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Using instream stationary antennas to monitor the movements of warm water fishes in a reach of stream bisected by a culvert

William Commins

A Thesis Presented in Partial Fulfillment of Requirements for the
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Department of Evolution, Ecology, and Organismal Biology

Kennesaw State University
1000 Chastain Road
Kennesaw, GA 30144
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Major Advisor: William Ensign, Ph. D.
Committee Member: Herman Ray, Ph. D.
Committee Member: Troy Mutchler, Ph. D.

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Abstract

In this study I investigated the differences in the non-migratory movement patterns of six fish species in a 280m reach of stream bisected by a culvert (impeded), and a 300m reach of stream with no movement barriers (unimpeded). This study took place between July 1, 2018 and November 14, 2018 in Raccoon Creek, Paulding County, Georgia. I used 12mm passive integrated transponder tags and four instream stationary antennas to monitor the movements 429 fishes. The antennas redetected 262 of the 429 individuals (61.1%), and 48% of fishes were redetected more than 10 times. The proportion of tagged individuals detected by species ranged from 53.3% (*Lepomis auritus*) to 90% (*Hypentelium etowanum*). The proportion of detected fishes that moved at least 150m in the unimpeded reach ranged from 41% for *L. auritus* to 100% for *Moxostoma duquesni*. A multi-state model was implemented to estimate the probability of weekly upstream and downstream movement in the unimpeded reach (upstream= 0.11, 95% CI = 0.08 - 0.16, downstream= 0.07, 95% CI = 0.04 - 0.10), and in the impeded reach (upstream= 0.01, 95% CI = 0.001 -0.04, downstream= 0.01, 95% CI = 0.004-0.02). The patterns of movement observed in this study suggest that conservation managers should consider movements of 150m as a potentially frequent weekly occurrence for the species monitored, and other closely related fishes. This study demonstrates the potential long-term impact a culvert can have on the natural movement patterns of stream fishes.

Keywords: Fish Movement, Culvert, PIT tags, Instream Antennas, Multi-state model

Chapter 1 –Literature Review

Fish Movement Patterns and Population Structure

W.H. Burt first proposed the ‘home range movement concept’ for terrestrial organisms in the early 1940’s (Burt 1943). Generally, a home range is described as the distance an organism travels to achieve the activities required for survival (Burt, 1943, Hayne 1949). Within an organism’s home range, movements are typically biased towards a location of increased fidelity (Spencer et al. 1990). In the 1950s, S.D. Gerking suggested that the home range concept also applied to riverine fishes (Gerking 1959). Over the next three decades, multiple mark-capture-recapture studies by Gerking and others led to broad acceptance of a ‘Restricted Movement Paradigm’ (RMP) for riverine fishes (Gerking 1950, Lotrich 1975, Hill and Grossman 1987). According to the RMP, stream fishes express a high level of site fidelity, with movements of adults typically limited to a single habitat unit (i.e. riffle or pool) (Gerking 1959). Although the RMP did not disregard the occurrence of movements that extended beyond a typical home range, these long distance movements were considered to be less frequent, and associated with migratory spawning (Gerking 1950, Cohen 1969).

In 1994, a review article by Gowan and others raised questions about how broadly the RMP described the movement patterns of riverine fishes (Gowan et al. 1994). The article pointed out that in nearly half (42%) of the studies considered the rate of recapture for marked fishes was below 25%. Additionally, the review pointed out that all the studies considered typically focused recapture efforts in areas where fishes were originally marked, and therefore were not able to detect long distance movements. Many of these traditional studies also used batch marking, a marking technique where all fishes from a section are given the same “mark”. Due to the limitation on the number of unique marks, batch marking makes it very difficult to investigate the movements of individual fishes. With low percentages of marked fish recaptured and the inability to track individual fishes, Gowan

suggested that there was still considerable uncertainty in regards to the movement pattern of an entire population (Gowan et al 1994).

Following Gowan's review article, subsequent fish movement studies using more advanced and thorough methods confirmed that many stream fishes were more mobile than previously reported. Young (1996) used radio telemetry to track the movements of 29 Cutthroat trout (*Oncorhynchus clarki*) and determined the median home range of the tracked fish to be 233 meters. This was substantially higher than a previous movement study using batch marking (Peterson tags), which had reported the home range of Cutthroat trout to be 20m or less (Miller 1957). Smithson and Johnson (1999) used passive integrated transponder tags (PIT) to monitor the movements of the Creek chub (*Semotilus atromaculatus*), Black-spotted topminnow (*Fundulus olivaceus*), Longear sunfish (*Lepomis megalotis*), and the Green sunfish (*Lepomis cyanellus*), and determined that all four species had a portion of the population (12% - 33%) that moved away from the habitat units in which they were marked. Additional studies investigating the movement patterns of multiple fish families showed that the RMP did not fully describe the movement patterns of stream fishes (David and Closs 2002, Rodriguez 2002, Radinger and Wolter 2014, Davis 2017).

One of the difficulties in determining the movement patterns for riverine fishes is distinguishing home range movements from movements associated with migratory spawning. Spawning strategies represent a distinguishing life history characteristic for many freshwater fishes. Many of the spawning behaviors for stream fish involve very long distance movements during specific time periods (Cohen 1969, Fausch et al. 2002). Trout species have been monitored moving hundreds of kilometers to headwater streams to spawn and then returning to the same pool after spawning (Fraley and Shepard 1989). Although migratory movements are typically associated with large river fishes like Salmonids and Catostomids, some of the smallest river fishes make migratory

movements taking them kilometers away from their respective home range (Doherty et al. 2010, Hicks and Servos 2017). Due to the unique ability of spawning migrations to temporarily displace fishes from their home range, studies considering the daily dispersal movements of a population typically monitor movement during non-spawning seasons (Radinger and Wolter 2014).

It is now generally accepted that a population of stream fish is comprised of two components, a stationary component and a mobile component. The stationary component (the stayers) of the population display high levels of site fidelity and maintain a defined home range. A home range size is typically less than 100m for most stream fishes (Skalski and Gilliam 2000, Rodriguez 2002, Davis 2017), however, some fishes, specifically in the family Catostomidae, have been reported as having home range sizes over 1000m (Radinger and Wolter 2014). The fishes in the mobile component (the movers) have a tendency to make movements that far exceed the typical home range size for that species. Members of the mobile portion do not typically stay in a perpetual state of dispersal, but instead dispersal movements may result in home range shifts (Crook 2004). Once a fish has dispersed to a new location, it will once again maintain a home range with a new site of fidelity. There is also evidence to suggest that individuals may be able to transition from one component to the other throughout their lifetime. A study investigating the movements of the European Bullhead (*Cottus gobio*) found that some fish showed periods of extended fidelity before transitioning and becoming more mobile (Knaepkens et al. 2004).

Movement of stream fishes is best described using a leptokurtic distribution (Fraser et al. 2001, Radinger and Wolter 2014). A leptokurtic distribution differs from a normal distribution in that it has a higher number of individuals grouped near the center, and has thicker tails on either end (Figure 1.1). The individuals grouped at the center of the distribution are the stayers, most of which display a similar level of increased site fidelity. The tails of the distribution represent the upstream and

downstream dispersal distances made by the mobile portion of the population (Radinger and Wolter 2014). The thickness of the tails on the distribution coincides with the proportion of the population that actively makes long dispersal movements. The lengths of the tails vary based on the dispersal distances of the species. Differences in the proportions of stayers and movers for different species will result in variation to the shape of the shape of the movement distributions.

Movement Comparisons across Taxa

Many studies have recognized differences in the proportion of movers and stayers across different taxa of stream fishes. A study in a large coastal plain stream in the southeastern United States reported that the Blackbanded Darter (*Percina nigrofasciata*) in the family Percidae, and the Redbreast Sunfish (*Lepomis auritus*) in the family Centrarchidae had different proportions of movers (Freeman 1995). Blackbanded Darter were more mobile with 42% of recaptured fishes moving away from their marking area, compared to just 23% for the Redbreast Sunfish. A 2009 study on the movement patterns of the Mottled Sculpins (*Cottus bairdii*) found that only 16% of the marked fish moved more than 100m, with the vast majority displaying a restricted movement pattern (Breen et al. 2009). In a large river in Idaho, a study reported that 24% of Smallmouth bass (*Micropterus dolomieu*) were mobile (recaptured outside of their original marking area) (Munther 1970).

Studies have also reported variation in the home range sizes for stream fishes. A study on a large river in Australia found significant differences when comparing the mean home range movements of two large-bodied fishes from the families Percidae and Cyprinidae (Crook 2004). The Cyprinidae (*Cyprinus carpio*) had a home range size of 109 m, and the Percidae (*Macquaria ambigua*) had a home ranges size of 525m. In the Saint Johns River, Canada, the home range size of the White Sucker (*Catostomus commersoni*) averaged 2600m during non-spawning periods (Doherty

et al. 2010). In contrast, the home range size of the Longnose Dace (*Rhinichthys cataractae*) was reported to only be 12.9m (Hill and Grossman 1987).

Closely related fishes are typically reported as having similar home range sizes and proportions of mobile fishes. The Central Stoneroller (*Campostoma anomalum*) was reported to have a home range of 35.2m in a small Ohio stream (Mundahl and Ingersoll 1989). In two streams in Georgia (one rural and one urban), the Largescale Stoneroller (*C. oligolepis*) had an average home range size of 36.1m (Davis 2017). Both the Central and Largescale Stoneroller have long slender streamlined body forms, and prefer riffle habitats. In a small urban stream, the Redbreast Sunfish (*L. auritus*) was determined to have a mobile component of 14 % of the population (Davis 2017). The closely related Longear Sunfish and the Green Sunfish, all of which share similar body morphology and habitat preferences were reported as having a mobile component of 12% and 14% respectfully (Smithson and Johnston 2004). The similarities in movement patterns may result from similar body forms and habitat preferences. A study that used radio telemetry to investigate three species of black bass found daily movement rates did not vary for the Shoal Bass (*Micropterus cataractar*), Largemouth Bass (*M. salmoides*), and the Spotted Bass (*M. punctulatus*) (Goclowski et al. 2013). This study suggests that the closer species are in terms of phylogeny, the more likely they are to have similar patterns in mobility.

A meta-analysis by Radinger and Wolter (2014) examined the movements of 62 fish species from 10 fish families and summarized the within and across family variation in fish movement patterns. The study determined that the median movement distance for the stationary component for the 10 fish families was 36.4m, and that the median distance travel by the mobile component was 361m. The study revealed high levels of variation across families in median distance travelled by the stationary component (3m to 1000m) and the mobile component (30m to over 10,000m). The analyses

in this study support the concept of heterogeneity for the movement behaviors of stream fish populations. However, there is still uncertainty concerning what factors contribute to the differences in the proportions of mobile fishes across taxa. A better understanding of what promotes the variation in movement patterns across taxa could aid conservation efforts for impaired fishes, and help evaluate how a disturbance will affect a community of fishes.

Influences on Movement

Variations in the morphological features of stream fishes allow for mobility advantages in different water velocities (Nikolski 1933, Gatz 1979, Ross 1986, Gaston and Lauer 2012), resulting in different locomotive strategies and preferences towards specific habit types (Webb 1984, Sambilay 1990). The fundamental morphological features that influence the swimming capacities and movement strategies of a fish are body depth ratio (maximum depth/total length), and caudal fin aspect ratio (Aspect ratio = height of the caudal fin ²/surface area of fin) (Gatz 1979, Webb 1984). The relative variation in these two morphological features typically result in increased reliance on either undulatory or oscillatory movements of the body and fins. In fast flowing waters, the wave-like undulatory motion of a streamlined fish's body and caudal fin allow it to rapidly accelerate to maintain its' position in the water column (Webb 1984). In comparison, a high body depth ratio is associated with increased oscillatory motion of body and paired fins, allowing for increase maneuverability in the complex habitats of slower moving water (Webb 1984).

In general, fishes with common habitat preferences share similar morphological features and swimming strategies. Fish with streamlined body forms and low body depth ratios are found more often in higher velocity habitats associated with riffles (Webb 1984, Gaston and Lauer 2012). Alternatively, fish with high body depth ratios are more suited for the slower water velocities found in

pool habitats (Gaston and Lauer 2012). Movement between suitable habitats can be limited by different ecological or physical factors depending on body form. Differences in body morphologies and the distance between adjacent suitable habitat units may result in differences in movement rates for stream fishes (Schaefer 2001, Matthews et al. 1994, Niebuhr et al. 2015). A high body depth ratio results in considerably more drag in fast flowing water compared to a low body depth ratio. Therefore a deep-bodied fish would require more energy to traverse riffles compared to a streamlined fish (Webb 1984). Although a riffle dwelling fish may be able to traverse the slowly moving waters of a pool, the presence of potential predators in pools has been shown to influence movement rates for smaller fishes (Werner et al. 1983).

The physical characteristics of a stream can also influence movement for fishes. Stream discharge, cover, habitat complexity, and temperature have all been shown to influence fish movement for at least one species of stream fishes (Albanese et al. 2004). Stream morphologies are diverse and differ based on elevation, topography, flow regime, and geology. A stream with large changes in elevation can produce multiple natural movement barriers within a watershed, restricting fish movement and isolating populations (Wofford et al. 2005). Alternatively, lowland streams can consist of large reaches of homogeneous habitat with few physical obstructions to movement (Sedell et al. 1990). The relative location to a confluence with another stream can also influence movement patterns for stream fish. In a study that compared movement patterns of four fish species in a network of Virginia streams, increased distance to a mainstem river reduced the dispersal frequency of two fish species (Albanese et al. 2004).

Increases in fish movement are linked to seasons with more precipitation. High flow events or flood conditions can increase water depth at shallow or previously impassable portions of a stream and have the potential to increase fish dispersal. Jeffres and Klimley (2006) investigated the movements of

the Sacramento Sucker (*Catostomus occidentalis*) under flood conditions and showed that before a flood fish moved on average less than 550 meter, however during flood times some individuals moved over 8100 meters. A study using radio telemetry reported that over 70% of Giant kokopu (*Galaxias argenteus*) moved and settled into a new location during flood events (David and Closs 2002). Additionally, a study in a network of Virginia streams found that four benthic dwelling and four water column fishes were more likely to move into a bi-directional weir during flow events (Albanese et al. 2004).

Movement Barriers

The increasing urbanization of many watersheds can make it difficult to identify the natural movement patterns for stream fishes. Urbanization negatively impacts fish movement due to the installation of dams and culverts at roadways (Meyer et al. 2005, Bouska and Paukert 2010, Wenger et al 2010). Many studies have investigated the effects of movement barriers on local fish movement patterns and assemblages (Warren & Pardew 1998, Benton et al. 2008, Eisenhour and Floyd 2013, Evans et al. 2015). Long-standing barriers to movement, both dams and culverts, have even been shown to produce assemblage level differences upstream and downstream of the barrier. A study on a complex of streams in the Great Plains determined that extirpation events became more common for eight native species when the distance between movement barriers decreased (Perkins and Gido 2011). The installation of the Altus dam on the Red River in Oklahoma, USA, extirpated the populations of 4 species of cyprinids that were unable to move upstream of the dam (Winston et. al. 1991). At a single culvert on Lick Creek in Kentucky, a diverse upstream community of 9-13 fishes was so heavily affected that only two species of fishes remained common upstream (Eisenhour and Floyd 2013).

Road culverts are one of the most pervasive forms of movement barrier in many smaller streams. Culverts at road crossings have been shown to decrease fish passage for multiple species due

to hydrological alterations in the natural stream flow (Gibson et al. 2005, Benton et al. 2008, Kemp and O'Hanley 2010, Bouska and Paukert 2010). Decreased fish passage through culverts disrupts migrations, prevents colonization of new habitats, and reduces gene flow between stream fish populations (Warren and Pardew 1998, Benton et. al. 2008, Kemp and O'Hanley 2010, Eisenhour and Floyd 2013). Fish with restricted movement patterns are increasingly susceptible to population decline when barriers are constructed between suitable habitats (Niebuhr et al. 2015).

Differences in culvert design can influence passage rates for fishes. Multiple studies have reported that metal tube culverts negatively affect fish passage (Warren and Pardew 1998, Benton et al. 2008). Additionally, box culverts, which are normally constructed in a manner that replaces the original stream bottom with a smooth concrete surface, have been shown to have variable effects on fish movement. A study in the Etowah River basin, Georgia, investigated the movements of 22 species across box and tube culverts and found a significant reduction in movement compared to upstream movement in unimpeded stream reaches (Benton et al. 2008). However, an early study investigating movement through similar box culvert structures reported an increase in movement compared to unimpeded stream reaches (Warren and Pardew 1998).

Many agencies have developed criteria for measuring the extent to which a structure acts as a movement barrier for fishes, with the goal of prioritizing the removal of structures in areas containing critical habitat for threatened and endangered species (Kemp and O'Hanley 2010, Bourne et al. 2011, Gottlieb et al. 2017). When a high priority barrier is located it can be removed or replaced with a clear span bridge. The replacement of a box or tube culvert with a clear span bridge has been reported as an effective method for increasing fish passage at roadways. In a network of Michigan streams, the removal of three culverts reestablished stream connectivity and fish populations downstream and upstream of the removal sites had an increase in similarity within just three years (Evans et al 2015).

Monitoring Movement

New advances in fish monitoring technologies have provided increasing evidence that stream fishes are more mobile than previously thought (Young 1996, David and Closs 2011, Bunnell et al. 1998, Gocłowski et al. 2013). Currently, the two primary techniques used to monitor fishes are radio transmitters and passive integrated transponder (PIT) tags. Both of these techniques allow for the identification of individual fishes, as well as consideration of individual correlates to movement (Albanese et al. 2004). PIT tags are miniaturized transmitters which when excited by an electromagnetic field communicate a unique serial number (Zydlewski et al. 2006). Radio telemetry also allows for the monitoring of individual fishes via surgically implanted radio transmitter with a unique frequency. Once implanted with radio transmitter individuals can be nearly continuously tracked over large areas using a receiver (Crook 2004, Young 2011).

Although radio telemetry and PIT tags have provided crucial new evidence on the movement patterns of stream fishes, each method has its limitation. Radio transmitters have a high cost per unit and typically result in relatively few individuals of a population being tracked. Additionally, radio transmitters run on batteries, which can limit the temporal scope of studies. With only a small portion of the population being monitored, there is still some uncertainty in the movement patterns of the population. PIT tags have allowed studies to track individual fish at a low relative cost per individual when compared to radio telemetry. Due of the difference in cost, studies using PIT tags typically tag hundreds if not thousands of individuals. Unfortunately, PIT tags alone do not intrinsically allow for increased rates of detection for free ranging fishes. For a PIT tagged fish to be detected it must be in close proximity to an antenna (typically less than a meter) (Zydlewski et al. 2006).

Many studies have used PIT tags along with extensive electrofishing, trapping, or handheld antennas to produce substantial fish movement data sets (Davis 2017, Albanese et al. 2004, Smithson

and Johnson 1999). However, these studies are still limited by the extensive labor required to repeatedly sample study areas, and the inability to monitor movements that may occur between sampling periods. One way to accomplish sustainable long-term continual monitoring on a large number of free ranging fishes is with an array of stationary in stream antennas capable of detecting PIT tags (Zydlewski et al. 2006). A stationary instream antenna offers both the low per individual cost to tag, as well as the ability to continuously monitor movement in an area of stream. Utilizing an array of multiply antennas provides evidence on which fishes maintain fidelity to a specific site and which are more prone to making longer distance movements. Additionally, antennas can increase the confidence in analyses of fish movement by providing higher percentages of redetected fish compared to physical recapture methods (Baker et al. 2017).

Purpose for Study

Over the last 20 years, advancements in the methods for monitoring fish movement combined with new statistical techniques has led to an increase in the awareness of the ecological importance of movement for stream fish populations (Albanese et al. 2004, Zydlewski et al. 2006, Davis 2017). The movements of the mobile component are now considered to play a vital role in maintaining gene flow between populations of fish (Heggenes et al. 2006). The size of the mobile portion of a population is also a proxy for the number of individuals available to recolonize areas of stream affected by a disturbance (Albanese et. al. 2009). Whether or not a population has an active mobile component may indicate if a species is at risk of extirpation from low genetic diversity, or at risk for extirpation from a disturbance (Ensign et al. 1997, Wofford et al. 2005, Goclowski et al. 2013)

Anthropogenic disturbances associated with the rapid rate of urbanization are contributing to

an increased rate of extirpation for many species around the world. Unfortunately, the linear nature of the systems occupied by stream fishes can make populations susceptible to genetic isolation or extirpation if long uninhabitable reaches or barriers to movements (i.e. dams, and culverts) exist within a stream system (Winston et. al. 1991, Wofford et al. 2005, Perkin et al. 2015). Within the Southeastern United States many watersheds have been have become urbanized leading to an increase in road crossings at streams (Walters et al. 2003). Road crossing can become barriers to movement by physically impeding fish passage, or by altering the hydrology of the stream (Warren and Pardew 1998, Benton et al 2008).

The Etowah River basin in north central Georgia has been heavily affected by urbanization. A 2003 study on 30 different sub-basin of the Etowah River reported that increased urbanization was a primary predictor for the loss of endemic species (Walters et. al. 2003). The basin is of high concern for conservationists as it contains the only populations of the federally endangered Etowah Darter (*Etheostoma etowahae*), and the federally threatened Cherokee Darter (*Etheostoma scotti*) (Storey 2000, Jelks et. al. 2008). Unfortunately, within the Etowah basin it is estimated that 34% of culverts are impassable for small-bodied fishes (Bowen et al. 2008). Of the 256 culverts investigated within the basin, the culvert on Raccoon Creek at Raccoon Creek Road was prioritized as number 1 for removal, and it was estimated that replacement of the single culvert would restore access to 5,784 meters of stream for the Etowah Darter and 43,700 meters for the Cherokee Darter (Gottlieb et al. 2017).

The ability for stream fishes to survive in an increasingly fragmented landscape has been a concern for researches for over four decades. The differences in the proportion of movers and stayers across different species may be one of the key factors determining which fishes are most impacted by barriers to movement. Unfortunately, the differences in home range sizes and variation in the

proportions of mobile to stationary fishes across taxonomic groups makes it difficult to determine how stream fragmentation will affect a community of fishes.

In this study I used PIT tags and an array of stationary instream antennas to monitor the movements of fishes over extended periods in Raccoon Creek, Georgia. The goal of this study was to investigate the differences in the non-migratory movement patterns of fishes with different body forms, and to determine how the variations in body form contribute to changes in passage rates through a culvert. I monitored the movement of 6 species from three different families, allowing for movement comparisons on a diverse assemblage of body forms and habitat preferences. By monitoring multiple fish families in the same system at the same time I was able to control for a variety of physical correlates to movement (stream size, temperature, day length, habitat complexity, water velocity, and occurrence of flow events), which typically confound cross study comparisons. To differentiate between spawning and non-migratory long distance dispersals movements, the study was conducted after the spawning seasons for the target species. By conducting the study in a reach of stream impacted by a culvert and a reach with no natural movement barriers, I allowed for direct comparisons of how barriers disrupt the typical movement patterns of stream fishes. The design of this study has allowed me to estimate the occurrence and rate of non-migratory dispersal for stream fishes in both unimpeded and impeded reaches of stream. Given the diversity of fishes, the information obtained is broadly applicable to other diverse systems in the Southeastern United States.

Hypothesis I: The proportion of a fish population that makes long distance dispersal movements will differ among species.

Hypothesis II: The reach of stream bisected by the culvert on Raccoon Creek at Raccoon Creek Road will reduce the proportion of mobile fishes compared to a reach of unimpeded stream.

Chapter 2 – Study Design

Study Site

This study took place in Raccoon Creek, an Etowah River tributary in Paulding and Bartow Counties, Georgia, from April 2018 to November 2018. The Raccoon Creek watershed covers 143 km² and is one of the least impacted streams in the area. The watershed is dominated by rural forest (74.6% coverage) and agricultural landscapes (14.4%) (Stroud Watershed Research Center 2017). Raccoon Creek was considered to have high global significance in the 2015 Georgia State wildlife action plan primarily due to the aquatic biodiversity found in the watershed (Figure 2.2). Raccoon Creek contains 47 (over half) of the native Etowah River system fish species, including the federally endangered Etowah darter (*Etheostoma etowahae*) and the federally threatened Cherokee darter (*Etheostoma scotti*) (Gottlieb et al. 2017).

The study area encompasses a 580-meter reach of stream directly upstream and downstream of the Raccoon Creek Road culvert (site coordinates - 33.9973, -84.8952). The culvert is constructed of 4 concrete box enclosures and on the downstream edge has a perched lip. (Figure 2.1). During summer base flow the majority of flow passes through small cracks in the bedrock foundation under the concrete floor of the culvert. During high summer and winter flow levels the water passes as sheet flow over the concrete apron of the downstream lip (Figure 2.1). It has been estimated that for small fishes the culvert has a 93.7% chance of impeding movement (Gottlieb et al. 2017). Above the culvert, the reach is characterized by a series of 7 riffle-pool habitat sequences. The culvert bisects the stream at 140m from the downstream border of the study reach (Figure 2.3). There are no natural barriers (waterfalls/steep changes in channel slope) to fish passage in the study reach.

Methods

The methods described in the following paragraphs represent the generalized study design that was used to address both of the hypotheses tested. Methods specific to the predictions made in later chapters will be addressed in those chapters.

Capture methods: Fish sampling began in April 2018; we used two steel double throated fyke nets (Duluth Nets, Minnesota) placed in the stream channel 140 m above, 300 m above, and 140 m below the culvert on Raccoon Creek. The front and rear collection bins of the fyke nets are constructed from rectangular metal frames. The center portions of the fykes have five metal hoops to support two interior throats. The two throats help prevent fish from exiting the collection bin after being captured. The fyke nets have mesh wings that extend to the banks at an oblique downstream angle that direct fish into the throat of the fyke net. The wings have floats on the top and lead lines on the bottom that function to maintain them in a vertical position in the water column (Figure 2.4). Multiple 40 pound sand bags were added to the base of each wing to secure the bottom of the wing to the stream bottom. Each fyke net set was positioned to capture fishes swimming in the upstream direction. The nets were left in place for up to 4 days or until capture efficiency declined. Each net was checked daily, and all fish were removed and identified to species. The total length of each fish was measured, and appropriately sized individuals of study species were marked with PIT tags.

Occasionally, debris from flow events, throat collapses, or animals tearing through the net would severely reduce the capture efficiency of the nets. To supplement low capture rates, electrofishing and seining were also used as capture methods. A 6 ft. x 4 ft. minnow seine was used in upstream and downstream habitats adjacent to the fyke nets locations. Seining was performed sporadically, however, given the level of experience required for the technique, it ultimately did not prove to be an effective capture method. On two occasions, backpack electrofishing was used to sample in the pool habitats

adjacent to each fyke net location. The capture method for all fishes was documented to investigate any variation in movement of individuals captured by different methods. Sampling was only used as a method for marking new individuals. If a tagged fish was recaptured during sampling it was released at the location it was captured. The location a fish was recaptured during sampling was not considered for any of the movement analyses.

Tagging procedure: All captured target species were measured for total length and recorded to the nearest millimeter. We used 12 mm half-duplex passive integrated transponder (PIT) tags (Biomark, Idaho) to tag fishes. Previous research has shown increased mortality for fishes less than 60mm total length (Davis 2017) therefore only fish greater than 60 mm were tagged. All target species greater than 60 mm in length were anesthetized with MS-222 and abdominally injected with a PIT tag using a handheld MK25 Implant Gun (Biomark, Idaho) (Figure 2.6). Once a fish was implanted with a tag it was scanned using an HPR Plus portable PIT tag reader (Biomark, Idaho) and the unique serial number was documented. Tagged fishes were placed in buckets of fresh stream water until they fully recovered. PIT tags were removed from any individual that did not survive the procedure. All fishes captured by fyke net were released upstream of the fyke net block wings to avoid subsequent recapture of the same individuals during a fyke net deployment. Fishes captured by seining or electrofishing were returned to the nearest point of original capture.

Target Species: A pilot study performed in the fall of 2017 identified six species that were abundant within the reach and that vary in body form and habitat preference: *Campostoma oliglepis*, *Lepomis auritus*, *L. megalotis*, *Micropterus coosae*, *Hypentelium etowanum*, and *Moxostoma duquesni*. I consider these six species as the target species for this study. Body morphologies were obtained from measurements of preserved laboratory specimens, while habitat preferences were identified using Metee et al (1996). *Lepomis auritus* is a laterally compressed pool dwelling fish with an average body depth

ratio of 0.31. *Lepomis megalotis* is also a laterally compressed pool dwelling species with an average body depth ratio of 0.31. *Micropterus coosae* is a pool dwelling species with an average body depth ratio of 0.23. *Campostoma oliglepis* is a riffle and shallow pool dwelling fishes with an average body depth ratio of 0.17. *Moxostoma duquesni* is a pool dwelling fish with an average depth ratio of 0.20. *Hypentelium etowanum* prefers riffle and run habitats and has a body depth ratio of 0.15.

Redetection: Tagged individuals were redetected using HDX RFID Antenna systems (Oregon RFID, Washington). The HDX RFID antennas are constructed from 10 Gauge American Wire (AWG) THHN wires. Calibration of antenna structure was conducted on site in order to determine the configurations that would maximize the detectable range of the antennas. Due to substantial noise interference encountered from nearby power lines, the antennas contain two outer (2.5m x 1m) “noise canceling” loops, and one large (4m x 1m) inner loop. Due to changes in distance from overhead power lines, some variation (less than 1m) in the size of noise canceling loops was necessary to standardize the detection range. One inch PVC piping was used to secure the conformation of the outer noise canceling loops and to provide a structure for anchoring the antennas to the stream bottom (Figure 2.5). Sand bags were used to hold the center antenna wire to the stream bottom. The series of three loops are attached to an antenna auto tuner, which maintains the tuning for the antenna. The auto tuner is attached to an RFID data logger cable 5 to 10 m up the streambank away from the active channel using twinex cable. The antennas are powered by 100 amp- hour deep cycle batteries, allowing each antenna to run for up to 6 days on one charge cycle. Batteries were replaced with pre-charged batteries to minimize periods of antenna down time during the study. The use of similar antenna systems have reported detection efficiencies from 55% up to 97% for PIT tagged fishes depending on PIT tag size (Baker et al. 2017, Zydlewski et al. 2006).

Four antennas systems were used to monitor movement. One antenna was installed 140 m downstream and a second antenna 140 m upstream of the culvert. This design allowed for fish movement to be monitored over a 280 m distance that was bisected by the culvert at 140 m. The two additional antennas were both upstream of the culvert, one was 300 m above the culvert and the other was 450 m above the culvert. The upstream antenna locations allowed for movement to be monitored at both a 150m distance and a 300m distance of unimpeded stream (see Figure 2.3 for antenna placements within the stream reach). Some variation in antenna placement (distance from adjacent antennas) was necessary in order to standardize for stream depth at base flow conditions but the distance from adjacent antennas never varied by more than 15 meters. The antennas were located in shallow, narrow areas of stream to minimize the possibility that a fish could pass through that section of stream without being detected.

Flow levels in Raccoon Creek were monitored during the duration of the study using a Hobo water depth data logger (Onset, Massachusetts). The logger was housed in a 2" PVC tube and secured to a 5 ft. fence post. The fence post was driven into the stream bottom so that the data logger would remain submerged under base flow conditions. The logger continuously monitored temperate and absolute pressure of the stream. Changes in stream pressure were considered a proxy for the occurrence of flow events.

Chapter 3: Movement through the Culvert

Introduction

The importance of dispersal for stream fishes is suggested by reductions in fish diversity within watersheds where movement barriers have been introduced (Poulos et. al. 2014). Road culverts are one of the most pervasive forms of movement barrier in many smaller streams. Culverts at road crossings have been shown to decrease fish passage for multiple species due to hydrological alterations in natural stream flow (Gibson et al. 2005, Benton et al. 2008, Bouska and Paukert 2010). At a culvert, stream area is reduced and water is funneled into a constrained area, increasing both the velocity and turbulence of water moving through the culvert (Olson et. al. 2017). If the water velocity exceeds that of the swimming ability of a fish, the culvert becomes impassable (Ilanos 2011). Culverts can also impede fish movement during low flow events. When a low flow event occurs in a natural stream channel, water funnels into the lowest portions within the stream, and some passable areas are maintained. In contrast, within a culvert the channel morphology is typically fixed and stream depth is homogeneous. During times of low flow, streamflow through the culvert may remain at a depth that is impassable for some fishes. Additionally, the formation of a perched lip at the downstream end of a culvert can cause large abrupt drops in the stream channel reducing the upstream movement of fishes (Prowell et al. 2012).

Monitoring movement at different flow levels has been recognized as being especially important for evaluating fish movement through a culvert (Norman et al. 2009). The different body morphologies of stream fishes allow for mobility advantages in different water velocities (Nikolski 1933, Gatz 1979, Ross 1986, Gaston and Lauer 2012). To investigate to what extent a culvert impacts the movement patterns for fishes with different body morphologies, passage rates need to be monitored over a period when high and low flow events occur. Additionally, movement through the culvert must be compared to

movement in a stream reach with no barrier. This will determine if any observed differences in movement result from the hydrological changes of the culvert or just natural variation in movement patterns.

In this study I investigated the differences in the passage rates of fishes with different body depth ratios through a reach of stream bisected by a culvert compared to a stream reach with no natural movement barriers. I monitored the movement of six species from three different families, allowing for movement comparisons on a range of body depth ratios. By monitoring multiple fish families in the same system at the same time I was able to control for a variety of physical correlates to movement (stream size, temperature, day length, habitat complexity, water velocity, and occurrence of flow events) which typically confound studies across multiple systems. To differentiate between spawning and non-migratory long distance dispersal movements, the study was conducted after the spawning seasons for the target species. The study took place over a 20-week period during which multiple high and low flow events occurred. By conducting the study in a reach of stream impacted by a culvert I allow for direct comparisons on how a barrier disrupts the typical movement patterns of stream fishes.

Prediction I: There will be less movements detected across the stream reach bisected by the culvert (total distance 280m) when compared to the number of movements detected across the unimpeded stream reach (total distance 300m).

Prediction II: Fishes with lower body depth ratio will have a higher rate of passage through the culvert than fishes with high body depth ratios.

Methods

Data Collection: See Chapter 3 for information regarding fish capture, tagging procedures, methods used for redetection, and the monitoring of flow level.

The effect of the culvert on the proportion of mobile fishes was determined by comparing differences in the proportion of fishes detected moving in the reach of stream bisected by the culvert and the unimpeded stream reach. The proportion of fishes tagged or detected below the culvert (location D1), that were later detected above the culvert were considered upstream movers. For a fish to move from D1 to U1 it would have to move approximately 140 meters, pass through the culvert, and move an additional 140 meters (i.e. 280+ m). The proportion of fishes tagged or detected above the culvert (location U1), that were later detected at D1 below the culvert were considered downstream movers. Fishes tagged or detected at the first antenna above the culvert (U1), that were later redetected at the furthest upstream antenna (U3) were considered upstream movers in the unimpeded reach. For a fish to go from U1 to U3 it would have to move 300 meters through unimpeded stream. Fishes tagged or detected at the furthest upstream antenna (U3) that were later redetected at the first upstream antenna (U1) were considered downstream movers in the unimpeded reach.

The proportion of movers in the reach bisected by the culvert was then compared to the proportion of movers in the unimpeded reach. The proportion of movers for each species was determined by dividing the number of fish redetected at the furthest upstream antenna by the total number of fishes originally tagged or previously redetected at the first upstream antenna. The proportion of downstream movers for each species in the unimpeded reach was determined by dividing the number fish redetected at the first upstream antenna by the total number of fishes originally tagged or previously redetected at the furthest upstream antenna.

Modeling: A multistate model for live recaptures was used to estimate apparent survival,

detection probabilities, and weekly (7 day) estimates for movement across the two stream reaches. The models were implemented in the program MARK. The model structure used is an extension of the Cormack-Jolly-Seber model (CJS) for estimating transitions among multiple states (Cormack 1964, Jolly 1965). Each antenna locations (D1, U1, and U3) represents one of three possible states for a marked fish. Due to the length of the study and the number of tagged fishes, I chose to run a simple model with two movement parameters, one survival parameter, and three fully time-dependent parameters for detection (one for each antenna). One of the movement parameters combined transition estimates for upstream and downstream movement in the reach bisected by the culvert, and the other parameter estimated upstream and downstream movement in the unimpeded reach. Detection represented an individual fully time dependent parameter within the model, allowing for the model to consider variation in detection probability over time.

Data consolidation: Data retrieved from the individual antennas was transferred from the original text file to an excel sheet. The raw data contained the date, time, and tag ID of each fish detected. Due to the high number of detections, multiple detections of the same individual at the same antenna were binned by hour and considered to be one detection event. The detection data was then reformatted into a capture history file. A capture history file is a string of consecutive entries in a pre-designated time period for an individual. Each entry into the capture history file represents the state of the individual during the designated time. The capture history consisted of 4 possible states: “0” representing non-detection, “1” representing detection below the culvert, “2” representing detection events at the first antenna above the culvert, and 3 representing detection at the furthest upstream antenna. The location at which a fish was originally marked was the first detection in the capture history format (1, 2, or 3). Due to limitations in the computing power of the MARK software I was unable to input a capture history with an entry for every hour. To reduce the number of entries into the capture history file, detections

were binned by week (7 days). However, if an individual was detected at two antennas within the same week, the previous entry in the capture history files was altered to reflect the transition.

Results

During 2018 I tagged a total of 429 fishes at 4 separate locations within the 580m reach of Raccoon Creek (Table 2). Starting June 1, 2018 through November 14, 2018 the antennas made over 400,000 combined detections, resulting in detection of 61.1% of tagged individuals (Figure 3.1). The proportion of redetected fish was determined by dividing the number of redetected fish by the number of tagged fish for each species.

In this portion of the study I investigated the movements through the 300m unimpeded reach and the 280m reach bisected by the culvert over a 19-week period from July 1, 2018 through November 14, 2018. The movement portion of the study was delayed until July 1, 2018 to ensure the migratory season was over for the target species. In order to detect a 280m movement through the reach bisected by the culvert, or a 300m movement in the unimpeded reach, a fish had to be marked or detected at either D1, U1, or U3. Of the total 429 fishes tagged, 342 fishes were tagged at locations D1, U1, or U3. The 87 fish tagged at location U2 were not considered for this study unless they were at some point detected at either D1, U1, or U3 (Table 3). Not all the fish were in the reach when the movement portion of the study began, as 237 of the 342 fishes were tagged in the month of July. The total operation runtime for each antenna was 132 days for D1, 75 days for U1, and 87 days for U3.

There were 3 fishes originally marked downstream that were detected upstream of the culvert, resulting in an overall passage percentage of 2.4%. One *C. oligolepis*, one *L. auritus*, and one *H. etowanum* were detected moving through the reach bisected by the culvert (Figure 3.4). The proportion

of movers for each species was determined by dividing the number fish redetected upstream by the total number of fishes originally tagged or previously redetected below the culvert. There were 16 fishes originally marked at the first upstream location (U1) that were redetected at the furthest upstream antenna (U3), resulting in an overall passage percentage of 7.21% for the unimpeded reach. The proportion of tagged fishes that moved upstream through the unimpeded reach was 0.11 for *C. oligolepis*, 0.02 for *L. auritus*, 0.15 for *H. etowanum*, 0.15 for *L. megalotis*, 0.00 for *Micropterus coosae*, and 0.013 for *Moxostoma duquesni* (Figure 3.4). The proportion of downstream movers for each species in the impeded reach was determined by dividing the numbers of fish redetected at the downstream antenna by the total number of fishes originally tagged or previously redetected at the first upstream antenna. There were very few downstream movements in both reaches. In total, one *M. duquesni*, one *L. auritus*, and two *C. oligolepis* moved downstream in the impeded reach. In the unimpeded reach, one *H. etowanum* and one *M. duquesni* were detected moving downstream (Figure 3.6).

In addition to the descriptive results, I implemented a multi-state model to determine weekly transition estimates for upstream and downstream movement through the unimpeded reach compared to the reach bisected by the culvert. The estimated probability of weekly movement through the unimpeded reach was 0.112 (95% CI = 0.076 - 0.160) for upstream movement and 0.065 (95% CI = 0.043 - 0.097) for downstream movement (Figure 3.2). The estimated probability of weekly movement through the reach bisected by the culvert was 0.008 (95% CI = 0.001 - 0.035) for upstream movement and 0.009 (95% CI = 0.004 - 0.022) for downstream movement (Figure 3.2). Sample size in the downstream reach was too small to consider movement comparisons between body forms.

Discussion

The goal of this portion of the study was to compare the movements of fishes through a reach of stream bisected by a culvert and an unimpeded reach. I predicted that there would be (1) less movements detected across the impeded stream reach bisected by the culvert (total distance 280m) when compared to the number of movements detected across the unimpeded stream reach (total distance 300m), and that (2) fishes with lower body depth ratio would have a higher rate of passage through the culvert compared to fishes with high body depth ratios. The results from the study indicate that the culvert at Raccoon Creek at Raccoon Creek Road is a partial barrier to fish movement.

Model Results: The results indicate that weekly movement rates in the impeded reach are significantly lower than movement rates in the unimpeded reach (Figure 3.2), and show that the culvert does impeded the natural movement patterns of the local fish community. The multi-state model allowed for weekly estimates of upstream and downstream movement across the two reaches, and incorporated both detection probability and survival estimates for all tagged fishes. The results from the model allow for a better understanding of passage between the two reach compared to descriptive data or analyses that are unable to account for survival, emigration, and the probability of redetecting an individual.

Low battery or changes in antenna conformation periodically resulted in antenna downtime. Due to longer durations of downtime for antenna U1 there were instances where fishes moved from D1 to U2 but were never detected at U1. If a fish moved through the reach bisected by the culvert and was never detected at U1 but was detected at U2 it was entered into the capture history file as a detection at U1. This was done so that comparison across the two reaches could still account for the movement through the impeded reach. However, this was not an option for fishes that may have moved from U1 to beyond U3 without being detected, because the movement would remain undetected. The result of the data alteration underestimates transition probabilities through the unimpeded reach. Even though the model

has biases toward decreased movement through the unimpeded reach, the results still show significantly more movement in the unimpeded reach. Additionally, the antenna below the culvert had a longer runtime compared to the other two antennas. The longer runtime results in a bias of increased detection for downstream movement. This bias may be the reason for a slightly higher estimate for downstream movement through the impeded reach compared to upstream movement. Although there were fewer downstream movements detected in the unimpeded reach, the model still estimated a high transition probability compared to the impeded reach. This is an effect of sample size, as there were relatively few fishes tagged at U3 compared to U1.

Eisenhour and Floyd (2013) investigated the effect of a culvert with perched lip and reported a loss in species richness in the upstream reach as a result of decreased fish movement and hydrological alterations to the stream. Norman et al. (2009) reported that no benthic fishes were detected moving through a culvert with a perched lip, however approximately half of water column fishes were able to move through the culvert with a perched lip compared to an unimpeded reach. My results suggest that the Raccoon Creek culvert impeded water column fishes much more than the culvert in the Norman et al. (2009) study.

The results from my study improve on previous studies in evaluating the passage rate of warm water fishes through a culvert by increasing the duration of monitoring and the percentage of recaptured fishes (Warren and Pardew 1998, Benton et al. 2008, Norman et al. 2009). Benton et al. (2008) redetected 33.1% of marked fishes, Warren and Pardew (1998) had an average redetected percentage of 19.5% over a two-year study, and Norman et al. (2009) had an average redetection of 24%. All of these detection percentages are considerably lower than the 61.1% redetection in this study. However, these studies do offer their own advantages. Benton et al. (2008) considered 22 different species and marked considerably more individuals, and Warren and Pardew (1998) evaluated movement through multiple

different culvert types. All mentioned studies have reported that culverts act as partial barriers to fish movement. This study has increased the confidence that culverts alter the movement patterns of a population by increasing the percentage of redetections, the frequency of redetections, and the use of a multistate model capable of incorporating survival estimates and detection probabilities.

Culverts have the ability to impede fish passage at both low and high flow levels (Olson et al. 2017). Therefore monitoring needs to occur over long durations with multiple flow events in order to better understand the extent of the impacts a culvert has on the movement patterns of a community of fishes (Norman et al. 2009). During this 19-week study five increased flow events occurred, as well as extended periods of base flow conditions. Since this study included near-continuous monitoring of movement during a variety of flow conditions it allows for increased confidence in the inference that this culvert acts as a long term impediment to fish movement.

Descriptive Data: Due to the low number of detected movement in the unimpeded reach (16) and the impeded reach (3) I was unable to perform any statistical analysis addressing differential movement rates for each species. However, the results obtained in this study show reduced movement through the reach of stream bisected by the culvert compared to the unimpeded reach for all species, *L. auritus* being the one exception. It is however possible that the higher rate of movement for *L. auritus* in the reach bisected by the culvert is a function of small sample sizes in the reach downstream of the culvert. Only 1 of the 11 *L. auritus* tagged below the culvert was detected in the upstream reach, compared to 2 of the 153 *L. auritus* that moved through the unimpeded reach. This assumption is consistent with another movement study which found that the mean movement distance for the mobile portion of a population for *L. auritus* was under 200m (Davis 2017). Additionally, in a study that marked 624 *L. auritus* in a large lowland river, only a single movement over 200 m was detected (Freeman 1995). These results suggest that in general *L. auritus* do not frequently make movements over 280 m.

Overall, there was a low proportion of the total number of tagged individuals that were detected making a movement of 300 m in the unimpeded stream reach. Proportions ranged from 0.00 for *M. coosae* to 0.15 for *L. megalotis* and *H. etowanum*. Given the variation in movement distances for all species included in the study, 300 m may have been too long of a distance to fully investigate the impacts of the culvert. Although studies have detected similar passage rates for fishes through box culverts (Warren and Pardew 1998, Benton et al. 2008) the nearly continuously monitoring of movement may increase the ability to assess passage rates, especially if an instream antenna was installed at the culvert. Future studies should consider using more instream antennas and prioritize the placement of an antenna at the culvert structure.

Based on the actual number of detected movements, the culvert most heavily impacted the movement rates of *L. megalotis* and *Moxostoma duquesni*. The culvert had the least impact on the movements for *H. etowanum* and *C. oligolepis*, both with the lowest body depth ratio in their respective families for the families considered in this study. These results suggest that the body morphology may affect passage rate through a culvert but additional data is needed to support the prediction. The higher rate of movement through the culvert for *H. etowanum* and *C. oligolepis* conflicts with the results from a similar study that reported higher rates of movement for water column fishes through culverts with perched lips (Norman et al. 2009). Although I did not directly consider variation in benthic versus water column fishes, both *H. etowanum* and *C. oligolepis* prefer riffle habitat and have the low body depth ratios, characteristics typical of benthic dwelling species.

Conclusions

The results from this study indicate that an array of instream stationary antennas can be used to examine the differential movements of PIT tagged fishes and in turn inform conservation and management decisions. By implementing a multi-state model I was able to calculate weekly transition

probabilities across a reach of stream obstructed by a culvert compared to an unimpeded reach. The results from this study shows the potential long term impact of a culvert on a community of fishes by demonstrating that even at a very short time span (7 days) the natural movement patterns of stream fish are significantly altered. This study supports culvert removal as a strategy for maintaining fish populations, especially in systems where species may be imperiled if movement between suitable habitats is limited.

Chapter 4: Movement in an Unimpeded Stream Reach

Introduction

Riverine fishes make both local and long-distance movements. In general, populations can be divided into stationary (stayers) and mobile (movers) components, with stayers comprising the largest portion of the population (Skalski and Gilliam 2000, Rodriguez 2002, Crook 2004, Radinger and Wolter 2014). The movements of the stayers are described as home range movements, and the movements of the mobile portion are considered long distance dispersal movements. The relative proportion of a fish population displaying these two types of movements can vary by species, body type, total length, and stream size (Skalski and Gilliam 2000, Radinger and Wolter 2014, Albanese et al 2004) Long distance dispersal movements are different than seasonal spawning movement, as they may occur at any time and typically result in a shift in home range location (Crook 2004). A better understanding of differences in the dispersal patterns of riverine fishes could provide support for conservation efforts aimed at maintaining stream biodiversity especially within systems prone to disturbance (Albanese et. al. 2009).

The home range sizes of stream fishes can range 10m to 1000m depending on the species, but for most species home range sizes are typically less than 100m (Skalski and Gilliam 2000, Rodriguez 2002, Radinger and Wolter 2014, Davis 2017). The distance traveled by the mobile portion of the population has been shown to vary greatly by species (Rodriguez 2002, Hill and Grossman 1987, Mundahl and Ingersoll 1989, Lotrich 1975, Freeman 1995). The length of distances moved by the mobile portion of population will exceed that of the respective home range size, and typically result in a fish establishing a new home range location (Crook 2004).

Studies have suggested that differences in movement patterns for stream fishes result from variations in body form (Webb 1984, Sambilay 1990, Boily and Magnan 2002, Gaston et al. 2012),

body size (Albanese et al. 2004, Bunnell et al 2011), influences from physical and ecological characteristics of a stream system (David and Closs 2002, Albanese et al. 2004, Wofford et al. 2005, Jeffres et al. 2006), and habitat preference (Hill & Grossman 1984, Goclowski et. al. 2013). In general, fishes with common habitat preferences share similar morphological features and swimming strategies. Fish with streamlined body forms and low body depth ratios are found more often in higher velocity habitats associated with riffles (Webb 1984, Gaston and Lauer 2012). Alternatively, fish with high body depth ratios are more suited for the slower water velocities found in pool habitats (Gaston and Lauer 2012). A high body depth ratio results in considerably more drag in fast flowing water compared to a low body depth ratio, therefore a deep-bodied fish would require an increase in energy to traverse riffles compared to a streamlined fish (Webb 1984, Matthews 1998). The additional effort associated with traversing fast flowing waters may limit the rate of passage through riffle habitat for deep bodied fishes.

Species that have similar body depth may be limited in movement through non-favorable habitat by different factors. The low body depth ratio and generally small body size of riffle dwelling fishes allow them to navigate in fast flowing waters, however these traits may make them more susceptible to predation when passing through pool habitats (Metee et al 1996, Shaefer 2001). Although, pool dwelling species may be limited by the energy input required to traverse a riffle, variations in flow level may provide areas of manageable velocity. Additionally, the typically larger body size of pool dwelling fishes requires an increase energetic requirement and therefore the potential need to seek out new food sources (Minns 1995, Jeffery et al. 2011, Gaston et al 2012).

Prediction 1: There will be differences in the proportion of each species that stay at their original

marking location compared with those that move and are detected at an adjacent antenna.

Prediction II: There will be a higher proportion of individuals with low body depth ratios detected away from their original marking location.

Prediction III: Body size will be a predictor of increased movement.

Methods

Data Collection: See Chapter 3 for information regarding fish capture, tagging procedures, and methods used for redetection.

Statistical Analysis: I investigated the differences in the proportion of mobile fishes detected at adjacent antennas compared to fishes only detected at their original marking location. For a fish to go from U1 to U2, or from U2 to U3, they would have to move approximately 150 meters. This distance in antenna placement was chosen to limit the amount of home range overlap between fishes at a given antenna. Fishes below the culvert were not considered for this study. I assessed the differences in the proportions of movers descriptively by comparing the proportion of tagged fishes detected at antennas adjacent to their original marking area. Additionally, I used a chi-squared analysis to make comparisons on the number of movers and stayers with different body depth ratios and body size. Body size was determined by total length, with small individuals grouped into a “Small” or “Large” category based on natural breaks in the length measurements. The natural breaks in the length distribution result from the annual reproductive cycle of stream fishes and represent discrete year classes.

Modeling: A multistate model for live recaptures was used to estimate apparent survival,

detection probabilities, and weekly (7 day) estimates for movement for upstream and downstream movement. The models were implemented in the program MARK and are an extension of the Cormack-Jolly-Seber model (CJS) models for estimating transitions across multiple states (Cormack 1964, Jolly 1965). Models were run for each species individually using the same parameters for all models. Each of the antenna locations (U1, U2, and U3) represented one of three possible states in which a fish could exist. Due to the length of the study and the number of tagged fish I chose to run a model with two movement parameters. One movement parameter combined transition estimates for upstream movement from U1 to U2 and U2 to U3 jointly. The other movement parameter estimated downstream movement from U3 to U2 and U2 to U1 jointly. Due to limitations on model convergence, both movement parameters were estimated independent of time. Survival was also estimated independent of time and state (antenna) and represented a single parameters within the model. Detection represented three fully time dependent parameters, one parameter for each antenna. This was done to account for variability in detection efficiency of the antennas during the study. One additional model was run with a single fully time dependent parameter to estimate detections for all species jointly across all three antennas. Detection estimates for the likelihood of detection ranged from 0.11 to 0.83, and averaged 0.40 during the study (Figure 4.9).

Data consolidation: Data retrieved from the individual antennas were transferred from the original text file to an excel sheet. The raw data contained the date, time, and tag ID for each fish detected. Due to the high number of detections, multiple detection of the same individual at the same antenna were binned by hour and considered to be one detection event. The detection data was then reformatted into a capture history file. A capture history file is a string of consecutive entries during a designated time period for an individual with each entry representing the state of the individual. The capture history consisted of 4 possible states: “0” representing non-detection, a “2” representing

detection events at U1, a “3” representing detection at U2 and “4” representing detection at U3. The location a fish was originally captured (marked) was the first detection in the capture history format (a 2, 3, or 4). Due to limitation in the computing power of the MARK software I was unable to input a capture history with an entry for every hour. To reduce the number of entries into the capture history file, detections were binned by week (7 days). However, if an individual was detected at two antennas within the same week, the previous entry in the capture history files was altered to reflect the transition.

Results

During 2018 I tagged a total of 310 fishes within a 300 m stream reach of Raccoon Creek (Table 2). Within the 300 m stream reach there were no natural or artificial barriers to movement. I captured and tagged fishes at three locations above the culvert (Figure 2.3) and I used 3 instream antennas to monitor the movement of the tagged fishes. During the duration of the study 48% of the detected fishes were redetected more than 10 times, and on average a redetected fish was redetected 21 times during the study. Occasionally, low battery or changes in antenna conformation would result in downtime of antennas. The longest run time was at the furthest upstream antenna (+12 days), however upstream and downstream movement was considered jointly in the model so there is no overall bias expected in the transition estimates based on directionality of movement. The total operation runtime for each antenna was 75 days for U1, 80 days for U2, and 87 days for U3.

There were 80 individuals of the 310 tagged individuals that moved at least 150m and were detected by an adjacent antenna, resulting in a combined movement rate for all species of 25.8%. The proportion of all tagged fishes that moved at least 150 meters upstream or downstream by species was 0.36 for *C. oliglepis*, 0.18 for *L. auritus*, 0.44 for *H. etowanum*, 0.26 for *L. megalotis*, 0.40 for *M. coosae*, and 0.30 for *M. duquesni* (Figure 4.5). The proportion of movers for each species was

determined by dividing the number of fish redetected at an adjacent antenna by the total number of fishes originally tagged or previously redetected in the unimpeded reach. The proportion of redetected fishes that moved at least 150m and were detected at an adjacent antenna was 0.76 for *C. oligolepis*, 0.41 for *L. auritus*, 0.65 for *H. etowanum*, 0.62 for *L. megalotis*, 0.57 for *M. coosae*, and 1.00 for *M. duquesni* (Figure 4.4).

Chi-squared analyses were performed to investigate differences in the number of movers and the number of stayers with differing body depth ratio and body size. The analysis determined that there were significant differences in movement for *Lepomis* (*L. auritus* and *L. megalotis*) compared to Catostomidae (*H. etowanum* and *M. duquesni*) (p-value = 0.003). Chi-squared analysis also showed significant differences in movement for *Lepomis* compared to *C. oligolepis* (p-value = 0.026, Figure 4.6).

Chi-squared analyses were performed to investigate differences in the number of movers with differing body sizes for *L. auritus* and *C. oligolepis*. Fish over the length of 95mm were considered large for *L. auritus* and fish over the length of 112mm were considered large for *C. oligolepis*. There was a significant difference (P-value 0.013) in movement by total size for *L. auritus* with larger fish moving more than smaller fish. There was no significant difference (P-value 0.598) in movement by size for *C. oligolepis* (Figure 4.7).

Weekly estimates for the likelihood of movement (upstream or downstream) using a multi-state model was 0.06 (95% CI= 0.04-0.08) for *L. megalotis*, 0.07 (95% CI= 0.05-0.09) for *L. auritus*, 0.06 (95% CI= 0.03-0.13) for *M. coosae*, 0.30 (95% CI= 0.21- 0.41) for *C. oligolepis*, 0.95 (95% CI= 0.95-0.95) for *M. duquesni*, and 0.15 (95% CI= 0.11-0.20) for *H. etowanum* (Figure 4.1). In addition to movement estimates the multi-state model also determined weekly survival estimates. Survival rates were estimated to be 0.84 (95% CI=0.78-0.89) for *C. oligolepis*, 0.91 (95% CI= 0.88-0.93) for *L. megalotis*, 0.91 (95% CI= 0.89-0.92) for *L. auritus*, 0.94 (95% CI= 0.94-0.94) for *M. duquesni*, 0.94

(95% CI= 0.91-0.97) for *H. etowanum*, and 0.95 (95% CI= 0.83-0.99) for *M. coosae* (Figure 4.2).

Weekly detection estimate were determined using a time dependent parameter in the multi-state model and estimated for all species jointly. The weekly estimate for the likelihood of detection ranged from 0.11 to 0.83, and averaged 0.40 during the study (Figure 4.9).

Discussion

The goal of this portion of the study was to determine movement patterns of the target species in a reach of stream with no artificial barriers to movement. I predicted that:

(1) There would be differences in the proportion of each species that stay at their original marking location compared those that move and are detected at an adjacent antenna.

(2) There would be a higher proportion of individuals with low body depth ratios detected away from their original marking location.

(3) Body size will be a predictor of increased movement.

In this study I used three instream antennas to monitor the movement of tagged fishes nearly continuously over a 19-week period. As a result, I had a higher proportion of redetected fishes and a greater frequency of redetections compared to the majority of studies supporting the RMP (Gowan et al. 1994). Due to the higher proportion of redetected fishes and the increased frequency of redetection in this study I was able to create an extensive capture history file and ultimately implement a multi-state model able to produce estimates for the frequency of weekly movements for the target species that account for both survival and probability of detection.

The results indicate that weekly movement rates of at least 150m are significantly higher for *M. duquesni* compared to the other 5 fishes (Figure 4.1 and 4.2). This was an expected result from the study as the home range size of many members of the family Catostomidae have been reported as larger than 150m (Doherty et al. 2010, Radinger and Wolter 2014). The model determined that *M.*

duquesni had a 95% likelihood of moving 150m within a week. Within the study reach, a 150m movement would require movement through a minimum of two riffle-pool habitat units. Additionally, when only considering the movement of fishes that were redetected, 100% of *M. duquesni* moved at least 150m during the study. The movement of *M. duquesni* provides strong evidence against a broad application of the RMP for stream fishes (Gerking 1953).

The second highest estimate for weekly movement of at least 150m was for *C. oligolepis*. Although *C. oligolepis* has a low body depth ratio compared to fishes in the family Centrarchidae and was predicted to be more mobile, the species was considerably more mobile than expected. The model estimated that *C. oligolepis* had a likelihood of weekly movement of at least 150m to be 30%, and 76% of redetected individuals moved and were detected by an adjacent antenna during the duration of the study. Previous studies on the movement patterns of fishes in the genus *Campostoma* have not reported movement frequencies as high as I estimated. The Central Stoneroller (*C. anomalum*) was reported to have a home range of 35.2m (Mundahl and Ingersoll 1989), while *C. oligolepis* had an average home range size of 36.1m in a study in two streams in the same river basin as Raccoon Creek. (Davis 2017). The high level of mobility found in this study may indicate that past studies were unable to detect the frequency with which *C. oligolepis* move, or that *C. oligolepis* may be susceptible to system specific covariates driving increased movement.

There was no significant difference in movement for the three species in the family Centrarchidae. In general, Centrarchids are reported to have smaller home range sizes and have shorter distances traveled by the mobile component when compared to fish from the families Cyprinidae and Catostomidae (Hill & Grossman 1984, Freeman 1995, Crook 2004, Breen et al 2009, Radinger and Wolter 2014, Davis 2017). Since the likelihood of movement for the Centrarchids is lowest, they may be most susceptible to reduced gene flow between populations if movement barriers

are constructed between suitable habitats. Additionally, their restricted movement pattern may impede their ability to recolonize new areas following a disturbance compared to *C. oligolepis* and *M. duquesni*.

Movement estimates were higher for fishes with low body depth ratios. *Campostoma oligolepis*, *H. etowanum*, and *M. duquesni*, all had the highest estimates for weekly movement and the highest proportion of redetected individuals that moved during the duration of the study (Figure 4.1 and 4.2). All three species vary in their life history characteristics, including different habitat preferences and feeding habits, and all experienced the same environmental conditions during the duration of the study. Although it is unlikely that body depth ratio is the only correlate for increased movement for stream fishes given the diversity of characteristics across the three species, body depth ratio was a consistent predictor in this study. To my knowledge no study has investigated how body depth ratio correlates with changes in the proportion of stayers and movers across multiple fish families in the same system.

There was a significant increase in movement for large *L. auritus* compared to smaller fish. The increase in movement is consistent with many other studies which have reported an increase in movement for larger fishes (Minns 1995, Albanese et al. 2004, Brunnell et al 2011, Radinger et al. 2014). There was no significant increase in movement for large *C. oligolepis* compared to smaller fish. There were more small fish that moved for *C. oligolepis*, however these differences were not significant and may be due to small sample sizes.

One of the concerns raised regarding fish movement studies that supported the RMP was the high proportion of undetected fish. With a high number of fish that are never redetected there is considerable uncertainty in the movement patterns of the entire population (Gowan et al. 1994). Many studies have based fish movement analysis on only a single, or at most a few redetections of an

individual, and as a result many studies have been unable to implement a model to account for survival and the probability of redetecting an individual (Hill & Grossman 1984, Freeman 1995, Albanese et al. 2004, Davis 2017). The use of instream antennas in this study allowed for a much higher proportion of redetected fish and an increased frequency of redetection compared to other studies. The high frequency at which I was able to redetect individual fishes allowed me to analyze my data using a multi-state model. The multi-state model allowed for weekly estimates of movement and incorporated both detection probability and survival estimates for all tagged fishes. The results from the model allow for a better understanding of the frequency of movement compared to descriptive data or analyses that are unable to account for survival/emigration, and the probability of redetecting an individual.

Absolute pressure was measured as a proxy for flow level for the duration of the study. There were no statistical tests done to investigate how flow level influenced movement. Future studies utilizing a multi-state model with the capacity to investigate time dependent covariates to movement should prioritize the consideration of flow level. Due to the different movement strategies of riverine fishes, it is reasonable to anticipate variation in response to high flow events. An increase in water level can inundate the banks of pool habitat, potentially creating shallow areas for riffle fishes to pass. Although a higher flow level would increase the water depth at riffles, the movement of pool dwelling fish may still be limited due to the increase in water velocity that occurs during flow events.

Conclusions

The physical and financial costs to repeatedly sample stream reach with traditional methods such as electrofishing or seining has limited many studies to just a few resampling occasions (Warren and Pardew 1998, Albanese et al. 2004, Benton et al. 2008, Eisenhour and Floyd 2013). As a result, the

conclusions of many fish movement studies are made based on a single or few recapture events. With only a few recapture events per individual, there is uncertainty in whether or not the location in which a fish was recaptured was maintained for the duration of the study. During this study 48% of tagged fishes were redetected more than 10 times, and the average number of redetections per fish was 21. No other study to my knowledge has produced such a high frequency of redetection using traditional methods. The nearly continuous ability for an array of instream antennas to monitor movement results not only in high percentage of redetected fishes but an increase in the total rate of redetection for individual fishes. The high percentage of redetection, the frequency of redetection, and the use of a multistate model capable of incorporating survival and detection estimates allows for increase confidence in the movement patterns of an entire population.

The nearly continuous monitoring offered by the instream antennas and the implementation of a multistate model to estimate transition probabilities has allow for a better understanding of the occurrence, frequency, and potential correlates to movement for the six species considered for this study. The results from this study suggest that stream fishes may be more mobile than previous reported by the studies that support the RMP. The reason for the differences in the reported frequency of movement is likely to be a result of low proportion and frequency of recaptured fishes. The patterns of movement observed in this study suggest that conservation managers should consider movements of at least 150m as a potentially frequent weekly occurrence for both the target species and other closely related fishes.

Acknowledgements

This project was funded by the Kennesaw State University College of Science and Mathematics Department of Ecology, Evolution and Organismal Biology, The Nature Conservancy, Georgia Department of Natural Resources, and the United States Fish and Wildlife Service. Thank you to my adviser, Dr. William Ensign for providing continuous support, patience, and guidance during my time at Kennesaw State University. Thanks to my committee, Dr. Gene Ray and Dr. Troy Mutchler for your insight and assistance on the project. Lastly, thank you to the following field assistants whose hard work made this project possible: Miriam Branson, Tyler Everton, Matt Scholten, Tyler Schwartz, Jonathan Ray, Caleb O'Neal, and Chris Pruitt.

Integration of Thesis Research

This project integrated organismal biology, ecology, statistics, and a multi-state model to investigate patterns of movement for different fish species. The advantages offered by statistics and a multi-state model allowed me to investigate how species-specific variation contributes to the patterns of movement observed for a community of fishes. The integrative approach to this study resulted in weekly movement estimates for six species of fish from three fish families and showed how anthropogenic alterations to natural stream habitat impede movement patterns of stream fishes.

Figures

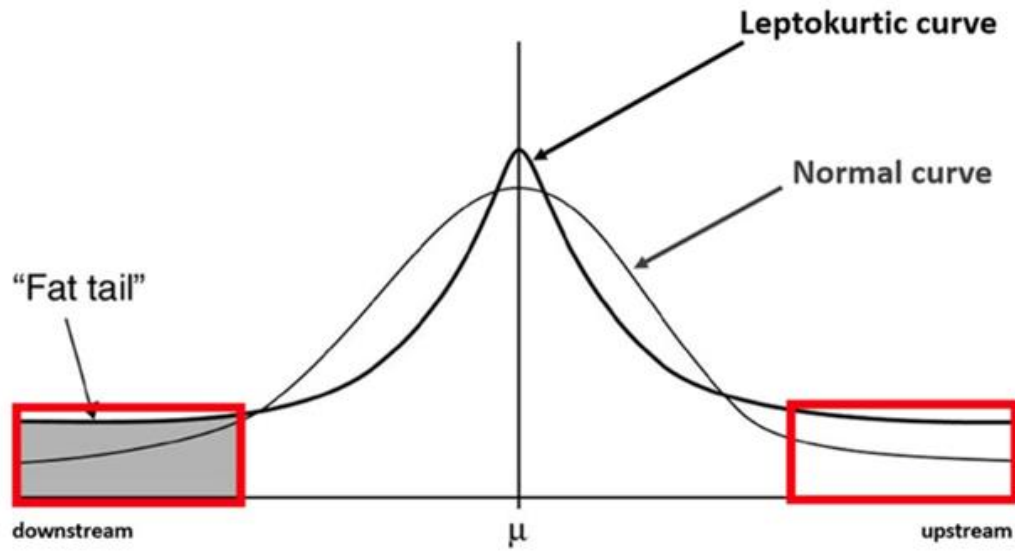


Figure 1.1: Leptokurtic distribution compared to a normal distribution.



Figure 2.1: The culvert at Raccoon Creek Road during low flow (top) compared to high flow (bottom).

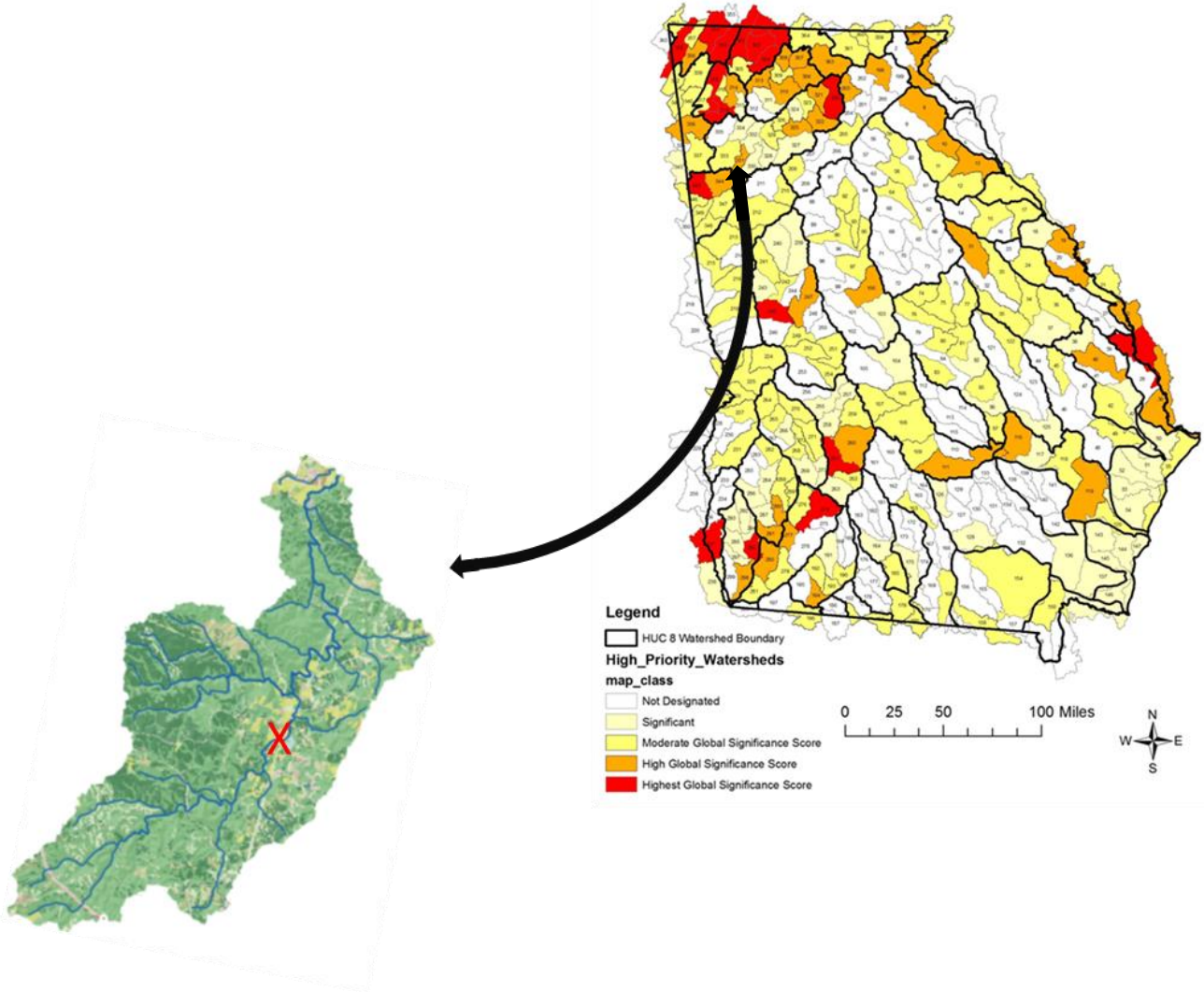


Figure 2.2: The location of the study area, and the Raccoon Creek watershed (left). Raccoon Creek watershed recognized as having high global significance on the 2015 Georgia State Wide Action Plan (left) (GA SWAP 2015).

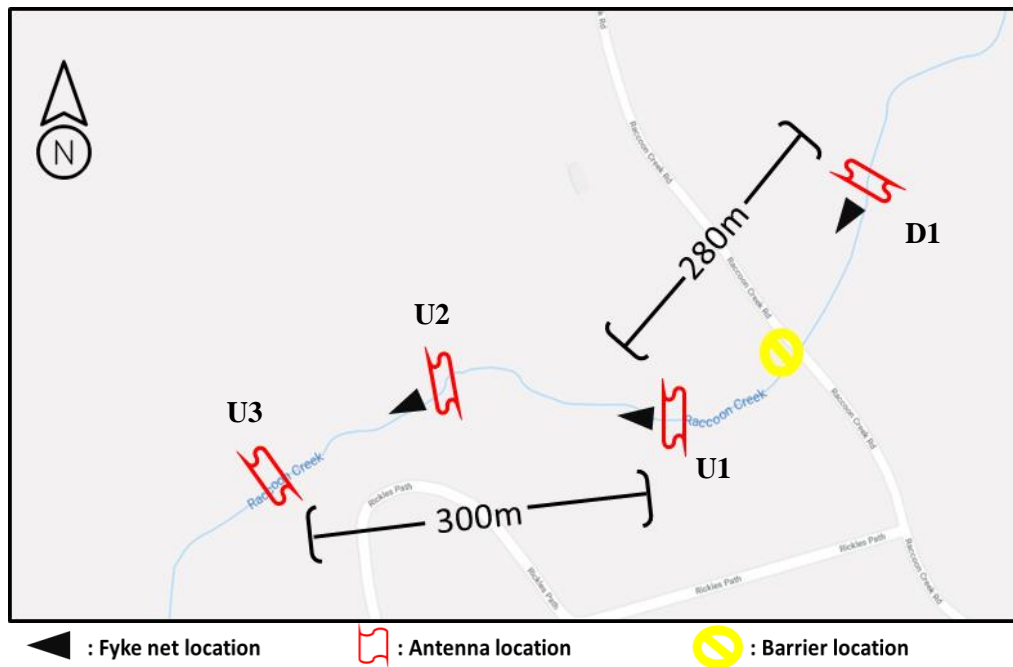


Figure 2.3: Map showing the 580m long study area on Raccoon Creek at Raccoon Creek Road. There are two separate study reaches; the downstream reach is 280m long and is bisected by the culvert at 140m. The upstream reach is 300m long and has no natural barriers to movement. There are two antenna locations in the downstream reach, D1, 140 below the culvert and U1, 140m above the culvert. There are three antennas in the upstream reach U1, U2, and U3. All of the antennas in the upstream reach are approximately 150m apart. Fyke nets were deployed at three locations within the two reaches. One fyke net was 140m downstream of the culvert, one was 140m above the culvert, and the third was 280m above the culvert.



Figure 2.4: Photo showing fyke net deployed in Raccoon Creek 140m downstream of the culvert at Raccoon Creek Road. Fyke net was used to capture fish swimming in the upstream direction.



Figure 2.5: Photos showing the half duplex antenna systems installed in Raccoon Creek to monitor fish movement.

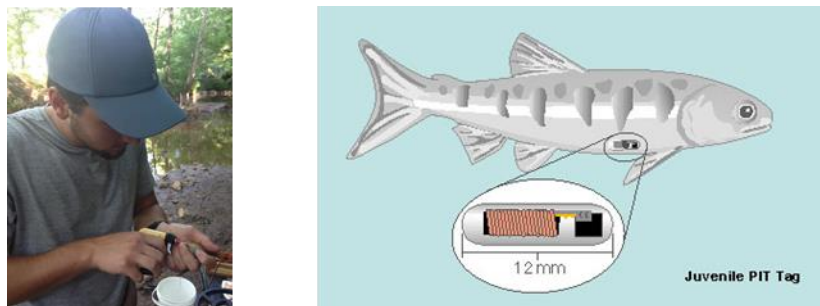


Figure 2.6: Photo showing the process of implanting a PIT tag in a fish (left). Diagram showing the location of the PIT tag within a tagged fish.

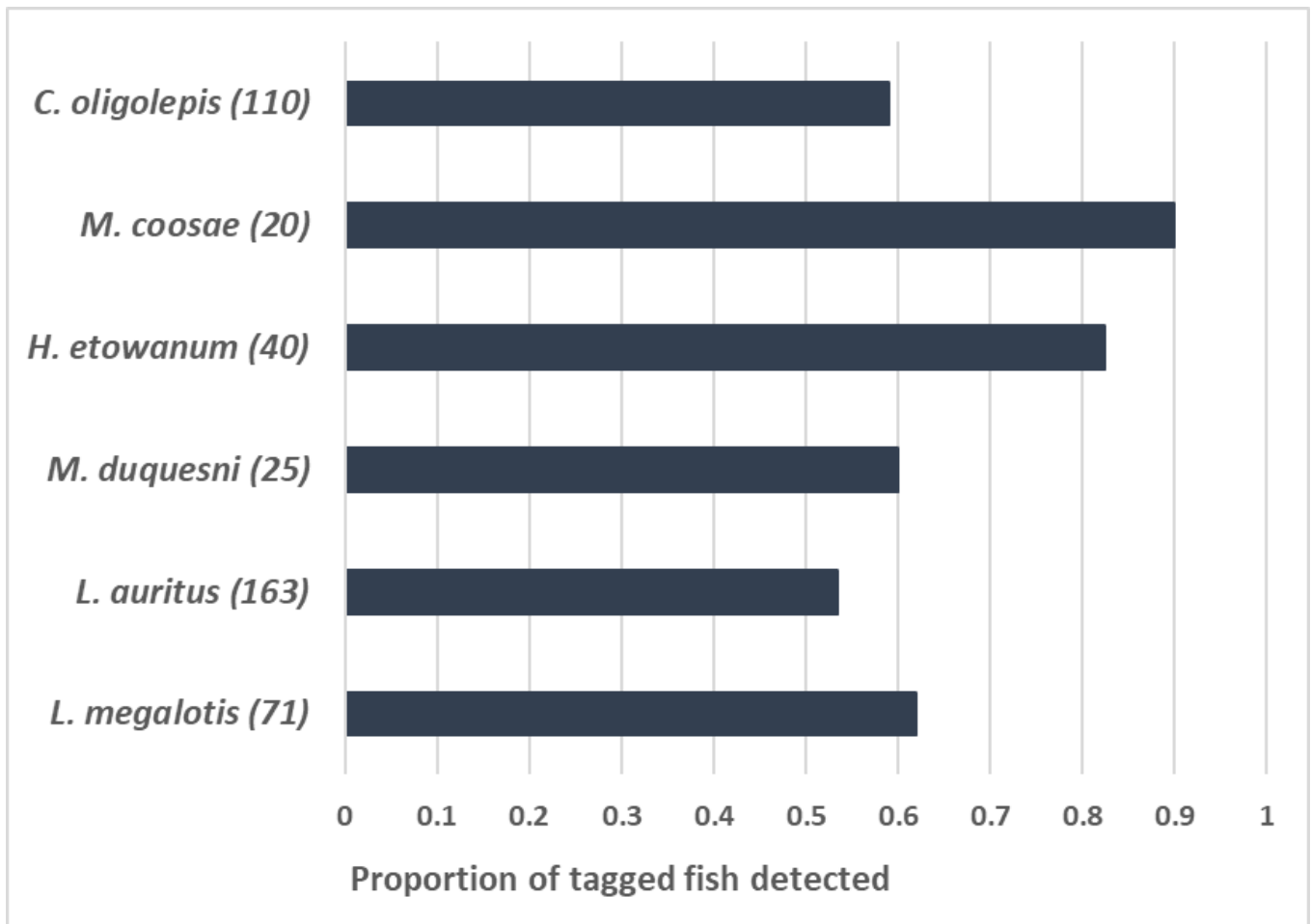


Figure 3.1: The proportion of tagged fishes detected between July 1, 2018 and November 12, 2018 by species. The proportion of redetected fish was determined by dividing the number of redetected fish by the number of tagged fish for each species. There were a total of 262 fishes detected of the 429 tagged fishes, resulting in a total redetection rate of 61.1%

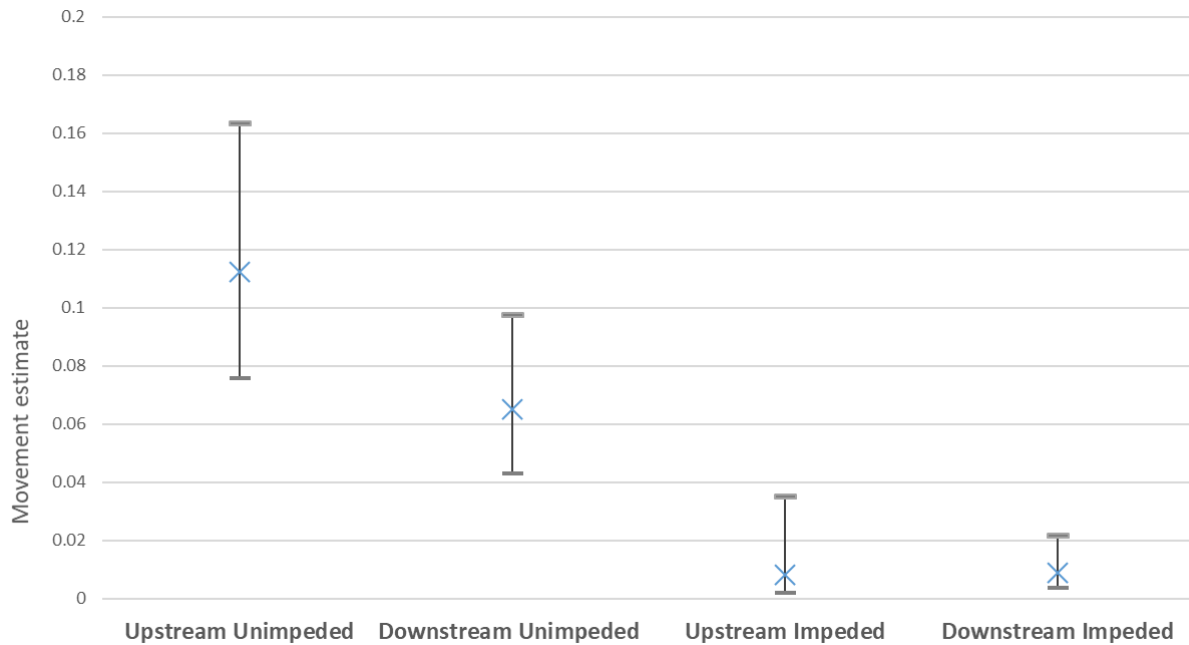


Figure 3.2: The weekly transition probabilities and upper and lower 95% confidence intervals for the likelihood of upstream and downstream movement through the unimpeded reach compared to the reach bisected by the culvert. Probabilities were calculated using a multi-state model for live recapture in MARK software. Weekly movement through the unimpeded reach is estimated to be 0.112 for upstream movement and 0.065 for downstream movement. Weekly movement through the reach bisected by the culvert is estimated to be 0.008 for upstream movement and 0.009 for downstream movement.

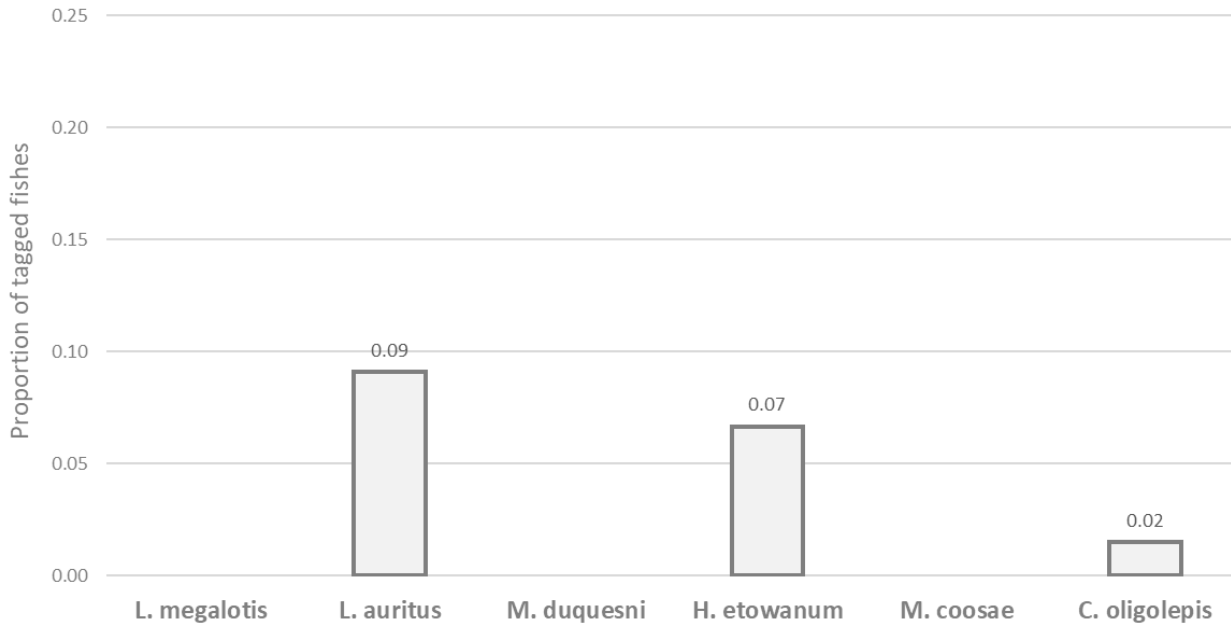


Figure 3.4: The proportion of tagged fishes that moved 280 meters through the stream reach bisected by the culvert at Raccoon Creek Road. The proportion of movers for each species was determined by dividing the number fish redetected upstream by the total number of fishes originally tagged or previously redetected below the culvert. There were a total of 3 fishes of the 123 fishes tagged or detected below the culvert that moved and were detected above the culvert, results in a passage rate of 2.4% for the reach bisected by the culvert.

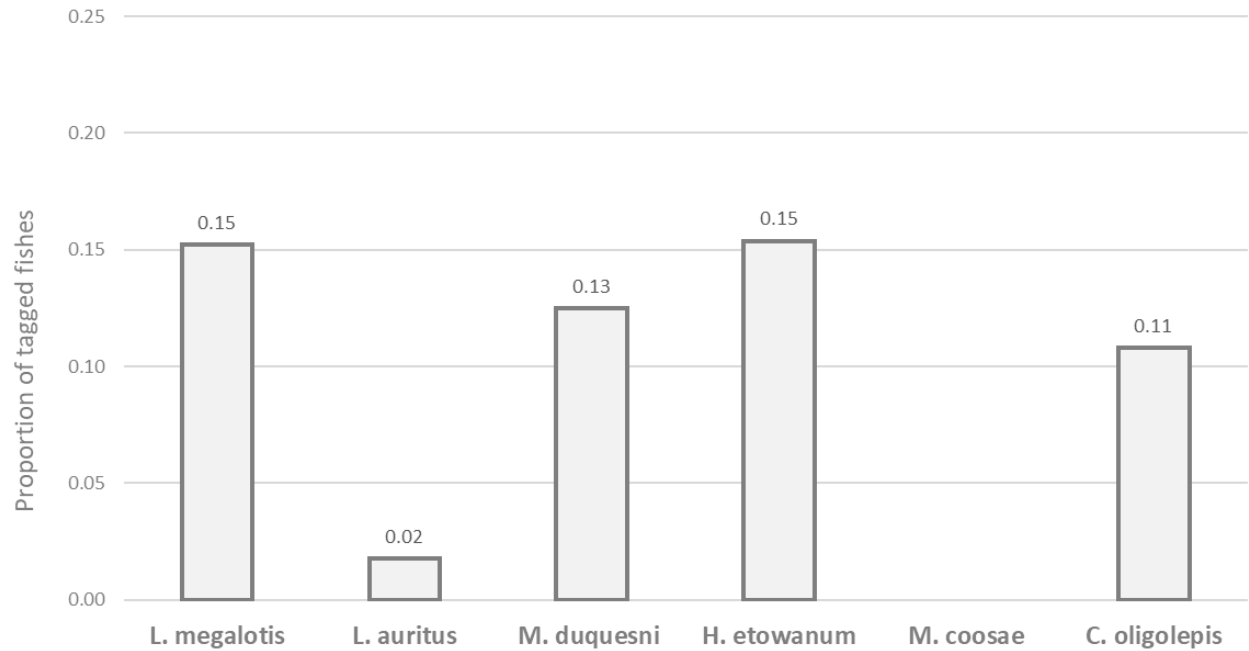


Figure 3.5: The proportion of tagged fishes that moved 300 meters through the unimpeded stream reaches by species. The proportion of movers for each species was determined by dividing the number fish redetected at the furthest upstream antenna by the total number of fishes originally tagged or previously redetected at the first upstream antenna. There were a total of fishes 16 of the 222 fishes tagged or detected at the first upstream antenna that moved and were detected at the furthest upstream antenna, resulting in a combined passage rate of 7.2% for the unimpeded reach.

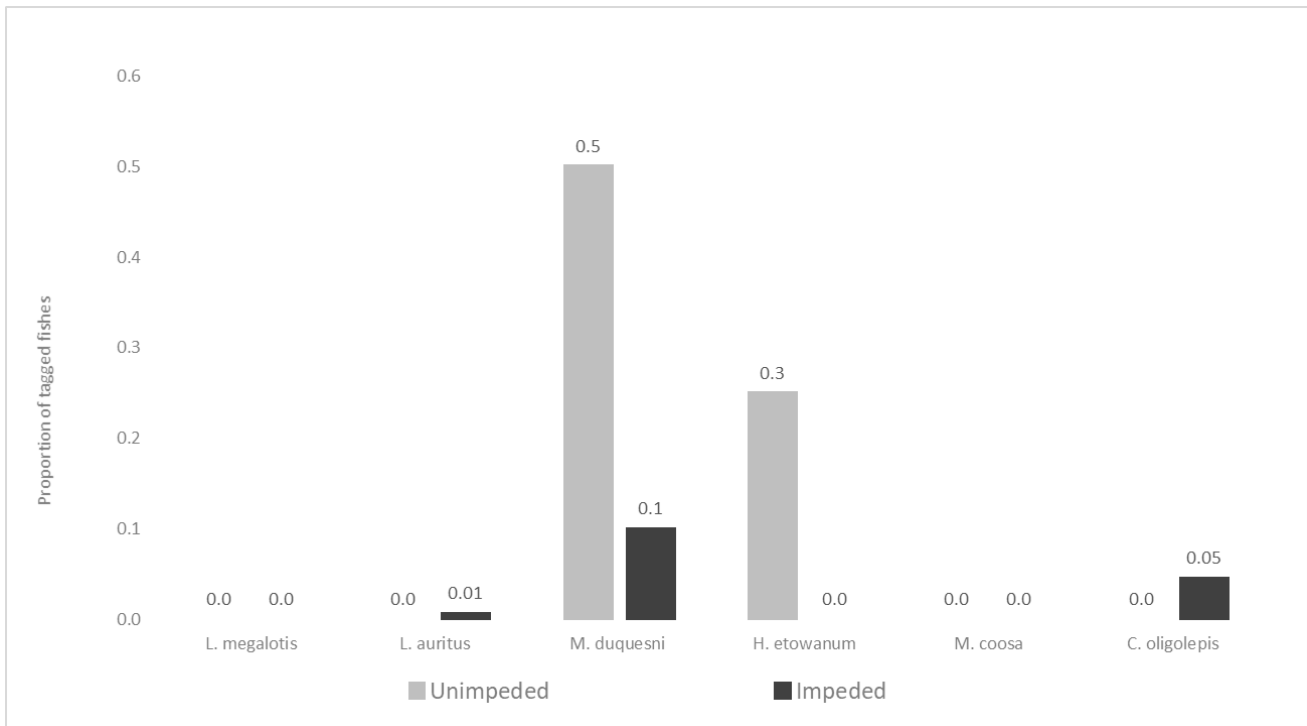


Figure 3.6: The proportion of tagged fishes that moved downstream 300 meters through the unimpeded and 280m downstream through the impeded stream reaches by species. The proportion of movers for each species in the unimpeded reach was determined by dividing the number fish redetected at the first upstream antenna by the total number of fishes originally tagged or previously redetected at the furthest upstream antenna for downstream movement. The proportion of movers for each species in the impeded reach was determined by dividing the number fish redetected at the downstream antenna by the total number of fishes originally tagged or previously redetected at the first upstream antenna.

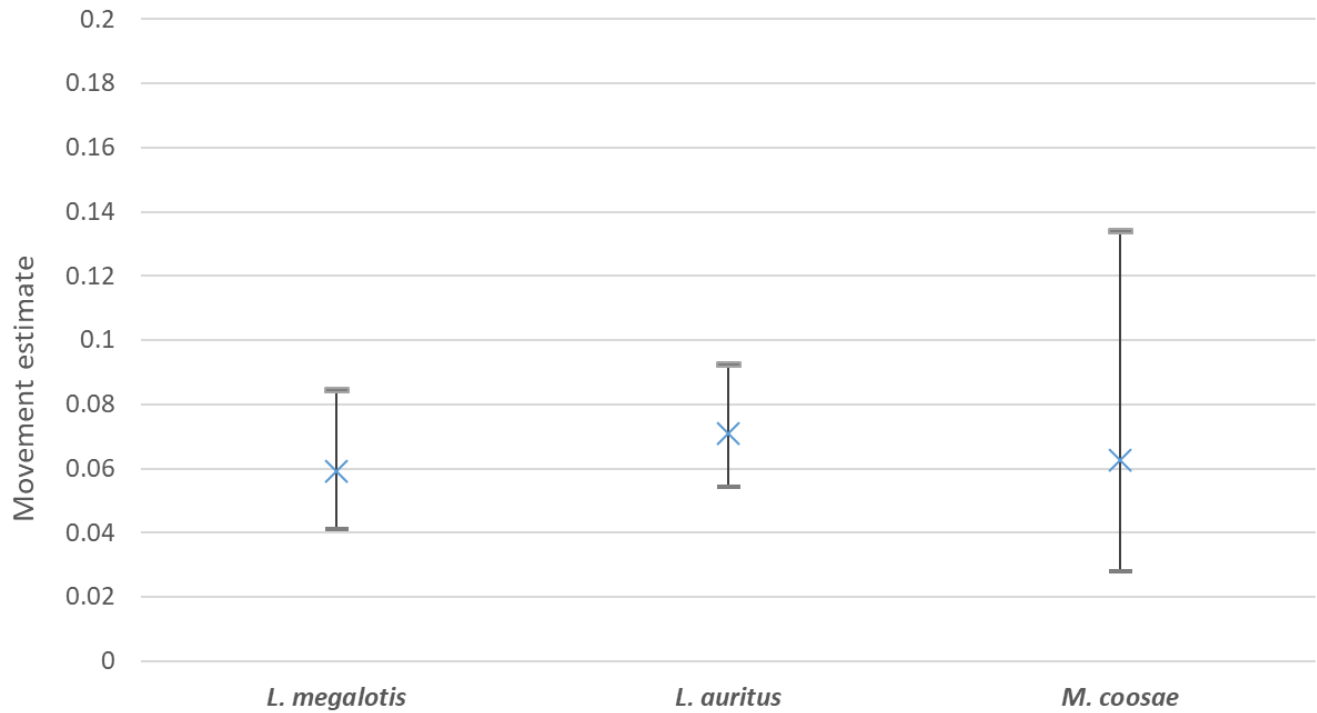


Figure 4.1: The weekly transition probabilities and upper and lower 95% confidence intervals for the probabilities of a fish moving $\geq 150\text{m}$ upstream or downstream. Estimates were calculated using a multi-state model for live recapture in MARK software. Weekly estimates for the likelihood of movement was 0.059 for *L. megalotis*, 0.071 for *L. auritus*, and 0.063 for *M. coosae*.

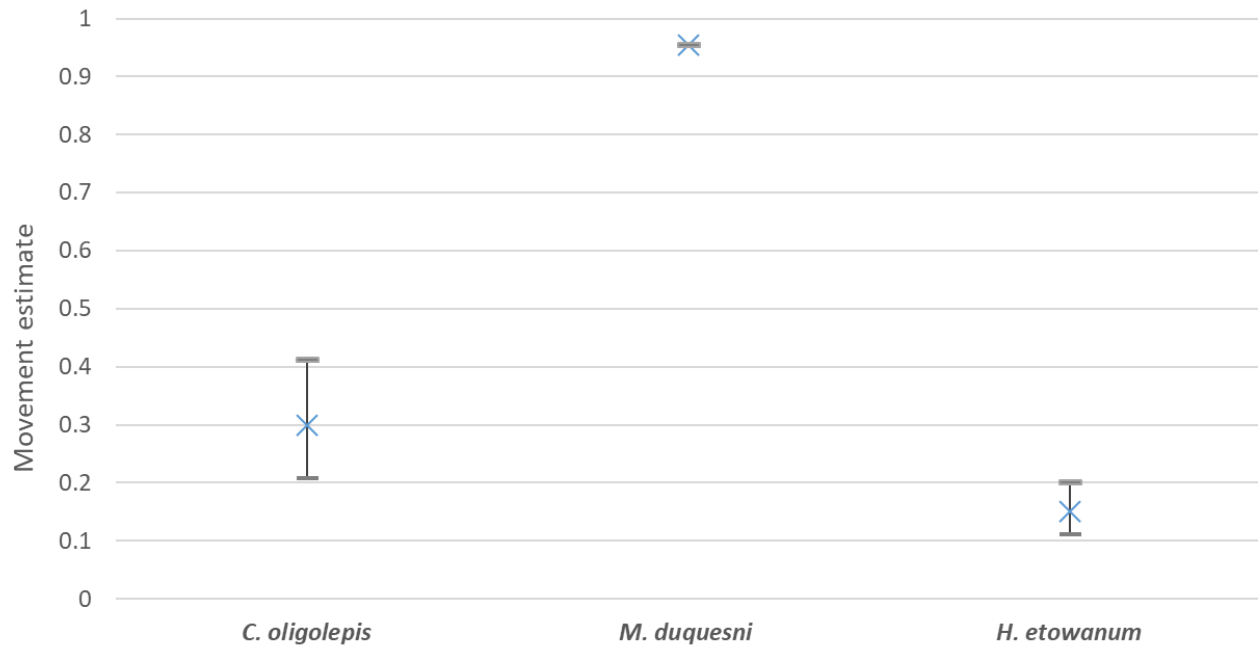


Figure 4.2: The weekly transition probabilities and upper and lower 95% confidence intervals for the likelihood of a fish moving $\geq 150\text{m}$ upstream or downstream. Transition probabilities were calculated using a multi-state model for live recapture in MARK software. Weekly estimates for the likelihood of movement 0.030 for *C. oligolepis*, 0.96 for *M. duquesni*, and 0.015 for *H. etowanum*.

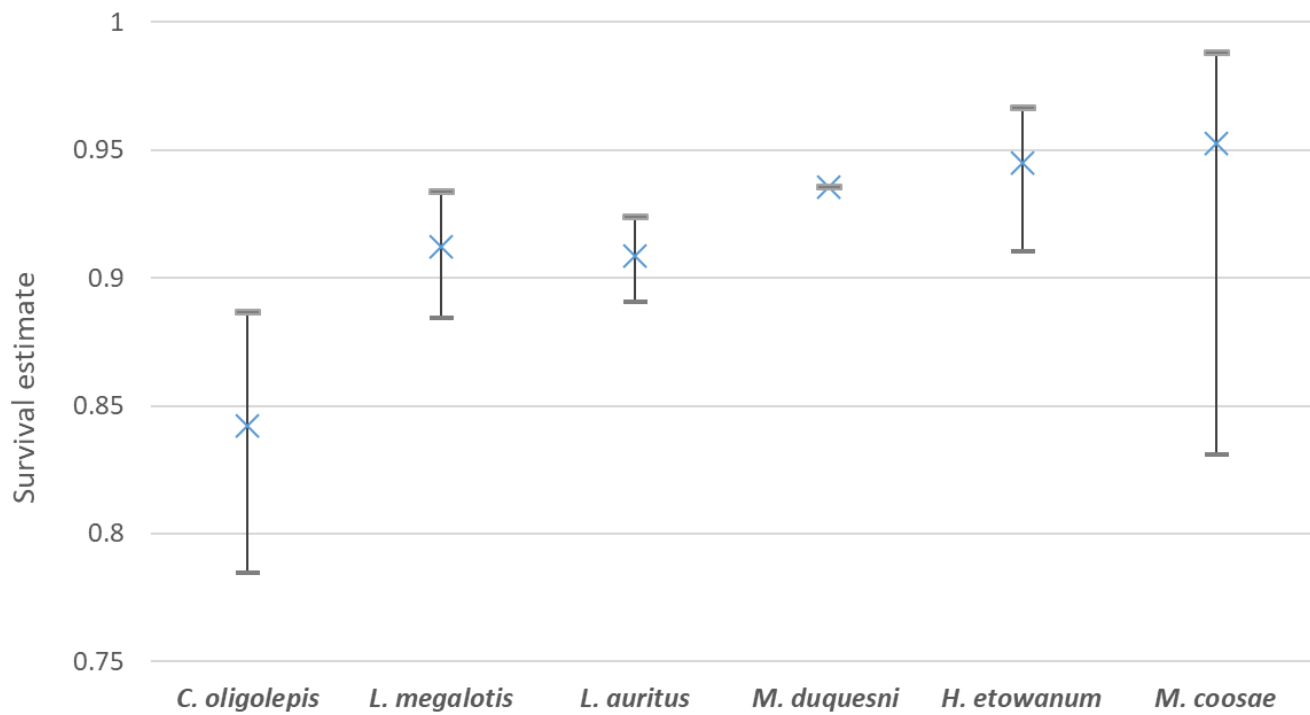


Figure 4.3: The weekly transition probabilities and upper and lower 95% confidence intervals for the likelihood of survival. Transition probabilities were calculated using a multi-state model for live recapture in MARK software. Survival rates were estimated to be 0.84 for *C. oligolepis*, 0.91 for *L. megalotis*, 0.91 for *L. auritus*, 0.94 for *M. duquesni*, 0.94 for *H. etowanum*, and 0.95 for *M. coosae*.

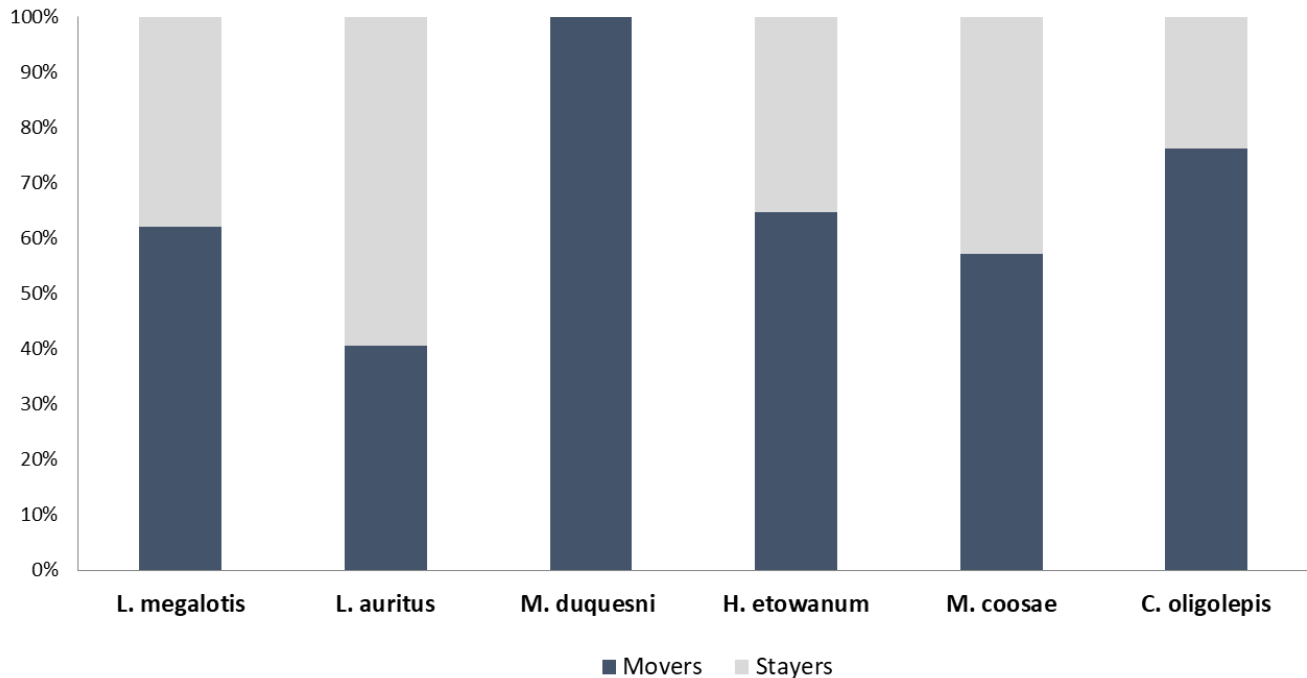


Figure 4.4: The proportion fish that were only redetected by the antenna at their original marking location (stayers), to the proportion of fishes redetected at an adjacent antenna (movers). This bar graph does not consider the fishes that were never redetected. Proportions of movers were determined by dividing the number of movers and stayers by the total number of redetected fish within the unimpeded reach.

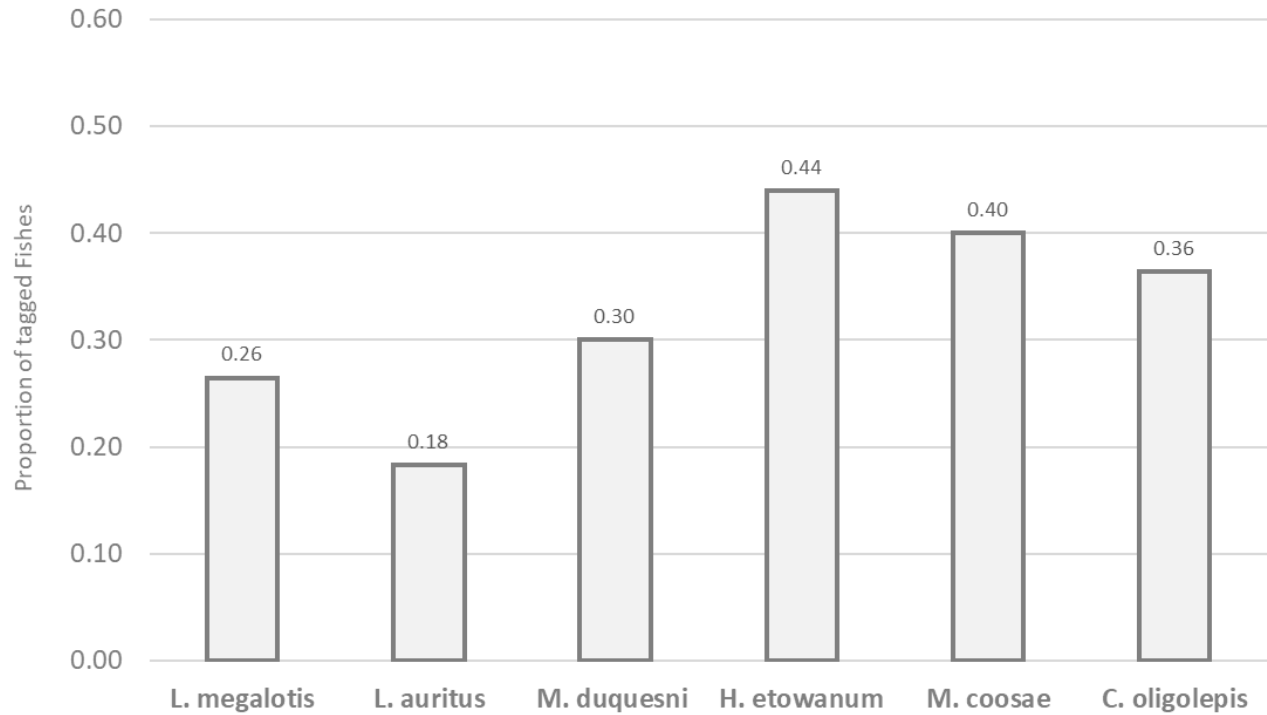


Figure 4.5: The proportion of tagged fishes that moved at least 150 meters upstream or downstream by species. The proportion of movers for each species was determined by dividing the number fish redetected at an adjacent antenna by the total number of fishes originally tagged or previously redetected in the unimpeded reach. There were a total of 80 fishes of the 310 fishes in the reach that moved and were redetected at an adjacent antenna, resulting in a combined movement rate of 25.8%.

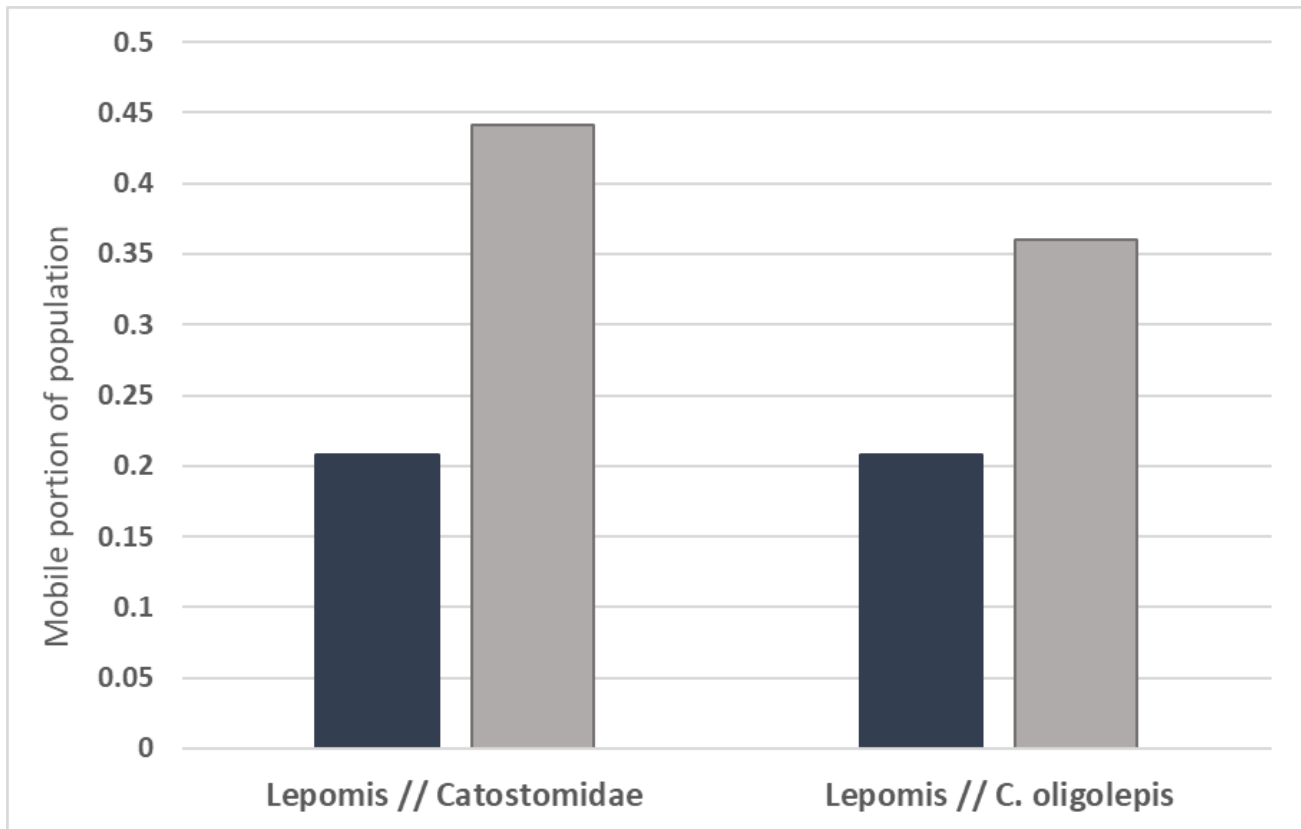


Figure 4.6: Comparisons in the differences in the number of movers and stayers for fishes with different body forms and habitat preferences. Chi-squared analysis determined that there were significant differences in movement for Lepomis (*L. auritus* and *L. megalotis*) compared to Catostomidae (*H. etowanum* and *M. duquesn*) (P value 0.003). Chi-squared analysis also showed significant differences (P value 0.026) in movement for Lepomis compared to *C. oliglepis*.

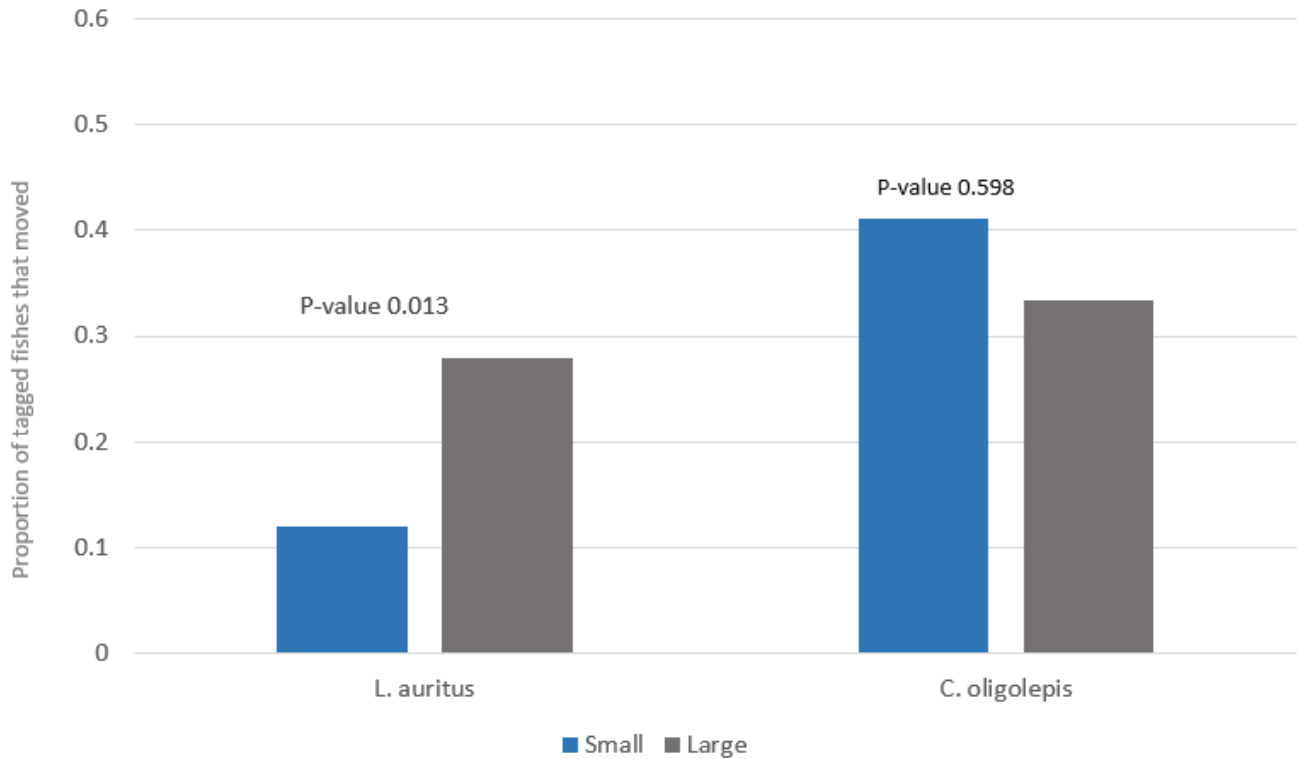


Figure 4.7: Comparisons in the differences in the proportion of movers and stayers for fishes of different body sizes (determined by total length). Fish over the length of 95mm were considered large for *L. auritus* and fish over the length of 112mm were considered large for *C. oligolepis*. Chi-squared analysis determined that there were significant differences in the number of movers versus stayers for *L. auritus*, with increased movement for large fish.

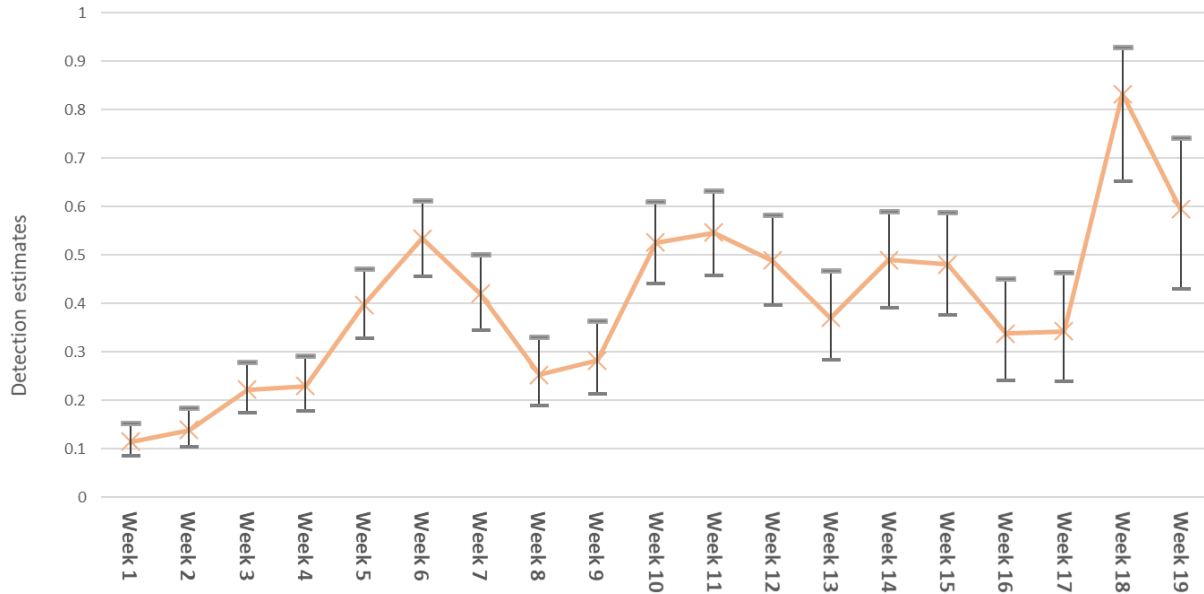


Figure 4.8: Estimates for detection by week with and upper and lower 95% confidence intervals. Estimates were calculated using a time depended model multi-state model for live recapture in MARK software. Weekly estimates for the likelihood of detection were for all species combined. Detection estimates ranged from 0.11 to 0.83, with an overall averaged 0.40 during the study.

Tables

Species	Marked at D1	Marked at U1	Marked at U2	Marked at U3	Total
<i>L. megalotis</i>	3	46	16	6	71
<i>L. auritus</i>	10	104	42	7	163
<i>M. duquesni</i>	15	8	0	2	25
<i>H. etowanum</i>	15	11	14	0	40
<i>M. coosae</i>	10	4	6	0	20
<i>C. oligolepis</i>	66	35	9	0	110
Total	119	208	87	15	429

Table 1: Number and species for all fishes tagged in Raccoon Creek in 2018. Fishes were tagged within a 580m reach directly upstream and downstream of the culvert at Raccoon Creek Road and considered for this movement analysis

Species	Fyke net	Electrofishing	Minnow Seine
<i>L. megalotis</i>	13	54	4
<i>L. auritus</i>	37	103	23
<i>M. duquesni</i>	21	3	1
<i>H. etowanum</i>	28	12	0
<i>M. coosae</i>	14	6	0
<i>C. oligolepis</i>	108	2	0
Total	221	180	28

Table 2: Method of capture for all fishes tagged in Raccoon Creek in 2018.

Species	Marked or Detected at D1	Marked or Detected at U1	Marked or Detected at U3
<i>L. megalotis</i>	3	46	19
<i>L. auritus</i>	11	113	23
<i>M. duquesni</i>	16	8	2
<i>H. etowanum</i>	15	13	3
<i>M. coosae</i>	10	5	1
<i>C. oligolepis</i>	68	37	9
Total	123	222	57

Table 3: Number and species for fishes in tagged or detected at the downstream antenna (D1), first upstream antenna (U1), and third upstream antenna (U3). Fishes must have been tagged or detected at in these locations in order to be considered for the movement comparison between the unimpeded reach and reach bisected by the culvert.

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