of these behavioral groups.

Many of the fluvial individuals tracked in this study had movement patterns analogous to adfluvial brook trout, albeit without the defining behavior of exiting the river. Other fish ranged over the entire length of the river and ended up at their original capture locations. These behaviors are indicative of a continuum of movement rather than two distinct movement patterns. Cucherousset et al. (2005) found similar behavior in brown trout, concluding that when freshwater (resident) brown trout movements were included with those of migratory brown trout, the result was a spatial and temporal continuum. Studies like this are reinforcing the idea that the differences observed between fluvial and adfluvial salmonids may be due to a lack of research identifying variation among fluvial movement patterns.

There is growing evidence to suggest that fluvial and adfluvial individuals do not differ genetically (D'Amelio and Wilson 2008; Scribner et al. 2012), or in some cases physically (Kusnierz et al. 2009). This information, when combined with my findings, suggests that the degree of movement in brook trout is set at the individual level with the population maintaining a range of conditionally determined options. A conditional strategy allows the individual to optimize its success based on its environmental

conditions by “selecting” a movement pattern (Gross 1996). There was no difference in condition or total length among the different fluvial movement patterns within Sevenmile Creek or Mosquito River. However, the relative abundance of conspecifics in a reach (CPUE) was associated with the frequency of mobile fluvial brook trout produced within that reach. Competition may vary throughout the river, based on the interaction of brook trout density and available resources. This may differentially affect brook trout according to their length or condition in each location.

Conversely, the lack of any significant difference in total length between movement patterns may suggest that movement pattern selection is affected by density-dependent, but not size-dependent, competition. This could be due to size-dependent fish distribution based on habitat quality, and therefore competition would act independently on each size class. If a distribution similar to this were in effect it would obscure any trend in total length or condition. Competition might act according to the size distribution within each patch of habitat. Unlike our streams, Gowan and Fausch (2002) found that the most dominant brook trout in their system moved throughout the stream in order to both monitor neighboring conditions and occupy the most optimal location based on seasonal variation. The patterns of dominant brook trout described in Gowan and Fausch (2002) are comparable to the nomadic movement patterns I observed. However, my findings did not suggest that nomadic fish were composed of the largest, most dominant individuals. It is possible that other large salmonids may replace brook trout in these systems in the role of large dominant fish.

I propose a model of brook trout movement based on a continuum of behaviors and eliminating the dichotomy that once separated fluvial from adfluvial brook trout. My results suggest a structure of brook trout movement that is evolutionarily stable. The patterns observed in the PIRO streams likely afford brook trout greater responsiveness to variable environmental conditions. Brook trout within these streams have the ability to move substantial distances within the stream in response to environmental stimuli; this flexibility also has the potential benefit of ensuring the recolonization of disturbed habitat. Fluvial brook trout within these streams also have the potential to search for optimal habitat. This allows for shifts in the distribution of brook trout with changes in habitat. Interestingly, a large proportion of individuals remained stationary throughout the study. This suggests that there is ecological value to these individuals in remaining in a relatively small area, but it is still unclear how these benefits are balanced with the potential to move throughout the system. It also is unclear whether this stationed behavior is a permanent strategy for a particular individual or if these fish could be expected to adopt a different movement strategy at a later date. Until it is discovered how the selection of movement pattern is genetically supported, it will be unclear what the consequences of these findings are at the population or evolutionary level. Further study within this field should include the examination of the fitness consequences of each movement pattern relative to each other through the use of individual growth and fecundity. This will allow for a greater understanding of the persistence of each movement pattern within individuals and the population.

Figures

Table 3.1: Description of selection criterion for each movement pattern as well as frequency and percent of each movement pattern from May 2004 to August 2011.

| Movement Pattern | Criterion | # of individuals Sevenmile | # of individuals Mosquito |
|-------------------------|---|---------------------------------------|--------------------------------------|
| Stationed | ≥3 captures with total movements within 300m of OCL | 48 (61%) | 113 (56%) |
| Downstream | ≥3 movements totaling ≥450m downstream of OCL | 14 (18%) | 44 (22%) |
| Upstream | ≥3 movements totaling ≥450m upstream of OCL | 9 (12%) | 31 (15%) |
| Nomadic | ≥3 movements with ≥2 movements of 300m in opposing directions | 7 (9%) | 14 (7%) |

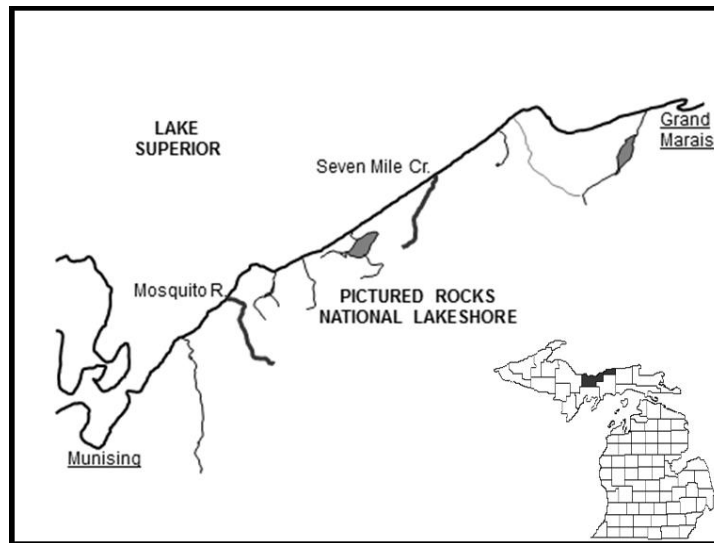


Figure 3.1 Sevenmile Creek and Mosquito River, Pictured Rocks National Lakeshore, Alger County, Michigan. Inset shows Alger County Michigan.

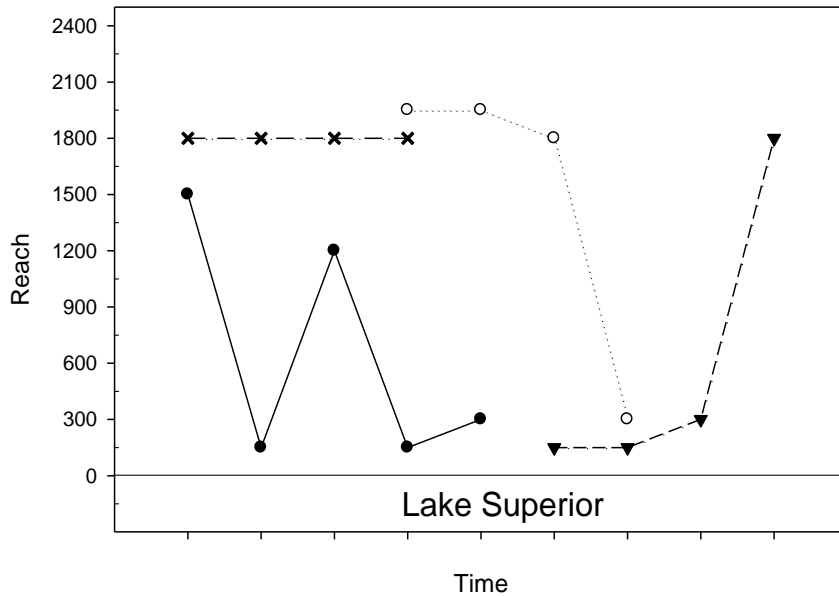


Figure 3.2 Brook trout movement patterns observed in Sevenmile Creek, MI in 2009. Fish number 1 (x) represents a stationary fish captured within the same stream reach each month. Fish number 2 (•) represents a nomadic movement. Fish number 4 (o) represents a downstream directed movement and fish number 5 (▶) shows an upstream directed movement.

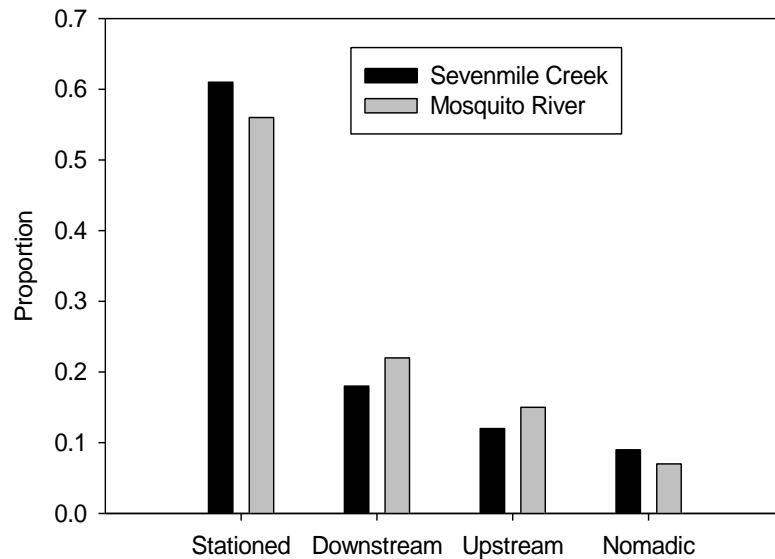


Figure 3.3 Percent of total individuals found in each movement pattern within Mosquito River and Sevenmile Creek, Pictured Rocks National Lakeshore, MI.

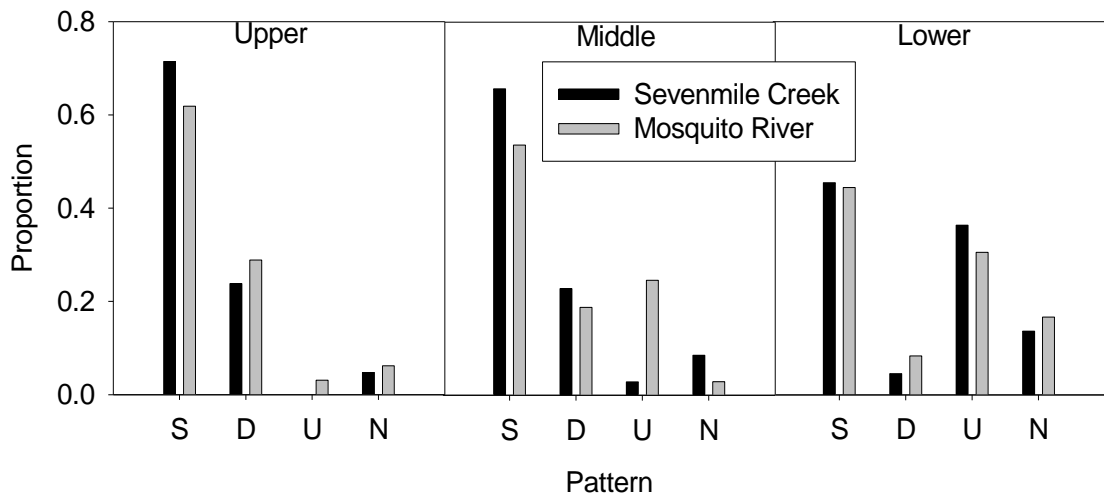


Figure 3.4 Proportion of movement patterns in Sevenmile Creek and Mosquito River, Pictured Rocks National Lakeshore, MI. The proportions are divided by river section.

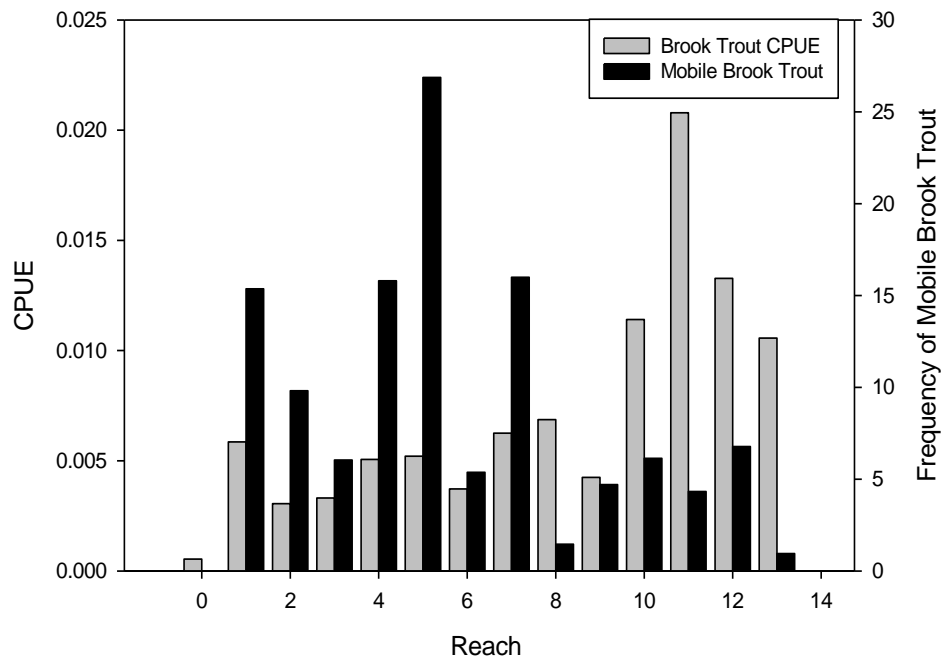


Figure 3.5 Patterns of mobile brook trout frequency and CPUE in Sevenmile Creek. Matched distributions would show direct correlation between brook trout CPUE and the frequency of mobile brook trout per OCL.

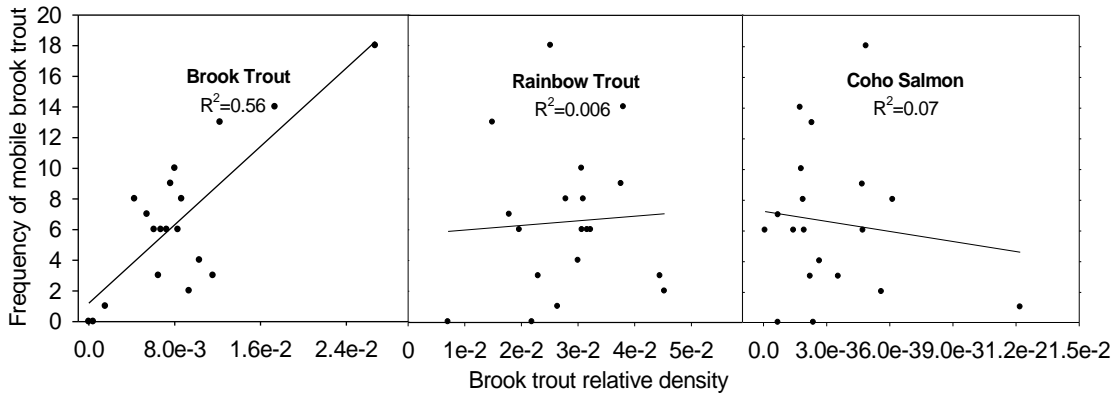


Figure 3.6 The relationship between by-reach brook trout, rainbow trout and coho salmon CPUE and the frequency of mobile brook trout tagged within that reach in Mosquito River, Pictured Rocks National Lakeshore, MI.

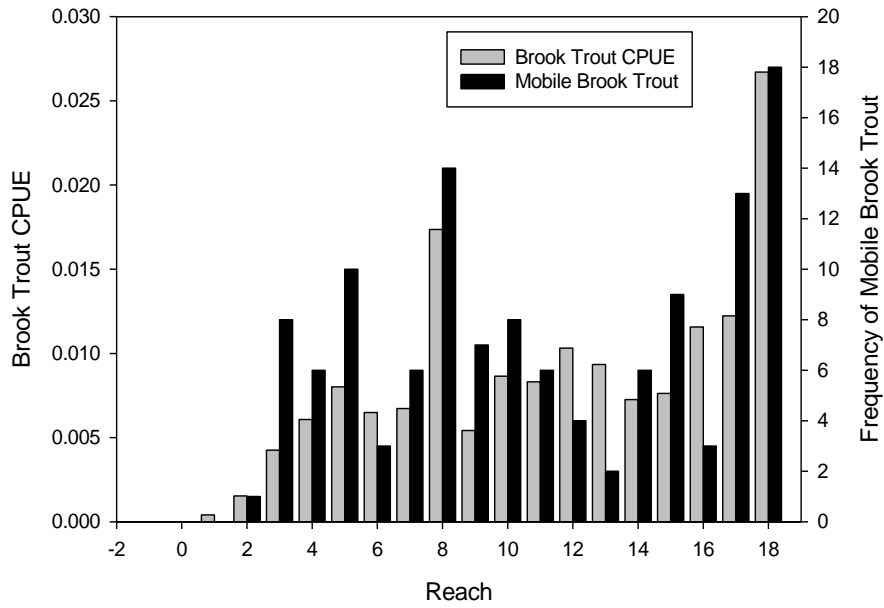


Figure 3.7 Distribution of mobile brook trout and CPUE in Mosquito River. Equal differences would show direct correlation between brook trout CPUE and the frequency of mobile brook trout per OCL.

CHAPTER 4: CONCLUSION

Sympatric populations of partially migrating brook trout exist within both Sevenmile Creek and Mosquito River. During my study, the two ecotypes were treated as mutually exclusive and compared to one another. However, my data provide evidence that these two ecotypes are actually part of a continuum of life history patterns within a single population of brook trout. Cucherousset et al. (2005) found that when all of the movement patterns found within their study sites were combined the end result was a continuum of movement patterns rather than a dichotomy of freshwater (residents) and saltwater individuals. My study also began with a dichotomy of movement patterns (adfluvial and fluvial). However, when combined, the movement patterns resulted in a behavioral continuum. Upon closer evaluation, fluvial brook trout had four subpatterns (stationed, downstream directed, upstream directed, nomadic) which further supports the continuum concept. This led to the question of what variables were responsible for the varying degrees of movement displayed in this population.

I found no physical difference (TL, K, W_r) between fish expressing the two main movement patterns (fluvial and adfluvial). The location in which individuals were first found in the stream (OCL) was a useful predictor of the expression of adfluvial behavior in Sevenmile Creek. OCL, however, did not correctly predict 100 percent of the movement patterns. This suggests that OCL has a strong influence on movement, but is not the sole determinant. The density of both conspecifics and other salmonids also had a significant influence on the number of mobile individuals, both adfluvial and mobile fluvial, that were found in each reach. This suggests that competition of some sort may play a role in brook trout movement.

With the absence of any genetic divergence between adfluvial and fluvial brook trout (D'Amelio and Wilson 2008; Scribner et al. 2012), it appears that movement patterns are determined at the individual level. Gross (1996) proposed a “conditional strategy” and attributed alternate life history traits to phenotypic plasticity. In this case, movement patterns are “chosen” in response to environmental conditions based on an individual’s phenotypic expression. Therefore, the way an individual’s body responds to environmental factors (based on its phenotypic expression) may influence its movement pattern. This strategy, as outlined by Gross (1996), allows for two alternate tactics to compete with one another on the individual level while not competing on an evolutionary scale (within the population). This strategy may explain why there is no detectible genetic divergence in populations while also explaining how movement patterns can be set at the individual level my study suggests. However, it is necessary to determine the fitness associated with the expression of fluvial and adfluvial behavior in order to understand the costs and benefits of each pattern. It is also important to determine the permanence of an individual’s movement pattern to better assign costs and benefits. Consequently, if fluvial movement patterns are not permanent then it may not be possible to assign them fitness.

In proposing a new model of brook trout movement, this study has determined four fluvial brook trout patterns. The population and evolutionary ramifications of these patterns are not yet known. However, these patterns along with adfluvial, and even anadromous, brook trout help to further explain the evolutionary stability of brook trout and highlight the importance of intraspecific diversity. Adfluvial and mobile fluvial brook trout may help to act as genetic vectors between concentrations of brook trout within larger systems. These

movement patterns may also help to repopulate disturbed habitat after a perturbation. Therefore, it is important to understand the variables that lead to the expression of these patterns, since they may aid in the persistence of brook trout during climate change or anthropogenic perturbations.

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APPENDIX



Continuing Education
1401 Presque Isle Avenue
Marquette, MI 49855-5301

MEMORANDUM

October 12, 2010

TO: Dr. Jill Leonard
Department of Biology

FROM: Terrance Seethoff, Ph.D. *RS*
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**
Modification to Application # IACUC 152
Approval Period: 01/25/2009-05/31/2011

The Institutional Animal Care and Use Committee, has approved the modifications to your application to use vertebrate animals in research, "Examination of resident and coaster brook trout response to exotic salmonid removal in Sevenmile Creek Pictured Rocks National Lakeshore".

If you have any questions, please contact me.

kjm

MEMORANDUM

August 27, 2010

TO: Dr. Jill Leonard
Department of Biology

FROM: Terrance Seethoff, Ph.D. *TSS*
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**
Application # IACUC 152
Approval Period: 08/15/2010-08/14/2013

The Institutional Animal Care and Use Committee have approved your application to use vertebrate animals in research, "Examination of resident and coaster brook trout response to exotic salmonid removal in Sevenmile Creek, Pictured Rocks National Lakeshore".

If you have any questions, please contact me.

kjm