

MOVEMENT, SURVIVAL, AND RESOURCE USE
BY STOCKED RAINBOW TROUT

By

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BY STOCKED RAINBOW TROUT

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Abstract: Non-native species introductions often have unintentional consequences. This has led to a gradual philosophical shift where aquatic management agencies now either consider the consequences of adding a new species prior to full-scale introduction or limit introductions to highly altered stream segments. Rainbow Trout *Oncorhynchus mykiss* is an emblematic non-native species regularly stocked to increase sport fishing opportunities. Understanding how Rainbow Trout introduction influences native species is limited by region-specific conditions, the spatial and temporal extent of investigation, and the limited mechanisms examined. Introduced Rainbow Trout at southern latitudes may seek critical thermal resources, along with other habitat characteristics, creating possible interspecific competition with native species. The goal of my thesis was to evaluate environmental conditions related to possible interactions between non-native Rainbow Trout and native warmwater fishes. My first objective determined habitat selection at two spatial scales by several native fishes to determine if the presence of Rainbow Trout altered their selection of important physicochemical resources. To evaluate the spatial extent of possible interactions between Rainbow Trout and native species, my second objective evaluated movement and dispersal patterns of Rainbow Trout following stocking. In addition, I quantified Rainbow Trout survival to assess persistence of this non-native fish over time. Collectively, my work provides key information on the spatial extent and possible interactions with native species over a 2-year period.

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CHAPTER I

INTRODUCTION

INTRODUCTION

The introduction of non-native species often results in both ecological and economic consequences. When non-native species become established, they may disrupt proper ecosystem function. For example, the accidental introduction of Asian carp *Hypophthalmichthys spp.* led to their range expansion throughout much of the Mississippi River catchment (Sampson et al. 2009). These filter-feeding species target the base of the food web, thereby altering energy flow throughout the system (Sampson et al. 2009). In addition to ecological effects, invasive species result in billions of dollars in damage annually (Pimentel et al. 2005; Lovell et al. 2006). For example, substantial infrastructure damages have resulted from the introduction of Zebra Mussel *Dreissena polymorpha* to the Great Lakes (Drake and Bossenbroek 2004), Sea Lamprey *Petromyzon marinus* to the St. Mary's River (Lupi et al. 2003), and the European Green Crab *Carcinus maenas* to the Pacific Northwest (Lafferty and Kuris 1996). Despite the documentation of negative outcomes related to non-native species introductions, the purposeful introduction of non-native species is also common.

Globally, introductions of non-native fishes are often driven by economics, and commonly associated with unintentional ecological consequences. In the United States, approximately 50,000 foreign species are estimated to have been purposely introduced (Pimentel et al. 2005). Aquatic species are often introduced as food sources (e.g., Common Carp *Cyprinus carpio*; Weber and Brown 2009) or to provide recreational opportunities (e.g., Brook Trout *Salvelinus fontinalis*; Dunham et al. 2002). For example, Common Carp was introduced from Europe to the United States during the 1800's as a food fish (National Park Service 2015). The Common Carp quickly expanded its range across North America, degrading water quality and negatively affecting native species (Weber and Brown 2009). Both Blue Catfish *Ictalurus furcatus* and Flathead Catfish *Pylodictis olivaris* were introduced into Virginia tidal rivers to create new sport fishing opportunities for anglers (Moran et al. 2016). Both of these top predators are now well established and comprise much of the total biomass in these systems (Schloesser et

al. 2011). Salmonids are perhaps the best example of a group of species with consistent non-native introductions (Halverson 2008). Rainbow Trout *Oncorhynchus mykiss* is the most widely stocked fish species in the United States and has been introduced to every state outside its native range (Fuller et al. 1999). Today, most state agencies maintain some form of a trout-stocking program, excluding only Florida, Louisiana, and Mississippi (Halverson 2008). Collectively, these introductions bring billions of dollars to states via fishing opportunities, but the ecological consequences to other native fishes are sometimes unknown.

Stocking Rainbow Trout in the United States provides both economic incentives and the ability to maintain fisheries in areas where native species have been reduced. Rainbow Trout anglers provide substantial financial support to state and federal fishery agencies through the purchase of licenses and associated fees (Hyman et al. 2016). In addition, Rainbow Trout anglers spend an estimated 3.6 billion dollars on fishing gear, travel, and other associated expenses (USFWS 2011). This translates to an estimated 8.6 billion dollars in total economic benefit (USFWS 2011). In areas where native species have been negatively affected or eliminated by human activity (e.g., impoundments), Rainbow Trout can provide a mitigation fishery. Rainbow Trout are commonly stocked in tailwaters of the southern United States to supplement the reduction in native species as a result of altered thermal conditions (Bettinger and Bettoli 2002; Runge et al. 2008; McManamay et al. 2015). Despite the economic benefits and recreational opportunities, there is some evidence to suggest there may be negative interactions between trout and native fishes under some circumstances.

Introducing Rainbow Trout and other salmonids may result in negative consequences to the native species. For example, Rainbow Trout influence both the feeding position and habitat selection of the threatened Little Colorado Spinedace *Lepidomeda vittata* (Blinn et al. 1993; Bryan et al. 2002). In laboratory studies, Brown Trout *Salmo trutta* influence individual forage and thermoregulation behavior of native Brook Trout (Hitt et al. 2017). At the population level, non-native Brook Trout replaced native Cutthroat Trout *Oncorhynchus clarkii* in Rocky

Mountain headwater streams (Peterson and Fausch 2003). Rainbow Trout introductions have led to site-specific declines (i.e., stocking site) in the relative abundance of native fish assemblages such as Smallmouth Bass *Micropterus dolomieu*, Bluegill *Lepomis macrochirus*, Southern Redbelly Dace *Chrosomus erythrogaster*, and Central Stoneroller *Campostoma anomalum* (Walsh and Winkelman 2004b). There is also evidence of some diet overlap between Rainbow Trout and native fishes (Metcalf et al. 1997; Fenner et al. 2004; Oklahoma Department of Wildlife Conservation, *unpublished data*). The presence of Rainbow Trout can disrupt food webs, causing native species to switch forage behavior to seek out alternate prey. For example, Baxter et al. (2004) showed that Rainbow Trout preyed upon the majority of terrestrial insects that dropped into a stream, causing the native Dolly Varden Char *Salvelinus malma* to switch from this food source to benthic invertebrates. In general, investigation into the effects of stocked salmonids has focused on native and non-native salmonid interactions (Turek et al. 2013), providing little insight to possible interactions with non-salmonid fishes (but see Walsh and Winkelman 2004b and Weaver and Kwak 2013).

Evaluations of interactions between introduced Rainbow Trout and non-salmonid native species reveal few patterns but have been limited in scope. The geographic extent of introductions make it difficult to make large generalizations about the possible ecological consequences (Fausch et al. 2001; Turek et al. 2013). Rainbow Trout have been introduced in warmwater streams (Walsh and Winkelman 2004a), coldwater lakes (Koenig et al. 2011), and in dam tailwaters (Bettinger and Bettoli 2002) to provide seasonal or year-round fishing opportunities. In some instances, no ecological effect has been related to trout introductions. For example, Weaver and Kwak (2013) found no measurable difference in native species richness, diversity, and microhabitat use following the introduction of three salmonid species including Rainbow Trout in coldwater Appalachian Mountain streams. The authors hypothesized that either these hatchery-raised trout were poor competitors in the natural stream landscape or that negative effects caused by trout were masked by environmental variability (Weaver and Kwak 2013). In addition,

existing studies have been both spatially and temporally limited (e.g., 1 – 2 years, Weaver and Kwak 2013), lacked reference sites (i.e., not accounting for environmental variation, Walsh and Winkelman 2004b), and evaluated only a few mechanisms (Turek et al. 2013). Lastly, Fausch et al. (2001) highlight that both invasion success and interactions among Rainbow Trout and native species may largely depend on the suitability of coarse-scale environmental factors in various ecosystems (e.g., flow regime).

The overarching goal of my thesis was to increase our understanding of interactions between non-native Rainbow Trout and native fishes with emphasis on spring-fed, warmwater streams. I accomplished this goal via two primary objectives. The first objective of my thesis was to examine the relationship between the presence of Rainbow Trout and shifts in spatio-temporal habitat selection by native fishes. I addressed this question at two spatial scales, microhabitat and channel unit complexes. Additionally, my study addressed seasonal differences at the microhabitat scale. To infer the spatial and temporal extent of changes in habitat selection related to Rainbow Trout presence, it was also important to evaluate Rainbow Trout movement extent and their ability to persist in this stream. Consequently, the second objective of my thesis was to determine the movement and survival of Rainbow Trout stocked in the lower portion of Spavinaw Creek. This allowed me to infer the temporal extent of any stressors caused by the presence of Rainbow Trout. Collectively, my thesis provides important baseline data to develop hypotheses about mechanisms related to observed patterns in resource use at multiple spatial scales.

STUDY AREA AND PROJECT BACKGROUND

Spavinaw Creek is emblematic of many streams of the Ozark Highlands ecoregion. The climate of this region is moderate and most streams are classified as warmwater. However, the ecoregion is characterized by karst geology with notable groundwater contribution (i.e., seepage of groundwater into the stream) and subsequent thermal patchiness in many streams. The influence of groundwater on the thermal regime of Spavinaw Creek and similar streams in the

Ozark region has resulted in stocking of coldwater species including Rainbow Trout to increasing angling opportunities. Spavinaw Creek also supports healthy populations of native fishes that are recreationally important and of conservation value.

Historic stocking in Spavinaw Creek has provided limited information on possible ecological interactions with other fishes. Spavinaw Creek has been stocked with both Rainbow Trout and to a lesser degree, Brown Trout, in Arkansas. Some stocking occurred in the 1950's (Baker 1954), and the last legal stocking was in 2013. Rainbow Trout continue to be observed in Spavinaw Creek on occasion, but it is unknown if the thermal characteristics allow persistence or if illegal stockings result in the current presence of Rainbow Trout (Brown and Moore 2008). Previous efforts characterized possible diet overlap between Rainbow Trout and native species and determined trout density at select locations (Brown and Moore 2008; Williams et al. 2011). These investigations provided little insight due to limited access to private lands, short sampling duration, and evaluations only considered Rainbow Trout, Brown Trout, and the adult life stage of two sport fishes (Smallmouth Bass and Shadow Bass *Ambloplites ariommus*). Our limited understanding of the interactions between existing Rainbow Trout and native species in this spring-fed system, combined with pressure to allow stocking at additional locations have emphasized the need to examine this system in more detail.

An application to stock Rainbow Trout in the lower portion of Spavinaw Creek (Oklahoma) was granted to a private angling group by the Oklahoma Department of Wildlife Conservation in October 2018. Since then, stocking has occurred in autumn 2018 and spring 2019 at a single stream reach (see Chapter 3). The stocked portion of Spavinaw Creek contains one of the highest densities of Neosho Smallmouth Bass in the region, an important native sport fish (Brewer, *unpublished data*). Additionally, Spavinaw Creek supports populations of several species of conservation concern. For example, the Redspot Chub *Nocomis asper* is listed by both the Oklahoma Department of Wildlife Conservation and the Arkansas Game and Fish Commission as a Species of Greatest Conservation Need under their respective Wildlife Action

Plans. Consequently, the situation presented an opportunity to expand our understanding of how non-native salmonid introductions affect native fishes of recreation and conservation value.

CHAPTER II

IDENTIFYING HABITAT SELECTION SHIFTS BY STREAM FISHES IN RESPONSE TO RAINBOW TROUT

ABSTRACT

Fishes select habitat at multiple spatial and temporal scales to maximize forage efficiency, reproductive success, and to seek cover from predators or harsh physiochemical conditions. Habitat shifts by some species may also be driven by the presence of non-native fishes, particularly under conditions where key resources are limited. My objectives were to 1) determine microhabitat selection by five native fishes (Smallmouth Bass *Micropterus dolomieu*, Redspot Chub *Nocomis asper*, Creek Chub *Semotilus atromaculatus*, Redhorse *Moxostoma spp.* and Northern Hogsucker *Hypentelium nigricans*) in the presence and absence of non-native Rainbow Trout *Oncorhynchus mykiss* and 2) determine the relationship between native fishes, the presence of Rainbow Trout, and reach-scale habitat factors. I conducted seasonal microhabitat surveys throughout my two-year study period. I found Rainbow Trout present within my study reaches were related to several native fishes shifting their seasonal microhabitat selection patterns: depth (e.g., shifted to greater depth), velocity (e.g., shifted to lower velocity), temperature (e.g., shifted to less use of unique thermal patches), and cover (e.g., used more cover); however, seasonal and site-specific differences in habitat availability are important considerations when interpreting these relationships. Reach-scale snorkel surveys over two years were conducted during summer, base flow conditions. I found little relationship between Rainbow Trout density and native fish densities at the reach scale with only Creek Chub having a significant relationship Rainbow Trout. However, residual pool depth, percent riffle, and maximum weekly maximum temperature were strong predictors of native fish density. If the conservation of native species is the management goal, then eliminating or reducing stocking to seasons where minimal perceived interactions occur with native fishes would seem warranted (see Chapter 3). Future efforts examining additional changes in habitat selection would be helpful if Rainbow Trout stocking is continued and may provide more clarity on potential interactions.

INTRODUCTION

Physicochemical habitat use and selection patterns (i.e., where use exceeds available conditions, Johnson 1980; Boyce et al. 2002) confer benefits to stream fishes and aid in developing conservation and restoration strategies. Fishes select physical factors (e.g., cover and substrate, Todd and Rabeni 1989), hydraulics (e.g., depth and velocity; Fore et al. 2007) and water-quality constituents (e.g., pH, temperature, and dissolved oxygen, Snucins et al. 1995) to increase survival and fitness. Selection of physicochemical factors increases feeding success (e.g., Bluegill *Lepomis macrochirus*, Mittelbach 1981), provides cover from predators (e.g., Bluegill, Shoup et al. 2003), and minimizes energy loss (e.g., salmonids, Fausch 1984). Understanding how fishes select habitat elements is useful for developing management strategies (Guthery et al. 2005). For example, Nislow et al. (1999) determined the most profitable feeding position for age-0 Atlantic Salmon *Salmo salar* and recommended large woody debris be incorporated into stream restoration activities to provide velocity refuge for age-0 fish. Habitat selection has served as a foundation for instream flow recommendations (Moyle and Baltz 1985), stream restoration guidelines (Bond and Lake 2003), and is a useful way to assess possible species interactions (Weaver and Kwak 2013). However, the relationships that underlie these conservation and management strategies are often scale dependent.

The population dynamics of stream fishes (growth, mortality, and recruitment) may benefit from physiochemical selection at multiple spatial and temporal scales. At coarse scales, climate (e.g., Ficke et al. 2007; Comte et al. 2013; Carlson et al. 2014), land use (e.g., Harding et al. 1998; Meador and Goldstein 2003; Brewer and Rabeni 2011), and geology (e.g., Esselman et al. 2006; Neff and Jackson 2012) relate to population functions often via secondary production (Stevenson 1997). For example, longitudinal differences in temperature (Rieman et al. 2006) and production (Vannote et al. 1980) relate to both changes in elevation and fish assemblage structure (Schlosser 1982; Rahel and Hubert 1991; de la Hoz Franco and Budy 2005). At a finer spatial scale, individual habitat selection can also relate to population dynamics via predation rates (e.g.,

predator avoidance, Grossman et al. 1987), reproductive benefits (e.g., suitable nesting habitat or associations, Peoples et al. 2014), and benefit fish bioenergetics (e.g., thermal refuge, Ebersole et al. 2003a). Selection patterns across multiple spatial scales are an important consideration (Frissell et al. 1986) and can provide a more-complete picture of habitat selection (e.g., see Torgersen et al. 1999). For example, adult Smallmouth Bass *Micropterus dolomieu* select pool habitats but population density is associated with increasing amounts of riffle habitat at the reach scale, presumably due to prey production (Sowa and Rabeni 1995; Brewer 2013a). In addition, habitat selection may vary temporally due to seasonal (e.g., cover use, Todd and Rabeni 1989; temperature, Wolf et al. 2019) or daily needs (cover, Cook et al. 2001; and depth, Salas and Snyder 2010). Examining habitat selection among scales is a useful strategy for both improving native fish conservation and management, but also for assessing possible limiting resources that benefit both native and non-native fishes.

Interactions between native and non-native species may be scale or condition dependent when a resource becomes limiting (Taniguchi and Nakano 2000). For example, Hitt et al. (2017) showed competition for patchy thermal resources between non-native Brown Trout *Salmo trutta* and native Brook Trout *Salvelinus fontinalis*. Native Warpaint Shiners *Luxilus coccogenis* shifted to higher-velocity environments and their home range size increased in response to the presence of Rainbow Trout (Elkins et al. 2019). Likewise, Baxter et al. (2004) showed shifts in forage behavior by native species following the introduction of non-native Rainbow Trout *Oncorhynchus mykiss*. At coarser scales, shifts in fish assemblage structure (Walsh and Winkelman 2004) and declines in native species abundance have been related to non-native species introductions (e.g., see Peterson et al. 2004). Although multi-scale investigations of habitat use or selection are relatively common (e.g., Torgersen et al. 1999; Bean et al. 2015), multiscale studies examining resource overlap between native and non-native species are rare (but see Weaver and Kwak 2013). Consequently, an important consideration when examining resource overlap among species is to consider seasonal shifts in selection. For example, many

fishes select coolwater habitat during the summer (e.g., Chinook Salmon *Oncorhynchus tshawytscha*, Ebersole et al. 2003a; Smallmouth Bass, Whitley et al. 2006; Southern Redbelly Dace *Chrosomus erythrogaster*, Walker et al. 2013), suggesting competition among species could be possible if these resources are limited. Consequently, multiscale evaluations examining resource overlap or shifts by native fishes in the presence of non-native fishes may identify seasonal or scale-specific interactions.

My first thesis objective was to determine habitat selection patterns by several native fishes at both microhabitat and reach scales. Specific to my overarching research question, I sought to identify selection patterns under both reference (i.e., no Rainbow Trout) and stocked (i.e., with Rainbow Trout) conditions. This allowed me to determine if the introduction of Rainbow Trout related to habitat selection shifts by native fishes. This information will be informative to agency stocking decisions assuming native fish conservation is the management goal.

METHODS

Study area

My study area was located in eastern Oklahoma and western Arkansas in the Ozark Highlands ecoregion. The Ozark Highland ecoregion has a moderate climate with average high temperatures of 9°C and 33°C in January and July, respectively. The average annual rainfall is approximately 120 cm (Woods et al. 2005). The western portion of the ecoregion is characterized by cherty clay soils and underlying karst geology (Woods et al. 2005). Vegetation is typically oak-hickory forest, though much of the lowland area has been converted to agricultural land uses (e.g., pasture). Within this ecoregion, I sampled sites on both Spavinaw and Spring creeks (Figures 1 and 2). Spavinaw and Spring Creeks are third- and fourth-order (Strahler 1952) streams, respectively (upstream drainage areas from the nearest USGS stream flow gauge 297 km² and 422 km²) and have similar fish assemblage structure (Brewer, Unpublished data). In

addition, both streams are classified by relatively high groundwater contributions (Mollenhauer et al. 2019).

Species and life stages

I determined habitat selection by five native fish species because of their hypothesized resource overlap with Rainbow Trout, recreation value, and conservation need (Table 1). All species chosen occupy pool and run habitats that are also used by stocked Rainbow Trout in warmwater streams (Walsh and Winkelman 2004). Some species including the Creek Chub *Semotilus atromaculatus* have relationships with cooler water which I hypothesized would create resource overlap with Rainbow Trout. Additionally, Smallmouth Bass, Northern Hogsucker *Hypentelium nigricans*, and fishes of the genus *Moxostoma spp.* provide important recreational fisheries in the Ozark Highlands ecoregion. The Redspot Chub *Nocomis asper* and Shorthead Redhorse *Moxostoma macrolepidotum* are listed as species of conservation concern by both Arkansas Game and Fish Commission (AGFC) and the Oklahoma Department of Wildlife Conservation (ODWC). In Spavinaw and Spring Creeks, “Redhorse” consisted of Golden Redhorse *Moxostoma erythrurum*, Black Redhorse *Moxostoma duquesni*, and Shorthead Redhorse. These species could not be identified from one another using snorkel surveys but sampling data associated with unpublished studies indicate the majority are Blackhorse (Zentner, unpublished data).

I considered juvenile and age-1+ Smallmouth Bass separately in my surveys. I considered “juvenile” Smallmouth Bass to be fish beyond the black fry stage (approximately 35 mm total length [TL]) but ≤ 85 mm TL. Juveniles were both Smallmouth Bass that survived their first winter (i.e., age 1 fish) but also young-of-year Smallmouth Bass that were sampled during autumn and winter microhabitat assessments. I did not consider young-of-year Smallmouth Bass in my reach-scale surveys because their numbers decline rapidly throughout their first summer due to natural mortality (Lukas and Orth 1995; Brewer and Orth 2015); thus, differences among

sites would not necessarily relate to the presence of Rainbow Trout. I considered Smallmouth Bass > 85 mm to be age-1+ (Reed and Rabeni 1989; Brewer and Ellersieck 2011). For all other species, I enumerated only the adult life stage using species-specific length criteria (Table 1).

Site selection

Microhabitat. – I sampled four sites (i.e., pool-run complexes 100 – 200 m long consisting of heterogeneous microhabitat conditions) seasonally 2017 – 2019 to determine microhabitat selection by native fishes (Figure 1). Each site was visited several times during my study (Table 2) and observations between visits were assumed to be independent given the dynamic nature of stream habitat conditions across fine spatial scales (Frissell et al. 1986). I selected sites based on Rainbow Trout distribution and microhabitat heterogeneity. Three of my study sites were located on Spavinaw Creek because of the proximity to previously (AR) and currently (OK) known Rainbow Trout stocking locations. I chose sites in both AR and OK to account for differences in thermal microhabitat because colder water is available in AR. My fourth site was located on Spring Creek (OK). The Spring Creek site was my control (i.e., no Rainbow Trout throughout my study) and sampled seasonally (Table 2). I sampled the upstream site of Spavinaw Creek (AR) in winter and summer, and the downstream sites (OK sites) in spring, summer, and autumn (Table 2). The site in AR had higher groundwater contribution compared to the Oklahoma sites (Bowman et al. 1996; Brewer *unpublished data*); thus, I hypothesized habitat conditions in the Arkansas site would be more favorable for some stream fishes including Rainbow Trout during seasons of thermal stress (i.e., summer and winter).

Reach. – I sampled reaches (length approximately 20x average wetted width) throughout the summer and autumn 2018 and 2019 (Figure 2). I chose reaches that appeared to have different Rainbow Trout densities and heterogeneous habitat characteristics. I sampled 13 reaches on Spavinaw Creek and 5 reaches on Spring Creek over the 2018 – 2019 sample seasons (Table 3). I

sampled each reach on multiple occasions during each sample season. Similar to microhabitat sites, I assumed fish counts (i.e., sampling visits) to be independent of one another during each survey.

Habitat availability

Microhabitat. – I systematically quantified microhabitat availability across each of my sites. I established transects perpendicular to stream flow at 5-m increments. I recorded habitat measurements at four locations along each transect. Two points were measured 1 m from each streambank to encompass near-bank habitat. The two inner measurements were equally spaced along each transect between these outer points. At each point, I measured water depth (0.05 m), approximate water-column velocity (0.1 m/s, at approx. 0.6 depth) and benthic water velocity (0.1 m/s, just above substrate), dominant substrate, presence of cover, and water temperature (0.5 °C, 1-h resolution; see below). Water velocity was measured using Marsh McBirney Flo-Mate 2000 flow meter (Marsh-McBirney Inc., Fredrick, MD) or a Global Water Flow Probe (Global Water, College Station, TX). I measured the water velocity at two points in the water column because of differences in water-column use among my study species. Specifically, I measured benthic velocity to quantify both use and available velocities associated with Northern Hogsucker due to the species' benthic ecology (Miller and Robison 2004). I visually estimated the dominant substrate within a 1-m² patch (Brewer and Ellersieck 2011) using classifications of McMahon et al. (1996): 0) unbroken, 1) silt (< 0.06 mm), 2) sand (\geq 0.06 – 2 mm), 3) gravel (> 2 – 16 mm), 4) pebble (> 16 – 64 mm), 5) cobble (> 64 – 256 mm), and 6) boulder (> 256 mm). I considered cover present if any of the following habitat elements were located in a microhabitat patch: 1) coarse wood (>10 cm in diameter and 3 m in length; Wohl et al. (2010), 2) smaller wood \leq 10-cm diameter (e.g., fallen tree limbs), 3) rootwads, or 4) boulders. Consequently, boulders contributed to both cover and substrate classifications. Lastly, I measured water temperature at each patch using multiple methods as described below.

I used a combination of temperature loggers (iButton, Maxim, San Jose, CA) and a fiber-optic distributed temperature sensing (DTS) system to measure temperature availability across each site. I waterproofed iButton loggers in plastic (Plasti Dip International; Blaine, Minnesota) following the methods of Roznik and Alford (2012). Each iButton logger was placed in white PVC pipe and anchored to the substrate to limit the effects of solar radiation on water temperature measurements. A detailed explanation of the theory and application of DTS is provided in Selker et al. (2006). Briefly, DTS systems consist of fiber-optic cable that transmits light from a connected control box. Temperature along the cable is determined by measuring the scattering effect of light at different wavelengths along the cable. I deployed the fiber-optic cable along the stream bed and allowed it to pass through each habitat patch. The fiber-optic cable was connected to the box located on the stream bank that recorded temperature along the cable at fine spatial (~ 1 m) and temporal (~ 1 min) resolutions. I spatially referenced each patch to a cable location; thus, providing a continuous measurement of temperature across each site. Comparisons between iButton and DTS temperature measurements from multiple sites indicated solar radiation did not influence DTS measurements (< 0.5 °C difference; Wolf, *unpublished data*; see also Neilson et al. (2010).

Habitat use

Microhabitat. – I quantified the same habitat measurements measured during habitat availability surveys at each marked fish location to provide microhabitat use data. For depth, substrate, and cover, habitat use variables at each fish location were measured using the aforementioned methods (i.e., see *Microhabitat availability*). However, I did not measure velocity or temperature at each fish location. Instead, I spatially referenced each fish observation to the nearest transect-point measurement. The spatially-referenced locations were later used to obtain both temperature (i.e., matched to the time of the survey, 1-hr resolution) and velocity measurements.

Reach. – I recorded physicochemical characteristics that I hypothesized would influence fish counts at the reach scale. Habitat measurements were quantified on one or more occasions depending on the variation in conditions over time. For example, groundwater during the summer base flow period would be expected to decline slowly (Adamski et al. 1995); thus, repeat measurements during each survey were not necessary. I used either an Acoustic Doppler Current Profiler (Sontek RiverSurveyor S5, San Diego, CA) or a flow meter and wading rod (Marsh McBirney, Flo-mate 2000, Fredrick, MD) to measure fine-resolution discharge at the upstream and downstream extent of each reach one time. I used the difference in these measurements to classify each reach as gaining or losing groundwater (i.e., seepage measurements, Zhou et al 2018; Mollenhauer et al. 2019). I quantified channel unit area across each reach for two purposes. First, I was able to quantify what proportion of each reach consisted of riffle habitat. I hypothesized that differences in the proportion of riffle habitat at each reach would be related to fish counts because secondary production of macroinvertebrates in riffles can provide important food sources (e.g., crayfishes, Brewer et al. 2009) for stream-dwelling fishes (Sowa and Rabeni 1995; Brewer 2013a). Second, having channel unit area quantified also allowed me to offset my counts (i.e., events) by the total reach area (exposer) so that model estimates were treated as a rate (fish/m²) during Poisson regression (see analysis). This was important because the length of each reach was determined by the average wetted width and consequently, each reach did not comprise the same surface area. I measured residual pool depth (RPD; 0.05 m) of all pools at each reach by subtracting the downstream riffle crest from the deepest point of the upstream pool (Lisle 1987). I used RPD measurements from each pool at a reach to calculate the average RPD at each reach. RPD is more informative of channel depth independent of water level at the time of sampling (Lisle 1987; Mollenhauer et al. 2013). During each survey, I visually estimated the percentage of instream cover at each reach consisting of both boulders and coarse wood structure. These forms of cover are important to stream fishes (Todd and Rabeni 1989; Fore et al. 2007) and typically did not change in proportion at each reach during summer conditions. I deployed temperature loggers

(HOBO ProV2, Onset, Bourne, MA) in white PVC and cemented them to bedrock located in a run (i.e., areas of well mixed water) at a depth of approximately 0.5 m. I used hourly temperature measurements to calculate thermal metrics relevant to warmwater stream fishes (i.e., MWMT, see *data analysis*).

Snorkel Surveys

I used multiple-pass snorkel surveys to both quantify microhabitat use and enumerate fishes because the conditions in Spavinaw and Spring creeks were ideal for effectively using this approach. Snorkeling is an efficient method for habitat-use and fish-count observations in moderate depths and high water clarity (Dunham et al. 2009; Brewer and Ellersieck 2011). Visibility during snorkel surveys was ideal for counting fish (average horizontal water clarity 6.3 m; range 2.1 – 11.5 m, horizontal distance of fish silhouette, Dunham et al. 2009). I limited snorkel surveys to 2 h after sunrise and 2 h prior to sunset to optimize light conditions for each snorkel pass (Thurow et al. 2012). Each site or reach remained undisturbed for at least 1 h between snorkel passes following recommendations of Brewer and Ellersieck (2011) to allow disturbed fishes to redistribute.

During each snorkel pass, two snorkelers surveyed designated lanes based on habitat complexity. The more-complex lane tended to be narrower and deeper with more cover (Dunham et al. 2009). Observers slowly swam in an upstream direction to minimize fright responses by fishes. When an individual was encountered, observers tallied that individual on a writing cuff. For microhabitat assessments, I placed a weighted flag with unique identification on the substrate at the approximate focal location of the observed fish (Fore et al. 2007; Brewer 2013b; Weaver and Kwak 2013). The snorkel team maintained communication when fishes were observed near lane boundaries to minimize double counting or marking. During reach-scale assessments, I conducted two snorkel passes during each survey to estimate count precision. During microhabitat assessments, I conducted two to three snorkel passes daily over two to four days.

Data Analyses

Microhabitat. – I adjusted my data prior to analyses to improve interpretation of the results and meet generalized linear mixed model assumptions. To create relative temperature values for seasonal comparisons, I calculated the median temperature across all habitat patches during the time period (typically 1 h) that a snorkel pass took place. I subtracted the median value from each individual temperature measurement (i.e., from the temperature of each “habitat patch”) during the same time period. For example, if the median temperature across all thermal patches was 21 °C (minimum – maximum: 19 – 22 °C) for a given snorkel pass, then the resulting values were -2 °C, -1.5 °C, -1 °C, -0.5 °C, 0 °C, 0.5 °C, and 1 °C which corresponded to the original measurements of 19 °C, 19.5 °C, 20 °C, 20.5 °C, 21 °C, 21.5 °C, and 22 °C. Negative values represented cooler patches relative to the median water temperature, whereas positive values reflected warmer patches. I natural-log transformed water depth and velocity due to a right-skewed distribution. I standardized all continuous variables to a mean of zero and a standard deviation of one to improve model interpretation and promote parameter convergence (Gelman and Hill 2007).

I developed a resource selection function (RSF) to determine if Rainbow Trout influenced microhabitat selection patterns of native fishes. An important aspect of developing a RSF is identifying a reasonable ratio of use-available data points (hereafter, sampling ratio). RSFs differ from resource selection probability functions generated from use and non-use study designs because they measure the probability of use with respect to other predicted values rather than a true probability (Manly et al. 2002; Johnson et al. 2006). However, varying sampling ratios may still influence predicted relationships and subsequent ecological inferences under a use-availability framework (e.g., Northrup et al. 2013; Nad’o and Kanuch 2018). For the purpose of my study, I evaluated subsets of availability points to determine a logical sampling ratio that allowed meaningful selection relationships to be interpreted while maintaining reasonable computation time and species comparisons. I determined that a 1:5 sampling ratio would be

appropriate for my analysis (see Appendix A). Consequently, I standardized this ratio across my dataset for each species and by each sampling event.

I used a generalized linear mixed model with a binomial distribution to develop my RSF. These models determine the probability of use (i.e., a fish being present) using a binomial response variable where a vector of habitat measurements associated with fish observations are coded as one, and a vector of measurements associated with habitat availability (i.e., transect) points are coded as zero. Binomial model assumptions are: 1) the response variable is binary, 2) observations are independent of each other, 3) predictor variables have little to no multicollinearity with each other, and 4) each independent variable is linearly related to the log odds.

I fitted a global model with the highest-order interactions I hypothesized to describe how the presence of Rainbow Trout related to seasonal habitat selection by native species while also accounting for nested observations. The global model contained four-way interactions between each microhabitat variable, species, my Rainbow Trout indicator variable, and sampling day (Table 4). This allowed me to determine if Rainbow Trout presence was related to microhabitat shifts and whether these shifts were species specific, habitat specific, and/or seasonally specific. I included species as a factor with six levels reflecting my study species or life stages (i.e., Smallmouth Bass). The number of Rainbow Trout at each site was represented using an indicator variable where high density (≥ 5 fish) was indicated by 1 and < 5 Rainbow Trout was indicated by 0. The limited distribution of Rainbow Trout counts among each of my study sites prevented me from including Rainbow Trout density as a continuous variable. Lastly, I included sampling day as a continuous time variable where values either increased by one each day from zero (December 21) to 182 (June 21) or decreased by one each day from 182 (June 22) to 0 (December 21). I checked correlation among my predictor variables using Pearson's pairwise correlation coefficient (r) and none exceeded $|0.37|$ (Table 5). I also included three grouping factors to account for nested (i.e., non-independent) observations within each sampling day ($N = 44$),

sampling visit (N = 12), and sampling site (N = 4; Wagner et al. 2006; Gelman and Hill 2007).

The global model I fit can be expressed as:

Model: probability (logit) $\sim L(\mu, \sigma^2)$

$$\begin{aligned}
\mu = & \alpha_{0[i]} + \sum_{j=1}^J \alpha_{j[i]} && \textit{intercept and species deflections} \\
& + \beta_{9[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * \sum_{j=1}^J \beta_{1j[i]} X_1 \} && \textit{species deflections by season} \\
& + \beta_{10[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * \sum_{j=1}^J \beta_{2j[i]} X_2 \} && \textit{species deflections by trout interaction} \\
& + \beta_{11[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * [\sum_{j=1}^J \beta_{3j[i]} X_3 + \sum_{j=1}^J \beta_{4j[i]} X_4 + \sum_{j=1}^J \beta_{5j[i]} X_5 + \sum_{j=1}^J \beta_{6j[i]} X_6 + \\
& \sum_{j=1}^J \beta_{7j[i]} X_7 + \sum_{j=1}^J \beta_{8j[i]} X_8] \} && \textit{species deflections by habitat interaction} \\
& + \beta_{12[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * \sum_{j=1}^J \beta_{1j[i]} X_1 * \sum_{j=1}^J \beta_{2j[i]} X_2 \} && \textit{species deflections by season and trout} \\
& && \textit{interaction} \\
& + \beta_{13[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * \sum_{j=1}^J \beta_{1j[i]} X_1 * [\sum_{j=1}^J \beta_{3j[i]} X_3 + \sum_{j=1}^J \beta_{4j[i]} X_4 + \sum_{j=1}^J \beta_{5j[i]} X_5 + \\
& \sum_{j=1}^J \beta_{6j[i]} X_6 + \sum_{j=1}^J \beta_{7j[i]} X_7 + \sum_{j=1}^J \beta_{8j[i]} X_8] \} && \textit{species deflections by habitat and season} \\
& && \textit{interaction} \\
& + \beta_{14[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * \sum_{j=1}^J \beta_{2j[i]} X_2 * [\sum_{j=1}^J \beta_{3j[i]} X_3 + \sum_{j=1}^J \beta_{4j[i]} X_4 + \sum_{j=1}^J \beta_{5j[i]} X_5 + \\
& \sum_{j=1}^J \beta_{6j[i]} X_6 + \sum_{j=1}^J \beta_{7j[i]} X_7 + \sum_{j=1}^J \beta_{8j[i]} X_8] \} && \textit{species deflection by habitat and trout} \\
& && \textit{interaction} \\
& + \beta_{15[i]} \{ \sum_{j=1}^J \alpha_{j[i]} * \sum_{j=1}^J \beta_{1j[i]} X_1 * \sum_{j=1}^J \beta_{2j[i]} X_2 * [\sum_{j=1}^J \beta_{3j[i]} X_3 + \sum_{j=1}^J \beta_{4j[i]} X_4 + \\
& \sum_{j=1}^J \beta_{5j[i]} X_5 + \sum_{j=1}^J \beta_{6j[i]} X_6 + \sum_{j=1}^J \beta_{7j[i]} X_7 + \sum_{j=1}^J \beta_{8j[i]} X_8] \} && \textit{species deflections by} \\
& && \textit{season, habitat, and trout interaction} \\
& + \omega_d + P_z + \varepsilon_r && \textit{grouping factors} \\
\alpha_{0[i]} \sim & N(0, \sigma^2), \text{ for } k = 1, 2, \dots, I \\
\alpha_j \sim & N(0, \sigma^2), \text{ for } j = 1, 2, \dots, J \\
\beta_{1j} - \beta_{sj} \sim & N(0, \sigma^2), \text{ for } j = 1, 2, \dots, J
\end{aligned}$$

$\omega_d \sim N(0, \sigma_\omega^2)$, for $k = 1, 2, \dots, D$ (*day*)

$P_z \sim N(0, \sigma_\omega^2)$, for $z = 1, 2, \dots, Z$ (*visit*)

$\varepsilon_r \sim N(0, \sigma_\varepsilon^2)$, for $r = 1, 2, \dots, R$ (*site*)

Where i are observations $1, 2, \dots, I$, j is species $1, 2, \dots, J$, α_0 is the grand intercept, α_j are species j deflections from the group-mean intercept, $\beta_{1j} - \beta_{8j}$ are the species j deflections from the group-mean predictor variable coefficient (all main effects), $\beta_{9j} - \beta_{15j}$ are the species-specific deflections from interactions between main effects, $X_1 = \text{time}$, $X_2 = \text{trout}$ (*factor with two levels - yes/no*), $X_3 = \text{depth}$ (*continuous*), $X_4 = \text{quadratic depth}$ (*continuous*), $X_5 = \text{velocity}$ (*continuous*), $X_6 = \text{temperature}$ (*continuous*), $X_7 = \text{substrate}$ (*continuous*), $X_8 = \text{cover}$ (*factor with two levels - yes/no*).

I fitted the model using program JAGS (Plummer 2003) via the package jagsUI (Kellner 2018) in the statistical software R (version 3.4.2, R Core Team 2017). I used broad normal priors for all model parameters and vague gamma priors for each associated standard deviation (Kruschke 2015). I estimated each posterior distribution using a Markov chain Monte Carlo method with 10,000 burn-in iterations, a thin rate of 10, and 50,000 final iterations. I assessed parameter convergence using the Brooks-Gelman-Rubin statistic (\hat{R} ; Gelman and Rubin 1992) where values ≤ 1.1 indicate convergence.

After fitting my global (i.e., most complex) model, I selected my final model using a backward-selection process to retain only important predictor variables and interactions (Fore et al. 2007; Mollenhauer et al. 2019). I assessed the importance of interactions and main effects using 95% highest density intervals (HDIs), beginning with terms for the highest-order interactions. I retained interactions if at least one of the HDIs for a species-specific deflection did not overlap 0. I also eliminated interactions that came with 0.01 of overlapping zero to account for differences in estimates after rerunning the model (i.e., I was more conservative in my retention of interactions). In cases where only the group mean (i.e., species mean) for an interaction was deemed important by my HDI criteria, I eliminated the species-specific

deflections but retained the interaction with the group mean. I eliminated all four-way interactions that overlapped zero in the same step. After eliminating four-way interactions, I re-fitted the model and eliminated three-way interactions using the same approach. The process was repeated for two-way interactions and main effects (unless they were included in an interaction). I retained all grouping factors throughout model selection and in the final model.

Reach-scale. – I made several adjustments and transformations to my data prior to analysis. I used hourly temperature data collected from each reach to calculate the maximum weekly maximum temperature (MWMT) for each survey. MWMT was calculated by averaging the maximum daily water temperature across the 7 days prior to each survey. The MWMT is better suited for characterizing the relationship between thermal patterns and fish count data because it can be considered a measure of both chronic and acute thermal stress. Additionally, MWMT captures diel fluctuation of water temperature in warmwater streams better than the thermal metric maximum weekly average temperature (Shelton et al. 2018). In some cases, I did not have temperature data for the week prior to a survey. In 2018, all temperature loggers were deployed during the first survey (i.e., not 7 days prior). In these cases, I used the average of the MWMT values for the other surveys within the same reach. Similar to Mollenhauer et al. (2019), I classified groundwater contribution using an indicator variable where “losing” were reaches with no change or loss of discharge and “gaining” were reaches with discharge increase. Losing reaches were more common than gaining reaches and consequently, served as the reference category. Reaches without seepage measurements due to equipment malfunctions were classified at the reference level (i.e., losing). I used channel unit measurements to calculate riffle area (m^2) and total area (m^2) of each reach. I used these measurements to determine the percent riffle at each site (percent riffle = riffle area/total area). I log transformed total reach area to serve as a count offset for reach area sampled in the model (Gelman and Hill 2007). I also divided the Rainbow Trout count during each survey by the log-transformed area to account for count

differences in area sampled. I added a constant of 1 and log-transformed percent riffle and Rainbow Trout predictor variables due to right-skewed distributions. I standardized RPD, percent cover, percent riffle, and MWMT to a mean of zero and standard deviation of one to improve model interpretation. I did not standardize the Rainbow Trout predictor variable so model estimates were interpreted at reference (i.e., no trout) conditions. Lastly, I calculated the Pearson's pairwise correlation coefficient (r) for all predictor variables and it did not exceed $|0.39|$ for any combination (Table 6).

I built a global model (i.e., a starting model for backward selection process) using a generalized linear mixed model with a log link and Poisson distribution. The model allowed me to determine how relationships between native fishes and habitat variables related to Rainbow Trout density. The assumptions of Poisson regression are: 1) the response variable is count data, 2) counts must be positive integers, 3) the response variable must follow a Poisson distribution, and 4) each observation is independent. To account for the uncertainty in counts, I used count data from each snorkel pass and nested these data within each survey (i.e., two snorkel passes per survey (Barker et al. 2018)). In addition, I included a random effect for each reach to account for differences in reaches that related to factors not measured (e.g., land use). I also included the model offset (log area) to account for correlation between counts and reach size (Gelman and Hill 2007). Consequently, the response variable was scaled to represent fish/m². For simplicity, I refer to the response variable as “density” hereafter. I fitted the global model with an interaction between each species (i.e., factor) and each predictor variable. I chose Redspot Chub to serve as the reference species for all interactive effects. Redspot Chub raw counts (unadjusted for area) were highest relative to other species during almost all of my surveys. My hypothesis was that Redspot Chub was a “generalist” species in Spavinaw and Spring Creek, thereby allowing identification of stronger habitat selection patterns for other species. The complex model contained six predictor variables and interactions with each species/life stage (Table 4). The model contained 42 terms and can be expressed as:

Model: probability (log) $\sim P(\mu, \sigma^2)$

$$\begin{aligned} \log(\mu_i) = & \log(t)_i + \sum_{j=1}^J \alpha_{1j[i]} + \beta_{1[i]}X_1 + \beta_{2[i]}X_2 + \beta_{3[i]}X_3 + \beta_{4[i]}X_4 + \beta_{5[i]}X_5 + \beta_{6[i]}X_6 \\ & + \sum_{j=1}^J \alpha_{1j[i]} * [\sum_{j=1}^J \beta_{7j[i]}X_1 + \sum_{j=1}^J \beta_{8j[i]}X_2 + \sum_{j=1}^J \beta_{9j[i]}X_3 \\ & + \sum_{j=1}^J \beta_{10j[i]}X_4 + \sum_{j=1}^J \beta_{11j[i]}X_5 + \sum_{j=1}^J \beta_{12j[i]}X_6] + \rho_k + \gamma_l \end{aligned}$$

$\alpha_j \sim N(0, \sigma^2)$, for $j = 1, 2, \dots, J$

$\beta_{1j} - \beta_{xj} \sim N(0, \sigma^2)$, for $j = 1, 2, \dots, J$

$\rho_k \sim N(0, \sigma_\omega^2)$, for $k = 1, 2, \dots, K$ (survey)

$\gamma_l \sim N(0, \sigma_\omega^2)$, for $z = 1, 2, \dots, L$ (reach)

where i are counts, t is the reach area (m²), α are species j specific intercepts, β_1 through β_6 are slopes associated with habitat variables X_1 through X_6 (RPD, trout, riffle, cover, discharge, and temperature), β_7 through β_{12} are species-specific interactive slopes with habitat variables X_1 through X_6 , and ρ and γ are grouping factors for survey k , and reach l , respectively.

I fitted the model using the package lme4 (Bates et al 2015) in the statistical software R (version 3.4.2, R Core Team 2017). After fitting my complex model, I used a two-step backward-selection process to retain only important habitat variables and interactions. I assessed variable importance using 95% confidence intervals (CIs). I estimated CIs by bootstrapping model coefficients and standard error using the “bootMer” function in the R package lme4 ($n = 1,000$ simulations). At the first step of the backward selection, I retained all two-way interaction terms with confidence intervals that did not overlap zero and all associated lower-order main effects. I repeated this process and eliminated main effects with CIs that overlapped zero and were not associated with retained higher-order interactions.

I assessed model fit and residual error using a combination of diagnostic tests. I calculated both the conditional R^2 (variation explained by both predictor variables and random

intercepts) and marginal R^2 (variation explained by predictor variables; Nakagawa and Schielzeth 2013) for my final model using the R package MuMIn (Barton 2018). I assessed the residual error by plotting the standardized residuals of the final model against the expected values (Gelman and Hill 2007).

RESULTS

Microhabitat. – Habitat availability was variable among my sites, surveys and differed seasonally (Appendix B, Table 1). The maximum depth differed between sites on Spavinaw Creek and Spring Creek. The maximum depth on Spring Creek was greater than sites on Spavinaw Creek, regardless of season. The greatest maximum recorded depth was over 5 m during the last survey of Spring Creek (June 2019). Velocity was lower during winter and summer and higher during spring surveys. Substrate was generally comparable among seasons, streams, and sites where size “4” was most common. As expected, ambient water temperatures differed among surveys, but the deviation in temperature was comparable between surveys conducted during the same season. A greater range of temperature deviations were encountered during surveys conducted in the spring and summer.

I conducted 12 microhabitat surveys across my four fixed sites during 2017 – 2019. Nine surveys served as references (i.e., no Rainbow Trout present) and three surveys were conducted with Rainbow Trout present. After adjusting to the correct use:availability ratio (Appendix A), the final data set contained use observations for 540 Creek Chub, 992 Redhorse, 492 Northern Hogsucker, 1,434 Redspot Chub, 1,032 Age-1+ Smallmouth Bass, and 1,168 Juvenile Smallmouth Bass. Using a 1:5 ratio of use to availability points, the final dataset contained 33,752 total observations.

I recorded microhabitat observations for 278 Rainbow Trout. Microhabitat data were not collected on Rainbow Trout during one survey (i.e., Cisco 1, December 2017) because of high densities of Rainbow Trout (i.e., a focal location for each fish could not be determined). Raw data

indicated Rainbow Trout used shallow to moderate depths (average \pm SD: 1.00 ± 0.25 m), moderate velocities (0.4 ± 0.3 m/s), average available substrate (4 ± 1) and were associated with cover 23% of the time. During seasonal extremes, use of discrete thermal patches (temperature deviations) appeared minimal (winter: 0.0 ± 0.0 °C) and summer (0.0 ± 1.0 °C). However, these data represent only the use of habitat resources by Rainbow Trout and inference on habitat selection cannot be made on use data alone. Microhabitat use data for Rainbow Trout were not included in my microhabitat selection model because the species was represented as a factored predictor (i.e., trout or no trout) for other species; thus, it would have been inappropriate to model selection by Rainbow Trout habitat selection under trout vs no trout conditions.

The final model retained all of the highest-order interactions and subsequent lower-order interactions and main effects. The final model contained 224 terms (six species/life stage intercepts and 27 habitat interactions for each intercept, plus group mean and error estimates for each beta, Appendix B, Table 2). However, not all species-specific deflections were important for each interaction; thus, some relationships between native species, habitat, and the presence of Rainbow Trout were time specific whereas others were independent of time (Table 7). All \hat{R} values were less than 1.1, indicating successful model convergence (Gelman and Rubin 1992).

My model results indicate reach-scale presence of Rainbow Trout was significantly related to microhabitat selection for all six species and life stages. For all species and life stages, habitat selection of at least one variable changed in the presence of Rainbow Trout over time (Table 7). Depth was related to patch selection by all native fishes studied and had relationships with both time (i.e., season) and the presence of Rainbow Trout. For all species, I retained significant interactions with depth and time under reference conditions (i.e., no trout) in the final model. Juvenile Smallmouth Bass, Redspot Chub and Creek Chub were related to shallow and moderate depths (1 – 2 m) during winter, and these relationships did not change over time. Age-1+ Smallmouth Bass, Northern Hogsucker, and Redhorse selected greater depths during winter (Figure 3). As the time of year progressed towards summer, age-1+ Smallmouth Bass shifted to

having the greatest relationship with moderate depths (~ 2 m, Figure 4). Rainbow Trout presence was significantly related to changes in depth selection by Creek Chub, Redspot Chub, and age-1+ Smallmouth Bass and the relationships were time specific (Figures 3 and 4). The relationship between Rainbow Trout, depth selection and native fishes was strongest during summer. For example, there was no relation between depth selection of age-1+ Smallmouth Bass and Rainbow Trout during winter but an apparent relationship between Rainbow Trout and continued use of deeper habitats by age-1+ Smallmouth Bass during summer (Figure 4).

The relationship between native species and velocity was also related to Rainbow Trout presence and was a function of time. Under reference conditions (i.e., no Rainbow Trout), the interaction between velocity and time was significant for all species/life stages (Table 7). In general, velocity selection was minimal in winter (i.e., slope of the line was less steep, Figure 5). As the time of year progressed towards summer, the strength of the relationship between velocity and several species increased (Figure 6). For example, Redhorse selected higher velocity habitats whereas Creek Chub, Northern Hogsucker and juvenile Smallmouth Bass selected lower velocity microhabitats. The interaction between Rainbow Trout presence and time was related to all species except the Northern Hogsucker. In winter, Creek Chub shifted to lower-velocity habitats in the presence of Rainbow Trout whereas Redhorse shifted to higher-velocity habitats (Figure 5). Redhorse, Redspot Chub, and age-1+ Smallmouth Bass shifted to lower-velocity habitats during summer when Rainbow Trout were present (i.e., Figure 6).

Substrate and cover were also important predictors of microhabitat selection. Substrate selection by species was time specific except for selection by Redspot Chub. In general, substrate selection was greater with coarser substrates (Figure 7). However, Creek Chub and Redhorse selected finer substrates. Substrate selection by Creek Chub, Northern Hogsucker, and juvenile Smallmouth Bass depended on the presence of Rainbow Trout, but the magnitude of the effect (i.e., change in slope) was relatively small compared to selection of other microhabitat variables (Figure 7). Creek Chub, Northern Hogsucker, Redspot Chub, age-1+ Smallmouth Bass and

juvenile Smallmouth Bass had significant relationships with cover. All species were more likely to use cover over no cover except for Northern Hogsucker (Table 8). All five species used cover more when Rainbow Trout were present relative to reference levels (Table 8). The shift was greatest for juvenile Smallmouth Bass which were 2 times as likely to use cover under reference conditions and 8.5 times as likely to use cover when Rainbow Trout were present.

Temperature selection was variable among species and depended on the presence of Rainbow Trout. Significant interactions between temperature, time, and Rainbow Trout presence were related to Redspot Chub and juvenile Smallmouth Bass. Without Rainbow Trout present, both species selected warmer water in the winter and cooler than average water in the summer (Figure 8). With Rainbow Trout present, juvenile Smallmouth Bass selected cooler patches in the winter. Both Redspot Chub and juvenile Smallmouth Bass selected warmer microhabitat patches during the summer when Rainbow Trout were present (Figure 8). Redhorse and age-1+ Smallmouth Bass selected cooler patches, regardless of time. Creek Chub and Northern Hogsucker were not significantly associated with temperature.

Reach-scale surveys. – I conducted 82 reach-scale surveys over 18 reaches during summer 2018 and 2019. More surveys were conducted in 2018 than 2019 due to high water (Table 3). Habitat availability was variable among reaches (Table 4). The average RPD across reaches was 1.50 m and the maximum RPD was 2.95 m. Percent riffle represented, on average, 10% of each reach (range 0% to 36%). MWMT ranged 20.5 °C to 26.2 °C among reaches. Percent cover at each site was, on average, 28% but was as high as 50% at some reaches.

There was considerable variation in fish counts between species and among reaches. Redspot Chub was the most common native species (average snorkel pass count \pm SD = 82 ± 41). Creek Chub and Northern Hogsucker were least common (20 ± 19 ; 20 ± 15 , respectively). Smallmouth Bass counts were higher for age-1+ (65 ± 45) compared to juveniles (26 ± 14).

Redhorse counts were the most variable among my species counts (46 ± 40). Counts of Rainbow Trout ranged 0 to 74 across my study reaches.

My final model relating fish density to reach-scale factors showed proper fit and model structure and explained reasonable variation in my data. The residual plot based on my final model indicated adequate model structure (Figure 9) and overdispersion was minimal (Pearson $\hat{c} = 1.11$). The amount of variation explained by my predictor variables was reasonable (marginal $R^2 = 0.48$). The inclusion of survey and reach as random effects accounted for unexplained variation and improved model fit (condition $R^2 = 0.96$).

My final model relating variation in fish density to reach-scale variables had 25 terms (Table 8). As expected, there were density differences between species that were independent of habitat variables and were retained in my model. Some habitat relationships were common to all species, whereas others were species specific (Figure 10). All species were positively correlated with increasing RPD. Relative to reference conditions, increasing percent riffle was related to decreasing densities of Creek Chub, Northern Hogsucker, and Redhorse. Though not statistically significant, Redspot Chub and juvenile Smallmouth Bass densities increased with percent riffle. The MWMT was significantly related to both Creek Chub (negative) and Redhorse densities (positive) relative to the reference relationship. Lastly, Creek Chub were significantly related to increasing Rainbow Trout density.

DISCUSSION

Although inferring competition from field-based studies is difficult (Fausch 1988; Thibault and Dodson 2013), my results indicate microhabitat shifts by several warmwater fishes in the presence of introduced Rainbow Trout. Behavioral adjustments by native fishes would be more likely observed at the microhabitat scale if either patch resources are limited (Baltz et al. 1991; Brown and Moyle 1991) or species aggressions prevent use of energetically-profitable stream habitats (Mason and Chapman 1965; Fausch 1984; Hitt et al. 2017). For example, native

Mottled Sculpin *Cottus bairdi* reduced time spent in refuge habitat in the presence of non-native Round Gobie *Neogobius melanostomus* (Dubs and Corkum 1996). In general, shifts in microhabitat by native fishes related to salmonids have been thoroughly examined within coldwater fishes (Baxter et al. 2004; Hasegawa and Maekawa 2006; Leunda 2010; Hitt et al. 2017), but my findings build on our knowledge of potential interactions in warmwater systems (but see Blinn et al. 1993; Penaluna et al. 2009; Weaver and Kwak 2013; Elkins et al. 2019).

Microhabitat shifts by native fishes in the presence of Rainbow Trout were species and often season specific. Shifts in depth selection in response to Rainbow Trout were most apparent for age-1+ Smallmouth Bass and Redspot Chub during summer. Both species selected a greater range of depths when Rainbow Trout were present. Displacement from important foraging habitat (e.g., Sabo et al. 1996; Piccolo et al. 2008) and reproductive habitat during warmer periods (Maurakis et al. 1991) could be problematic for both species, particularly following harsh cold-weather periods (Suski and Ridgway 2009). Shifts to lower-velocity habitat by Redspot Chub, Redhorse, and age-1+ Smallmouth Bass during the summer may reflect displacement from ideal foraging habitat. For example, Redspot Chub and sub adult Smallmouth Bass drift feed or seek prey in riffle habitats that are typified by higher current velocities (Simonson and Swenson 1990; Orth and Newcomb 2002; Miller and Robinson 2004). Rainbow Trout also seek higher-velocity habitats to drift feed (O'Brien and Showalter 1993; Guensch et al. 2001); thus, overlap in feeding position may have resulted in interspecific competition (Fausch 1984; Fausch and White 1986). I also found Rainbow Trout related to thermal patch shifts by juvenile Smallmouth Bass and Redspot Chub in the two harshest seasons (i.e., summer and winter). Small or juvenile fish may continue foraging during winter months to maintain baseline activity rates (Shuter et al. 2012; Suski and Ridgway 2009); thus, winter selection of warmer thermal patches may have been energetically profitable (Peterson and Rabeni 1996). Redspot Chub and juvenile Smallmouth Bass selected warmer patches during summer in the presence of trout. Use of warmer water may result in decreased growth (Whitledge et al. 2006). Use of thermal refuge is common by salmonid

species during warmer periods (Torgersen et al. 1999; Ebersole et al. 2003a; Hitt et al. 2017); thus, the availability of cool-water patches may be limiting to both non-native trout, juvenile Smallmouth Bass, and Redspot Chub. Examining short-term growth responses by these species when occupying the selected thermal environments would be necessary to confirm the hypothesized mechanisms.

Shifts in cover selection by native fishes in the presence of trout may relate to perceived predation risk. Rainbow Trout alter cover selection by several species including native salmonids (e.g., Brook Trout, Thibault and Dodson 2013) and Little Colorado Spinedace *Lepidomeda vittata* (Robinson et al. 2003). In some instances, naturalized Rainbow Trout populations have become conditioned to stream environments (Thibault and Dodson 2013) and learn the tradeoffs of residing in or defending certain habitats (Grant 1990; Johnson et al. 1999). In these instances, native species may be displaced from using cover as a resource (e.g., Robinson et al. 2003). However, Rainbow Trout may also be perceived as a threat by native species and cause them to tightly associate with cover (Tabor and Wurtsbaugh 1991; Alvarez and Nicieza 2003).

Unlike cover, shifts in substrate selection in response to Rainbow Trout presence was weak and likely not ecologically significant; however, substrate selection by native species was evident without trout present. Given the availability of different substrates at the microhabitat scale (Appendix B, Table 1), it is not surprising Rainbow Trout did not substantially relate to substrate selection patterns by native species. Across seasons, use of coarse substrate may provide velocity refuge to some fishes (e.g., Chubs, Lobb and Orth 1988; salmonids, Baltz et al. 1991; and Smallmouth Bass, Orth and Newcomb 2002; Wolf et al. 2019) or serve as cover (juvenile Smallmouth Bass, Sabo and Orth 1994). Alternately, Redhorse were associated with fine substrates where feeding efficiency may have been improved (Kwak and Skelly 1992).

Interestingly, temperature selection was not seasonally specific for some species. Creek Chub, Redhorse, Northern Hogsucker, and adult Smallmouth Bass each selected cooler patches regardless of season. It is possible that during cold periods, species are more strongly associated

with other microhabitat factors (see Wolf et al. 2019). Selection of thermal conditions are evident during winter by some warmwater fishes (Peterson and Rabeni 1996; Westhoff et al. 2016) and may be a function of availability or scale; thus, selection may be restricted to years with extreme temperatures or simply occur at coarser spatial scales than I examined.

In some instances, the strong selection patterns observed may relate to microhabitat availability differences at locations with or without trout. The most extreme example of availability discrepancies relates to differences in available water depths at sites with and without Rainbow Trout. The greatest depth encountered during my study was approximately 5 m, whereas the maximum depth at sites containing Rainbow Trout was only 2 m. Though grouping factors can help account for site-specific differences (Wagner et al. 2006; Gelman and Hill 2007), the uncertainty around predictions beyond encountered values (e.g., predictions of depth use beyond 2 m with trout present; Appendix B, Table 2) should be considered when interpreting possible interactions between trout and native species in the field. Although the results represent field observations, uncertainty increases in predictions associated with deeper water.

The same stocking rate of 1,360 kg per stocking occasion was used throughout my study, and it is unknown how habitat selection might differ depending on different stocking densities. Reported stocking density or rates (e.g., trout/area or trout/time) are often variable (e.g., 200 trout/ha, Hartman et. 2012; 4,000/month, Flowers et al. 2019) and often depend on available fish, season of stocking, and the management objective (Miko et al. 1995; Wiley 2006). I cannot speculate on how changing stocked numbers of Rainbow Trout would alter microhabitat selection by native species in Spavinaw Creek. However, habitat selection interactions may relate to fish density (e.g., Urabe and Nakano 1999) and higher densities of non-native species often related to greater interactions with native species (e.g., Robison et al. 2003). The experimental manipulation and controlled conditions required to elicit a clear density-driven response are typically reserved for lab studies (Fausch 1988), and would be difficult or impossible to achieve during my field

efforts. It would be beneficial if future efforts in a laboratory setting could examine resource selection in response to altered densities of non-native fishes.

In addition to examining behavioral responses to an introduced predatory fish, my findings of seasonal microhabitat shifts not related to trout presence are informative to conservation and management actions. My findings build on others who report seasonal shifts in microhabitat for a variety of warmwater, stream-dwelling species (e.g., Smallmouth Bass, Todd and Rabeni 1989; Wolf et al. 2019), Redhorse (Grabowski and Isely 2006; Butler and Wahl 2017) and minnows (e.g., Santos et al. 2004; Lapointe et al. 2007). An understanding of resource use across multiple seasons is needed to ensure critical habitats are protected throughout the year. Broadly, my results suggest maintaining heterogeneous habitat in streams would ensure key microhabitats were available across seasons. For example, natural (Poff et al. 1997) and semi-natural (Poff and Zimmerman 2010) flows maintain channel-unit diversity that provide heterogeneous depth, velocity, and substrate resources to stream fishes (Gordon et al. 2004; Brewer 2013a). More specifically, seasonal temperature selection by some species highlight the importance of groundwater interactions (Peterson and Rabeni 1996; Chu et al. 2008; Middaugh et al. 2016) and riparian shading (Ebersole et al. 2003b; Whitley et al. 2006) at fine spatial scales. Groundwater restoration is becoming more common as temperatures warm due to climate and land-use changes (Hancock 2002; Anderson et al. 2010). Protecting these critical resources would be beneficial given the cost associated with restoration of these habitats. Protection of the habitat elements that benefit microhabitat refugia also relate to maintenance of factors important to native fishes at the reach scale.

Changes in fish densities at the reach scale may be related to microhabitat-scale shifts in selection (Robson and Barmuta 1998; Lamouroux and Cattaneo 2006) but may take longer to realize because of differences in temporal response (Weins 1989). Additionally, the inexperience of introduced fish and the time needed to locate habitats further from the stocking site may also contribute to temporal differences between microhabitat and reach scale relationships. For

example, percent riffle may relate to high prey densities (e.g., Brewer et al. 2009) but prey availability might not be realized for many years by a novel predator due to lack of experience (i.e., spatial learning, Braithwaite and Salvanes 2005) or an abundance of food at the time of stocking (Beauchamp 1990). Likewise, Rainbow Trout in novel environments explore habitat patches and their knowledge of patches increases with time. A time lag between fish persistence in an environment and ability to hone in on habitats further from the stocking area are expected (e.g., advantage of resident fish in intra-salmonid studies, Glova and Field-Dodgson 1995; less dispersal from hatchery fish due to inexperience with social structure, Weber and Fausch 2003). Interannual variation in densities are also expected to be high and thus, many years of data may be necessary to examine questions at coarser spatial scales (Wiens 1989).

Increasing RPD is often positively associated with stream fish density including non-game species in headwater streams (e.g., several dace and chub species, Danehy et al. 1998), salmonids (Mollenhauer et al. 2013), and fish assemblages in the Great Plains (Rowe et al. 2009). All of the native fishes I examined were positively associated with RPD. At finer spatial scales (e.g., microhabitat), depth may serve as cover for stream-dwelling fishes (Fore et al. 2007; Wolf et al. 2019); thus, greater availability of deep habitats may have attracted individuals to these reaches. Greater RPD may also be correlated with other habitat elements (e.g., woody debris and limited siltation, Shields et al. 1994) including hyporheic flow (May and Lee 2004).

My non-significant relationships between Redspot Chub and both life stages of Smallmouth Bass and percent riffle were surprising but may relate availability due to the length of my reaches. Riffles provide habitat for many fish-prey items such as crayfish (e.g., for Smallmouth Bass, Sowa and Rabeni 1995; Brewer 2013a). Most of my reaches had relatively low percentage of riffle habitat (mean \pm SD: 10.5 ± 7.7) compared to other studies that used longer reach lengths and reported greater riffle percentages (e.g., reaches with low pool percentage (~20%) corresponded to high riffle percentage, Brewer 2013a). It is possible that low percent riffle across my sites would prevent the establishment of a relationship. However, the streams I

sampled are also located at the western edge of the Ozark Highlands; thus, availability of riffles may simply be lower. Further, my study examined the Neosho subspecies of Smallmouth Bass whereas previous reports examined interior Highland intergrades (Brewer 2013a). The Neosho subspecies of Smallmouth Bass may have underlying ecological differences when compared to the nominal subspecies or intergrades (Brewer and Long 2015).

Creek Chub, Northern Hogsucker, and Redhorse were associated with reaches with limited riffle habitat. Adults of these three species may not benefit from riffles as a source of food like other species/life stages. The Northern Hogsucker and several Redhorse species including the Black and Golden Redhorse feed on detritus, algae, and terrestrial insects that settle in pools (Kwak et al. 1992; Miller and Robinson 2004). However, feeding juveniles target benthic invertebrates typically associated with riffle habitats (Reid 2009); thus, riffle habitat may be important to young of year and other juvenile life stages that were not the focus of my study.

Although the mechanisms are unclear, Creek Chub was the only native fish where density was positively related to Rainbow Trout density. Both Creek Chub and Rainbow Trout were associated with MWMT (Table 6). I did not attempt to characterize habitat selection by Rainbow Trout, but salmonids commonly select coolwater resources at multiple spatial scales (e.g., Torgersen et al. 1999; Ebersole et al. 2003a; Shelton et al. 2018). Consequently, the selection of coolwater at the reach scale likely led to the positive relationship between Creek Chub and Rainbow Trout density.

The majority of species I examined had positive relationships with cooler water temperatures except Redhorse. Creek Chub were significantly related to cooler MWMT and have the lowest optimal growth temperature (21 °C, Moshenko and Gee 1973). Creek Chub do not grow at temperatures above 24 °C (Miller 1964; Moshenko and Gee 1973); thus, warmer reaches were likely not suitable for summer growth. Other species including Smallmouth Bass also have optimal growth thresholds below average temperatures encountered at my reaches (22 °C, Shuter and Post 1990; Whitley et al. 2002). Redhorse were very weakly associated with increasing

MWMT suggesting the relationship is either minor compared to other habitat factors or may not be ecologically significant. Other Redhorse species (e.g., Greater Redhorse *Moxostoma valenciennesi*, Bunt and Cooke 2001; Robust Redhorse *Moxostoma robustum*, Grabowski et al. 2016) are mobile throughout the year but have seasonally important habitats (e.g., spawning habitat, Curry and Spacie 1984). Redhorse in Spavinaw and Spring creeks may also be highly mobile (Zentner, *unpublished data*); thus, their apparent relationship with warmer sites may have been an artifact of movements lower in the watershed where there is less groundwater contribution.

Management implications. – If conservation of native species is a management objective, it would be beneficial for agencies to consider the potential implications of the microhabitat shifts observed during my study. I found that both sport fish (e.g., Smallmouth Bass and Redhorse) and non-game species of conservation concern (e.g., Redspot Chub) seasonally shifted their selection of depth, velocity, cover and temperature following the addition of Rainbow Trout to Spavinaw Creek. Selection of microhabitat reflects energetic benefits (Mittelbach 1981) and predator avoidance (Shoup et al. 2003) at the individual level but may have population-level consequences over a greater temporal scale (Grossman and Ratajczack 1998). The relationship between shifts in depth and velocity selection and Rainbow Trout may result in decreased feeding efficiency for native species (Crowder 1984; Sabo et al. 1996; Piccolo et al. 2008) and exclusion from key spawning habitats (Maurakis et al. 1991). Additionally, shifts to greater cover use may inhibit the ability of native species to forage successfully (Pritcher et al. 1988) and decrease overall fitness thereby reducing survival (e.g., over winter, Suski and Ridgway 2009). These interactions may become more alarming over time as Rainbow Trout that successfully over summer (see Chapter 3) may become more conditioned to the stream environment (Mesa 1991; Glova and Field-Dodgson 1995); thus, becoming better competitors with native species over habitat resources.

Several possible strategies may be considered for future stocking of Rainbow Trout in

Spavinaw Creek. Given the high summer survival rates of stocked Rainbow Trout and fidelity to the stocking location (see Chapter 3), one possibility is to stop stocking or reduce stocking intervals until laboratory studies can be completed and longer-term data collected. Limiting stocking to the current location may be helpful in reducing effects across stream reaches while monitoring is continued. However, even with continued stocking at a single site, annual survival (Chapter 3) may increase dispersal of Rainbow Trout over time and increase the density of Rainbow Trout in other portions of the catchment. A third consideration is to limit stocking to autumn (November), given microhabitat shifts are much more substantial during the warmer, spring and summer conditions. However, my study was limited to a single year post stocking and differing seasonal conditions (e.g., a harsher winter) may also have important implications for the response of native fish at the microhabitat scale. Continued sampling will be important if stocking continues, particularly at the reach scale where the effects from stocking may not be realized for several years or only be evident under specific conditions (e.g., drought years, Elliot 2006).

TABLES

Table 1. Study species chosen to evaluate changes in microhabitat and reach-scale habitat use. Species were chosen because of suspected habitat overlap with introduced Rainbow Trout and conservation status within each state. The Oklahoma Department of Wildlife Conservation lists species from Tier I to Tier III with Tier I having the highest conservation priority. The Arkansas Game and Fish Commission lists species from S1 to S5 with S1 having the highest conservation priority.

Common Name	Scientific Name	Age and identification	Source	Listing status
Smallmouth Bass	<i>Micropterus dolomieu velox</i>	Juvenile: 35 mm – 85 mm, tri-colored tail	Brewer and Ellersieck (2011)	Stable
Smallmouth Bass	<i>Micropterus dolomieu velox</i>	1+: > 85 mm, olive-colored body with vertical bands, loss of tri-colored tail	Robison and Buchanan (1988); Pflieger (1997)	Stable
Creek Chub	<i>Semotilus atromaculatus</i>	Adult: > 100 mm, dark spot at base of dorsal fin, dusky stripe along midline	Robison and Buchanan (1988); Pflieger (1997)	Stable

Redspot Chub	<i>Nocomis asper</i>	Adult: > 100 mm, red spot behind head is developed in both mature males and females	Robison and Buchanan (1988); Pflieger (1997)	Tier II* S3*
Northern Hogsucker	<i>Hypentelium nigricans</i>	Adult: > 200 mm, Sucker-like body characterized by dark saddles on body	Robison and Buchanan (1988); Pflieger (1997)	Stable
Redhorse**	<i>Moxostoma spp.</i>	Adult: > 200 mm, easily differentiated from Northern Hogsucker with by of mottling on body	Robison and Buchanan (1988); Pflieger (1997)	Tier III*

*Status under Oklahoma Department of Wildlife Conservation Comprehensive Wildlife Conservation Strategy
wildlifedepartment.com/cwcs/ApprovedOKCWCSAppendices.pdf

•Status under the Arkansas Game and Fish Commission Arkansas Wildlife Action Plan
https://www.wildlifearkansas.com/materials/2017/02%20Section%201_Wildlife%20Action%20Plan.pdf

**Listing status refers to Shorthead Redhorse *Moxostoma macrolepidotum*

Table 2. Microhabitat sampling events by season and site. Condition refers to the presence or absence of Rainbow Trout at the time of sampling.

Latitude (Lat) and longitude (Long) are in NAD83 format.

Season	Site	Dates	Condition	(Lat)	(Long)
Autumn	Middle Spavinaw	10/20/2017 – 10/24/2017	Pre-stock (no trout)	36.326227	-94.670346
Winter	Upper Spavinaw	12/16/2017 – 12/19/2017	Previously stocked trout*	36.344460	-94.576210
	Spring	1/8/2018 – 1/11/2018	Reference (no trout)	36.089339	-95.027646
Spring	Spring	5/18/2018 – 5/21/2018	Reference (no trout)	36.089339	-95.027646
	Lower Spavinaw	6/12/2018 – 6/14/2018	Pre-stock (no trout)**	36.324543	-94.705999
Summer	Upper Spavinaw	9/9/2018 – 9/11/2018	No trout**	36.344460	-94.576210
	Lower Spavinaw	9/19/2018 – 9/20/2018	Pre-stock (no trout)	36.324543	-94.705999
	Spring	9/28/2018 – 9/30/2018	Reference (no trout)	36.089339	-95.027646
Winter	Middle Spavinaw	2/8/2019 – 2/11/2019	Post-stock (trout)	36.326227	-94.670346
	Spring	2/15/2019 – 2/17/2019	Reference (no trout)	36.089339	-95.027646
Spring/Summer	Middle Spavinaw	6/14/2019 – 6/17/2019	Post-stock (trout)	36.326227	-94.670346
	Spring	6/19/2019 – 6/22/2019	Reference (no trout)	36.089339	-95.027646

*Rainbow Trout were present in higher numbers but stocking had not taken place in Oklahoma yet. It is unknown whether the fish observed during this survey were holdovers from previous stocking efforts in Arkansas or the result of more recent, illegal stocking.

**Rainbow Trout were encountered in limited numbers (< 5). Data were collected on Rainbow Trout habitat use but these sites were considered absent of Rainbow Trout in terms of my factored variable “trout” during microhabitat analysis.

Table 3. Reach locations and dates where fish were enumerated in summer of 2018 and 2019. Reaches locations include site name, stream, state, and latitude (lat) and longitude (long) in NAD83 format. Surveys indicate temporally-replicated sites. NAs indicate reaches either not sampled because of low flow, insufficient clarity, or denied access by a private landowner, or when a sample reach was added after the 2018 field season.

<u>Reach information</u>			<u>2018</u>				<u>2019</u>		<u>Coordinates</u>	
Reach name	Stream	State	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6	(Lat)	(Long)
Colston	Spavinaw	OK	6/1/2018	7/13/2018	NA	NA	NA	NA	36.32328	-94.68178
Mill Dam	Spavinaw	AR	5/31/2018	7/11/2018	8/6/2018	9/27/2018	7/2/2019	8/16/2019	36.36531	-94.55071
Goldstein1	Spavinaw	OK	6/22/2018	7/9/2018	8/11/2018	9/12/2018	7/13/2019	8/18/2019	36.32662	-94.69395
Goldstein2*	Spavinaw	OK	NA	NA	NA	NA	8/1/2019	8/18/2019	36.32562	-94.68997
Harrison	Spavinaw	OK	6/2/2018	7/10/2018	8/8/2018	NA	7/12/2019	8/17/2019	36.33211	-94.63127
Lavern	Spavinaw	OK	6/3/2018	7/9/2018	8/6/2018	9/14/2018	7/12/2019	8/17/2019	36.32450	-94.70643
Maris1	Spavinaw	OK	6/2/2018	7/9/2018	8/6/2018	10/6/2018	7/13/2019	8/19/2019	36.32632	-94.67139
Maris2*	Spavinaw	OK	NA	NA	NA	NA	8/1/2019	8/19/2019	36.32357	-94.67760
Sisco	Spavinaw	AR	6/21/2018	7/11/2018	8/6/2018	9/12/2018	7/1/2019	8/16/2019	36.34500	-94.57555
Walker1	Spavinaw	OK	6/3/2018	7/10/2018	8/7/2018	9/13/2018	NA	NA	36.32917	-94.65370
Walker2	Spavinaw	OK	6/22/2018	7/10/2018	8/7/2018	9/13/2018	NA	NA	36.33389	-94.63908
Wilkins*	Spavinaw	AR	NA	NA	NA	NA	7/14/2019	NA	36.38020	-94.50054
Wilson	Spavinaw	AR	6/21/2018	7/11/2018	8/8/2018	9/12/2018	NA	8/20/2019	36.35242	-94.56732
Moss	Spring	OK	6/23/2018	7/14/2018	8/10/2018	9/30/2018	7/31/2019	NA	36.08929	-95.02629
Neal	Spring	OK	6/26/2018	7/12/2018	8/9/2018	10/5/2018	7/16/2019	8/15/2019	36.14963	-95.14296
Rogers	Spring	OK	6/26/2018	7/12/2018	8/10/2018	10/6/2018	7/15/2019	NA	36.08653	-95.06931

Ross	Spring	OK	6/23/2018	7/14/2018	8/10/2018	10/6/2018	7/15/2019	NA	36.09133	-95.01084
Torrey	Spring	OK	6/25/2018	7/13/2018	8/9/2018	10/5/2018	7/16/2019	8/15/2019	36.14303	-95.17440

Table 4. Predictor variables used to determine microhabitat and reach-scale habitat selection by five species and two life stages of fishes (Table 1). For my microhabitat objective, calendar day corresponded to an increasing daily value from 0 (December 21) to 182 (June 21), and substrate was measured using a modified Wentworth Scale: 0) unbroken, 1) silt (< 0.06 mm), 2) sand ($\geq 0.06 - 2$ mm), 3) gravel (>2 – 16 mm), 4) pebble (> 16 – 64 mm), 5) cobble (> 64 – 256 mm), and 6) boulder (> 256 mm) (Mahon et al. 1996). Other microhabitat variables quantified were depth (0.05 m), velocity (0.1 m/s), temperature (± 0.5 °C deviation from the median site temperature), cover (present or absent), and Rainbow Trout (Trout were present or absent). Snorkel day, site visit, and site were grouping factors where snorkel passes were repeated within a day, multiple days comprised each site visit, and multiple site visits took place at the same site over my study period. Reach-scale variables were: average residual pool depth (RPD) (0.05 m), percent riffle (1%), maximum weekly maximum temperature (MWMT) (0.1 °C), percent cover (1 %), groundwater (losing or gaining), and Rainbow Trout (trout was continuous and scaled by reach area). Both survey and reach were nested grouping factors where survey accounted for repeated snorkel passes per survey and reach accounted for repeated surveys per reach.

Scale	Variable	Type	Mean \pm SD	Minimum - Maximum	Levels
Microhabitat	Calendar day	Continuous	96.74 \pm 55.62	2.00 – 182.00	NA
	Species	Factor	NA	NA	6
	Substrate	Continuous	4.13 \pm 1.23	0 – 6.00	NA
	Depth	Continuous	0.75 \pm 0.68	0 – 5.10	NA
	Velocity	Continuous	0.13 \pm 0.21	0 – 1.50	NA
	Temperature	Continuous	0.05 \pm 0.47	-3.00 – 7.00	NA
	Cover	Factor	NA	NA	2

	Trout	Factor	NA	NA	2
	Snorkel day*	Factor	NA	NA	44
	Site visit*	Factor	NA	NA	12
	Site*	Factor	NA	NA	4
Reach	Species	Factor	NA	NA	6
	Average RPD	Continuous	1.5 ± 0.75	0.30 – 2.95	NA
	Percent riffle	Continuous	10.5 ± 7.70	0 – 36.00	NA
	MWMT	Continuous	23.75 ± 1.30	20.5 – 26.20	NA
	Percent cover	Continuous	27.56 ± 11.00	5 – 50	NA
	Groundwater	Factor	NA	NA	2
	Trout	Continuous	2.69 ± 4.94	0 – 19.65	NA
	Survey*	Factor	NA	NA	492
	Reach*	Factor	NA	NA	18

*Grouping factors

Table 5. Pearson’s pairwise correlation coefficients for predictor variables associated with microhabitat selection of stream fishes in Ozark Highland streams. Calendar day increases from 0 (December 21) to 182 (June 21) and back towards 0 past June 21. Trout was classified as 0 (no trout) or 1 (trout present). Substrate was classified using a modified Wentworth Scale (McMahon et al. 1996) corresponding to 0) unbroken, 1) silt (< 0.06 mm), 2) sand ($\geq 0.06 - 2$ mm), 3) gravel ($>2 - 16$ mm), 4) pebble ($> 16 - 64$ mm), 5) cobble ($> 64 - 256$ mm), and 6) boulder (> 256 mm), depth (m), and velocity (m/s) and temperature ($^{\circ}\text{C}$) were continuous habitat variables. Temperature represented a deviation of each observation from the median temperature at the time of each snorkel survey. Cover was classified as 0 (absent) or 1 (present).

Variable	Calendar day	Trout	Substrate	Depth	Velocity	Cover	Temperature
Calendar day	1.00						
Trout	-0.30	1.00					
Substrate	0.05	0.03	1.00				
Depth	0.04	-0.03	0.18	1.00			
Velocity	0.37	0.08	0.04	-0.10	1.00		
Cover	-0.03	0.01	0.28	0.19	-0.11	1.00	
Temperature	0.01	-0.03	-0.05	-0.13	-0.02	0.03	1.00

Table 6. Pearson’s pairwise correlation coefficients for predictor variables associated with reach-scale count data for stream fishes in Ozark streams. Rainbow Trout data were scaled by the log area of each reach, residual pool depth (RPD; 0.05 m) was a measure of average reach depth, percent cover was visually estimated (1%), percent riffle was calculated using channel unit dimensions (1%), groundwater was classified as losing or gaining, and the maximum weekly maximum temperature (MWMT) represented trends in weekly temperature (°C).

Variable	Rainbow Trout	RPD	Percent cover	Percent riffle	Groundwater	MWMT
Rainbow Trout	1.00					
RPD	0.10	1.00				
Percent cover	0.13	0.36	1.00			
Percent riffle	0.00	-0.39	0.20	1.00		
Groundwater	0.12	-0.17	0.02	0.16	1.00	
MWMT	-0.28	0.09	0.15	-0.14	0.07	1.00

Table 7. Habitat variables and interactions associated with five species and two lifestages of native fishes. Significant interactions are denoted by Y and non-significant interactions are denoted by N. Significant was determined by 95% Highest Density Intervals that did not fall within 0.01 or overlap zero. Y* indicates importance because of a higher-order significant interaction (i.e., the estimate itself is not significant but should be retained because of its contribution to a higher-order significant interaction). Appendix B, table 2 contains all coefficient estimates and associated 95% high density intervals.

Model interaction	Beta	CRC	MOX	NHS	RSC	AGE-1+	AGE 0	Species-specific significance
Time	1	Y	Y	Y	Y	Y	Y	All species
Depth	2	Y	Y	Y	Y	Y	Y	All species
Depth ²	3	Y	Y	Y	Y	Y	Y	All species
Temperature	4	N	Y	N	Y	Y	Y	MOX, RSC, Age-1+, AGE 0
Velocity	5	Y	Y	Y	Y*	Y*	Y	All species
Substrate	6	Y	Y	Y	Y	Y	Y*	All species
RBT	7	Y*	Y*	Y*	Y*	Y*	Y*	All species
Cover	8	Y	N	Y	Y	Y	Y	CRC, NHS, RSC, AGE-1+, AGE 0
RBT * time	9	Y*	Y*	Y*	Y*	Y*	Y	All species
RBT * depth	10	Y	Y	Y	Y*	Y*	Y	All species
RBT * depth ²	11	Y	N	Y	Y*	Y	Y	CRC, NHS, RSC, AGE-1+, AGE 0
RBT * temperature	12	N	N	N	Y	Y	Y*	RSC, AGE-1+, AGE 0
RBT * velocity	13	Y	Y*	Y	Y*	Y	Y*	All species
RBT * substrate	14	Y*	N	Y*	N	Y*	N	NHS, AGE-1+, AGE 0
RBT * cover	15	Y	N	Y*	Y	Y	Y	CRC, NHS, RSC, AGE-1+, AGE 0

Time * RBT * cover	16	N	N	Y	Y	Y	Y	NHS, RSC, AGE-1+, AGE 0
Time * depth	17	Y*	Y	Y	Y	Y*	Y	All species
Time * depth ²	18	Y	Y	Y	Y*	Y	Y	All species
Time * temperature	19	N	N	N	Y	N	Y*	RSC, AGE 0
Time * velocity	20	Y*	Y	Y	Y*	Y*	Y*	All species
Time * substrate	21	Y*	Y	Y	N	Y	Y	CRC, MOX, NHS, Age-1+, Age 0
Time * cover	22	N	N	Y	Y	Y*	Y	NHS, RSC, AGE-1+, AGE 0
Time * RBT * depth	23	Y*	N	N	Y*	Y*	N	CRC, RSC, AGE-1+
Time * RBT * depth ²	24	Y	N	N	Y	Y	N	CRC, RSC, AGE-1+
Time * RBT * temperature	25	N	N	N	Y	N	Y	RSC, AGE 0
Time * RBT * velocity	26	Y	Y	N	Y	Y	Y	CRC, MOX, RSC, AGE-1+, AGE 0
Time * RBT * substrate	27	Y	N	Y	N	N	Y	CRC, NHS, AGE 0

Table 8: Odds ratios of cover use for five species of native stream fishes that were significantly influenced by the presence of Rainbow Trout. For each species/trout/cover effect combination, the top row represents the odds of cover use and the bottom row indicates the odds of no cover use. The odds ratio is calculated by dividing the odds of cover by the odds of no cover and can be expressed at “X times as likely to use cover over no cover”.

Species	Trout/cover factor	Odds	Odds ratio for cover use
CRC	Yes/yes	1.9	18.1
	Yes/no	0.1	
	No/yes	0.9	6.1
	No/no	0.1	
NHS	Yes/yes	0.1	0.6
	Yes/no	0.1	
	No/yes	0.1	0.5
	No/no	0.2	
RSC	Yes/yes	0.8	3.2
	Yes/no	0.2	
	No/yes	0.3	1.1
	No/no	0.3	
Age-1+ SMB	Yes/yes	0.1	6.6
	Yes/no	0	
	No/yes	0.1	2.1
	No/no	0	
Juvenile SMB	Yes/yes	2.5	8.5
	Yes/no	0.3	
	No/yes	0.1	2.0
	No/no	0	

Table 9. Final model parameters and 95% Confidence intervals (CIs) for my reach-scale assessment of habitat selection and effect of Rainbow Trout on native species. The model intercept and main effects for each habitat variable are in reference to Redspot Chub. Percent riffle, residual pool depth (RPD) and maximum weekly maximum temperature (MWMT) represent standardized variables where the coefficient is the magnitude of the effect with a 1 SD change. Discharge gain is in reference to discharge loss. Each coefficient estimate is interpreted with all other variables held at mean, zero (Rainbow Trout), or reference levels.

Parameter	Coefficient	95% CI
(Intercept)	-4.52 ± 0.16	-5.01, -4.15
Creek Chub	-2.10 ± 0.13	-2.34, -1.83
Redhorse	-0.87 ± 0.12	-1.06, -0.64
Northern Hogsucker	-1.63 ± 0.12	-1.88, -1.45
Juvenile Smallmouth Bass	-1.36 ± 0.12	-1.71, -1.45
Age-1+ Smallmouth Bass	-0.28 ± 0.12	-0.56, -0.01
Temperature (MWMT)	-0.16 ± 0.09	-0.29, 0.06
Percent riffle	0.06 ± 0.08	-0.14, 0.21
Residual pool depth (RPD)	0.15 ± 0.06	0.07, 0.26
Rainbow Trout	0.01 ± 0.08	-0.23, 0.20
Creek Chub * MWMT	-0.63 ± 0.11	-0.91, -0.45
Redhorse * MWMT	0.22 ± 0.10	-0.14, -0.42
Northern Hogsucker * MWMT	-0.11 ± 0.11	-0.38, 0.03
Juvenile Smallmouth Bass * MWMT	0.07 ± 0.11	-0.15, 0.22
Age-1+ Smallmouth Bass * MWMT	0.12 ± 0.10	-0.09, 0.28
Creek Chub * percent riffle	-0.22 ± 0.11	-0.47, -0.04
Redhorse * percent riffle	-0.27 ± 0.11	-0.44, -0.12
Northern Hogsucker * percent riffle	-0.45 ± 0.11	-0.69, -0.28
Juvenile Smallmouth Bass * percent riffle	-0.01 ± 0.10	-0.22, 0.29
Age-1+ Smallmouth Bass * percent riffle	-0.08 ± 0.10	-0.32, 0.09
Creek Chub * Rainbow Trout	0.32 ± 0.11	0.04, 0.54
Redhorse * Rainbow Trout	-0.02 ± 0.10	-0.29, 0.16
Northern Hogsucker * Rainbow Trout	0.03 ± 0.11	-0.27, 0.19

Juvenile Smallmouth Bass * Rainbow Trout	0.18 ± 0.11	-0.06, 0.50
Age-1+ Smallmouth Bass * Rainbow Trout	0.07 ± 0.10	-0.15, 0.35

FIGURES

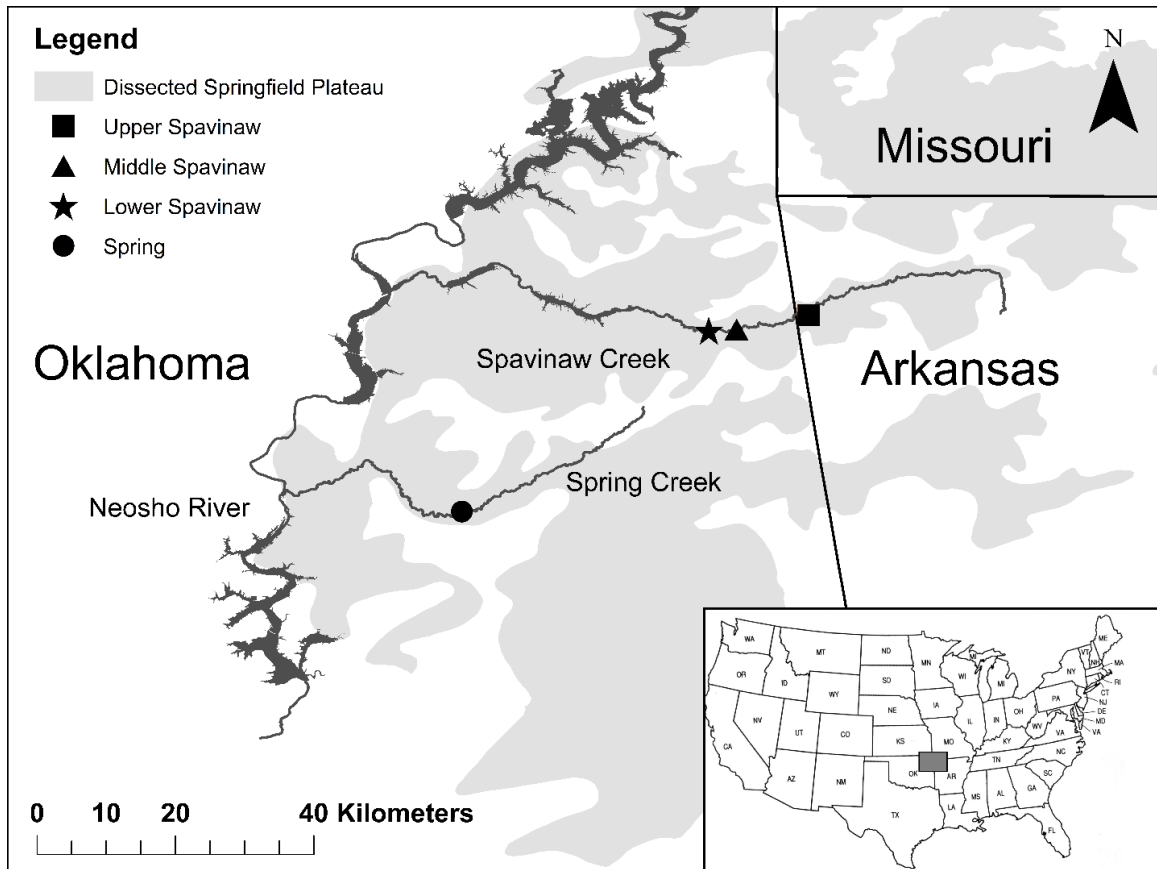


Figure 1. Location of microhabitat sites on Spavinaw and Spring creeks that I sampled seasonally 2017 – 2019. The middle and lower Spavinaw sites were sampled in autumn, winter, and spring. The upper Spavinaw site was sampled in winter 2017 and summer 2018. Spring Creek was sampled seasonally and served as a reference with no trout present (Table 2). Gray shading indicates extent of Dissected Springfield Plateau (Level IV ecoregion) within the map frame.

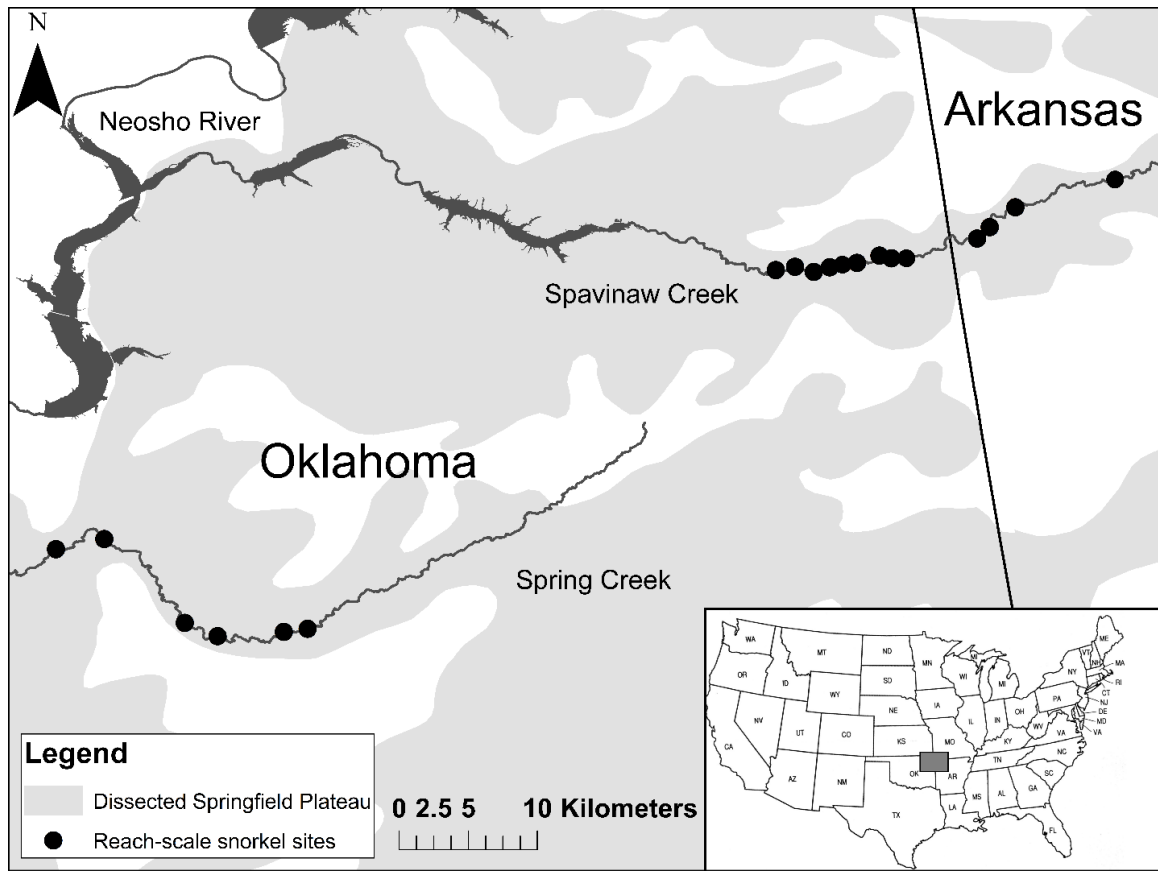


Figure 2. Location of reaches sampled on Spavinaw and Spring creeks during summer 2018 and 2019. Thirteen reaches were sampled on Spavinaw Creek and five reaches were sampled on Spring Creek. Not all reaches were sampled during both years (Table 3). Gray shading indicates extent of Dissected Springfield Plateau (Level IV ecoregion) within map frame.

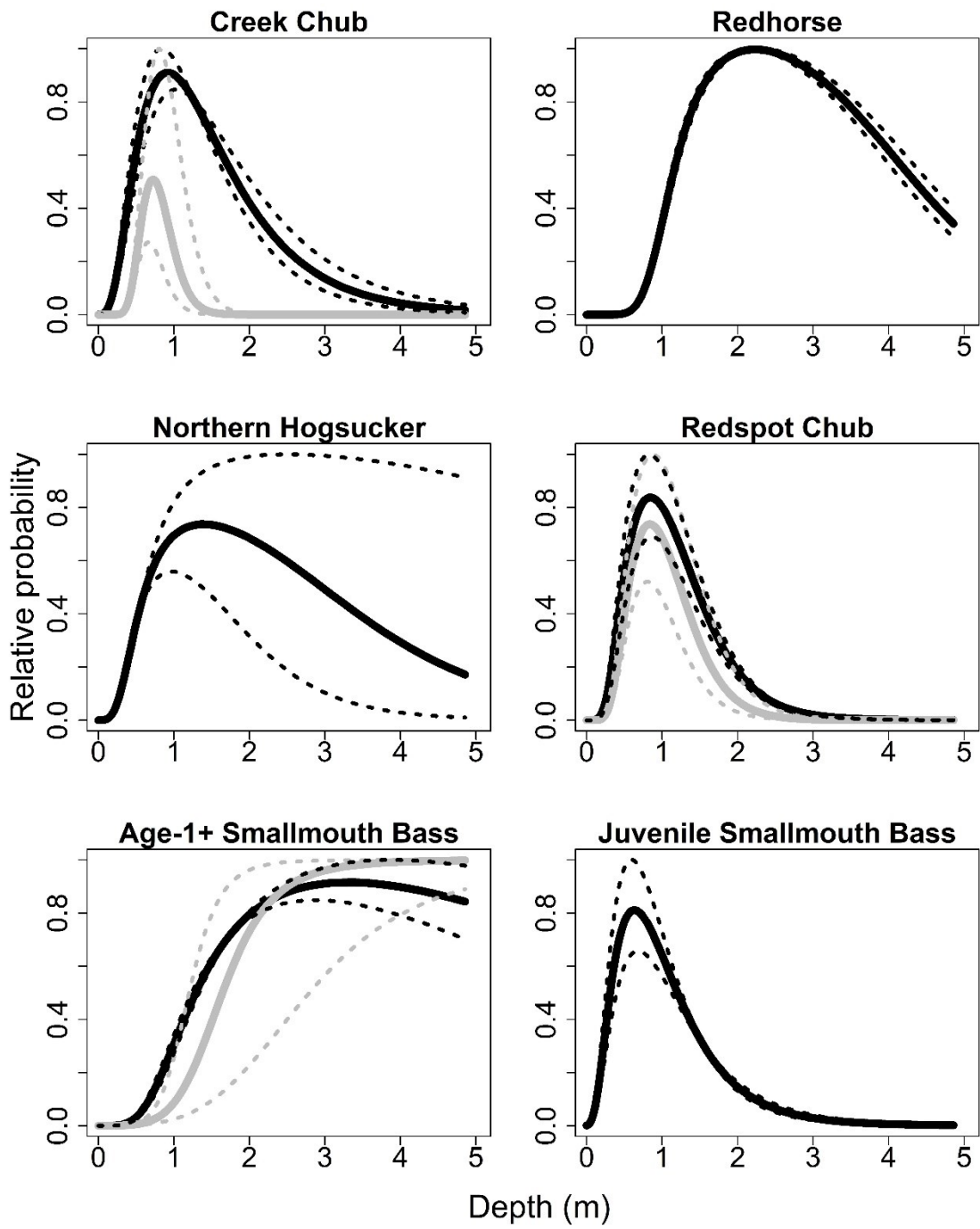


Figure 3.

Figure 3. Relative selection trends of depth (m) for six species/life stages of stream fishes encountered during microhabitat assessments. Selection trends are plotted as an interaction with time held constant at day 30 (i.e., ~ January 31). All species/life stages had significant relationships with the interaction between depth (depth + depth²) and time (relationships shown as black lines). For three species (Creek Chub, Redspot Chub, and age-1+ Smallmouth Bass), there were also significant relationships between depth, time, and the presence of Rainbow Trout (relationships shown as gray lines). In all plots, the estimates are scaled by the highest probability (e.g., X/highest probability) so that the highest predicted probability becomes a value of 1 on the y axis. All plotted relationships are deemed significant using a 95% High Density Interval criteria (dotted lines).

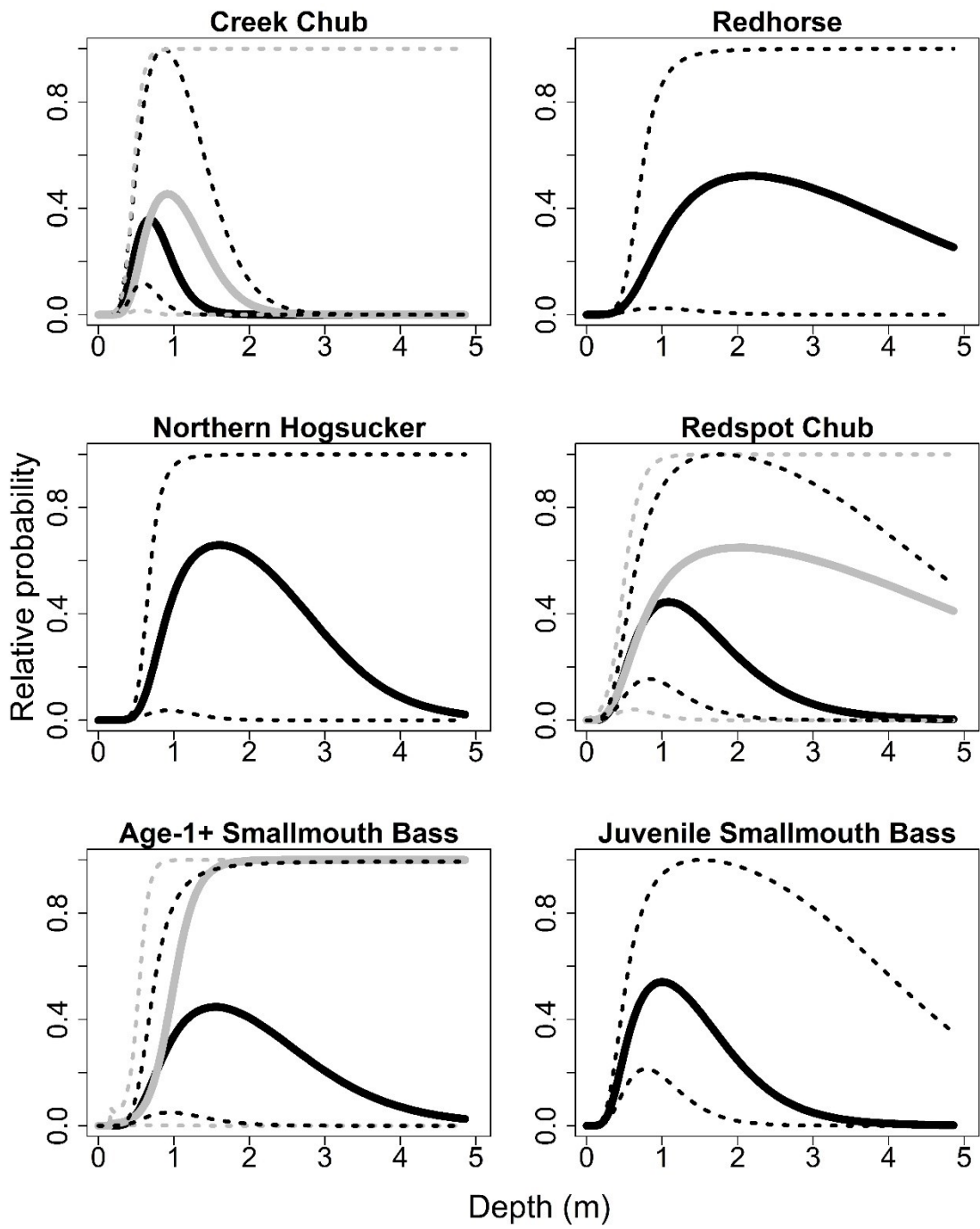


Figure 4.

Figure 4. Relative selection trends of depth (m) for six species/life stages of stream fishes encountered during microhabitat assessments. Selection trends are plotted as an interaction with time held constant at day 180 (i.e., ~ June 20). All species/life stages had significant relationships with the interaction between depth (depth + depth²) and time (relationships shown as black lines). For three species (Creek Chub, Redspot Chub, and age-1+ Smallmouth Bass), there were also significant relationships between depth, time, and the presence of Rainbow Trout (relationships shown as gray lines). In all plots, the estimates are scaled by the highest probability (e.g., X/highest probability) so that the highest predicted probability becomes a value of 1 on the y axis. All plotted relationships are deemed significant using a 95% High Density Interval criteria (dotted lines).

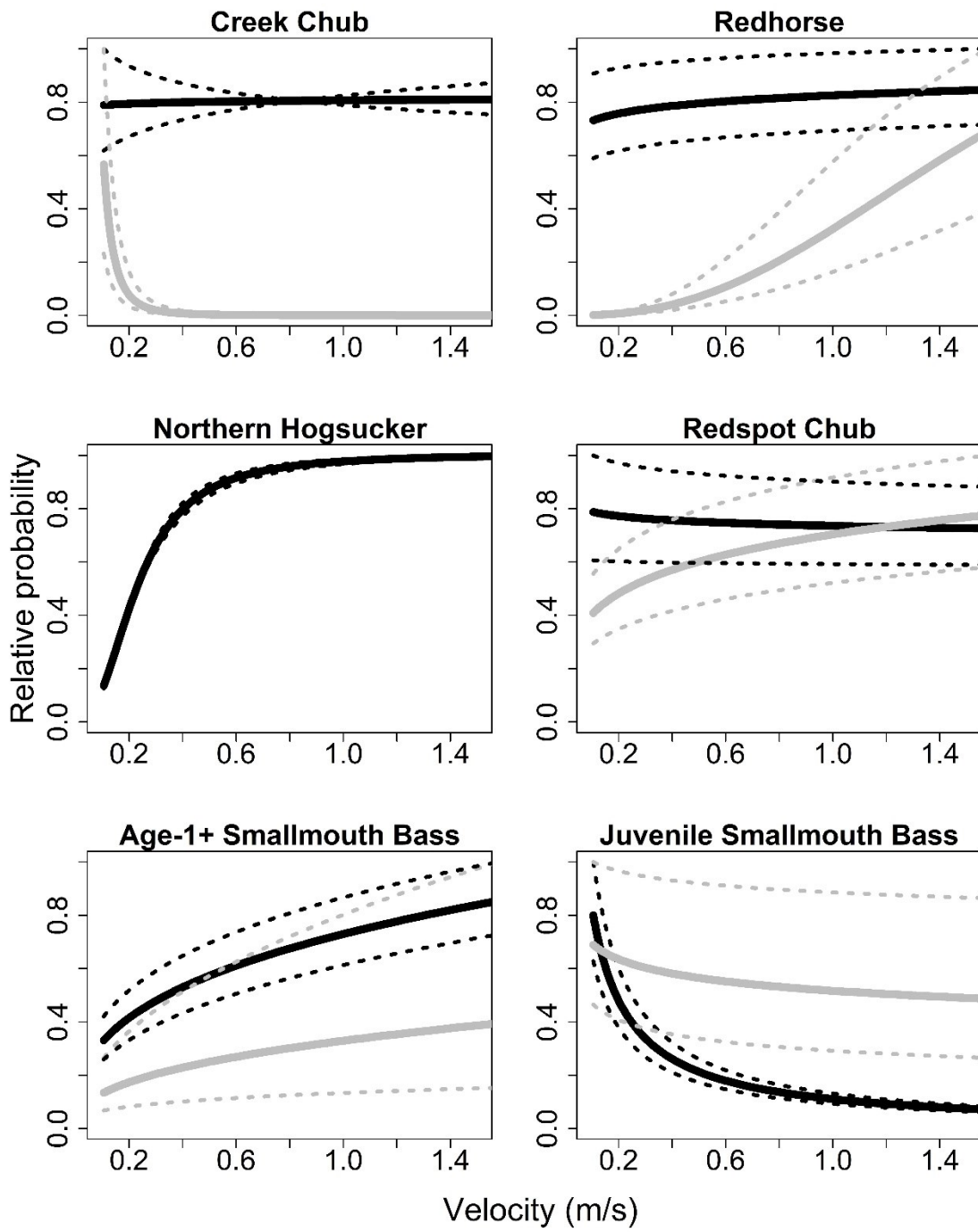


Figure 5.

Figure 5. Relative selection trends of velocity (m/s) for six species/life stages of stream fishes encountered during microhabitat assessments. Selection trends are plotted as an interaction with time held constant at day 30 (i.e., ~ January 31). All species/life stages had significant relationships with the interaction between velocity and time (relationships shown as black lines). For five species (Creek Chub, Redhorse, Redspot Chub, age-1+ Smallmouth Bass and Juvenile Smallmouth Bass), there were also significant relationships between velocity, time, and the presence of Rainbow Trout (relationships shown as gray lines). In all plots, the estimates are scaled by the highest probability (e.g., X/highest probability) so that the highest predicted probability becomes a value of 1 on the y axis. All plotted relationships are deemed significant using a 95% High Density Interval criteria (dotted lines).

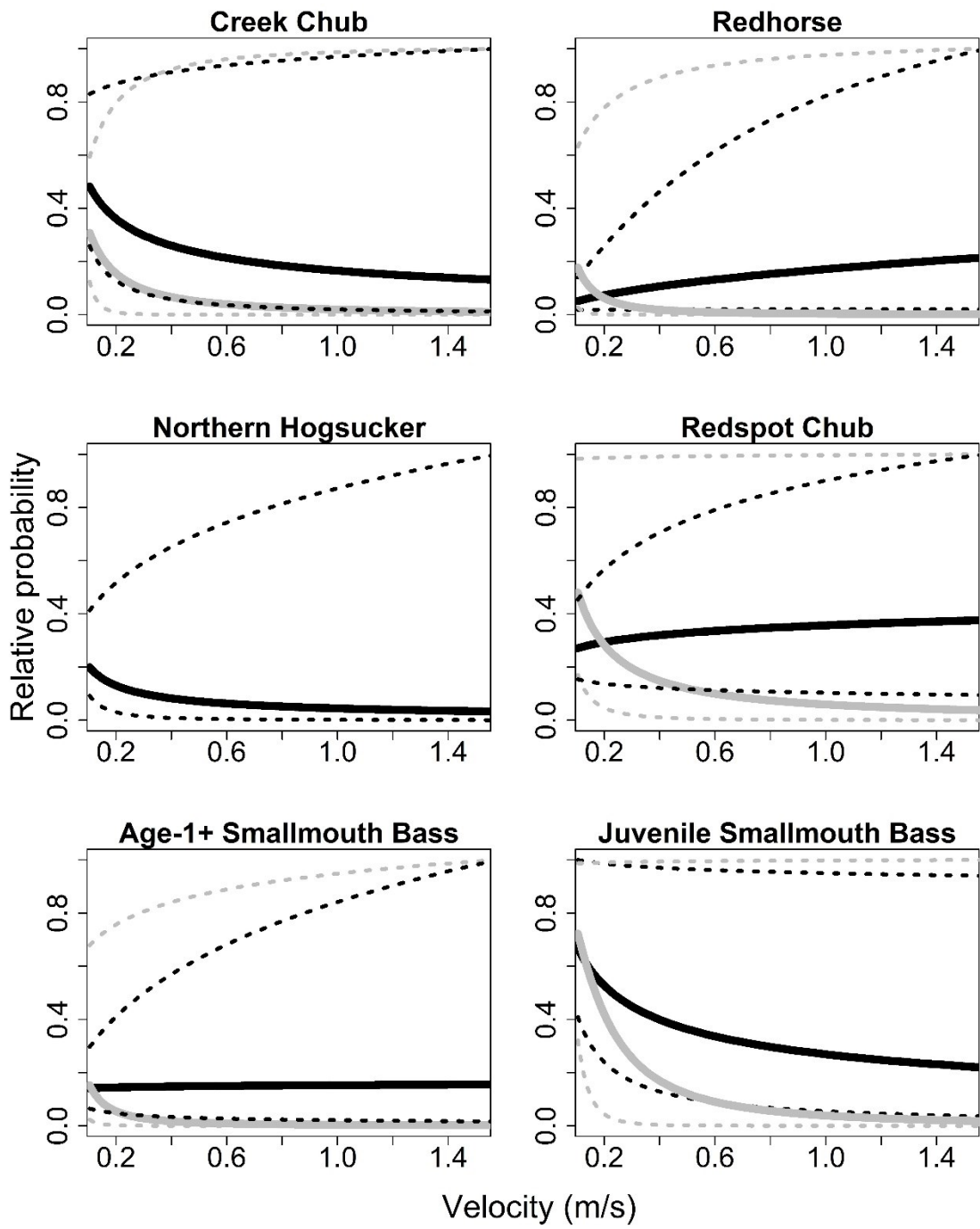


Figure 6.

Figure 6. Relative selection trends of velocity (m/s) for six species/life stages of stream fishes encountered during microhabitat assessments. Selection trends are plotted as an interaction with time held constant at day 180 (i.e., ~ June 20). All species/life stages had significant relationships with the interaction between velocity and time (relationships shown as black lines). For five species (Creek Chub, Redhorse, Redspot Chub, age-1+ Smallmouth Bass and Juvenile Smallmouth Bass), there were also significant relationships between velocity, time, and the presence of Rainbow Trout (relationships shown as gray lines). In all plots, the estimates are scaled by the highest probability (e.g., X/highest probability) so that the highest predicted probability becomes a value of 1 on the y axis. All plotted relationships are deemed significant using a 95% High Density Interval criteria (dotted lines).

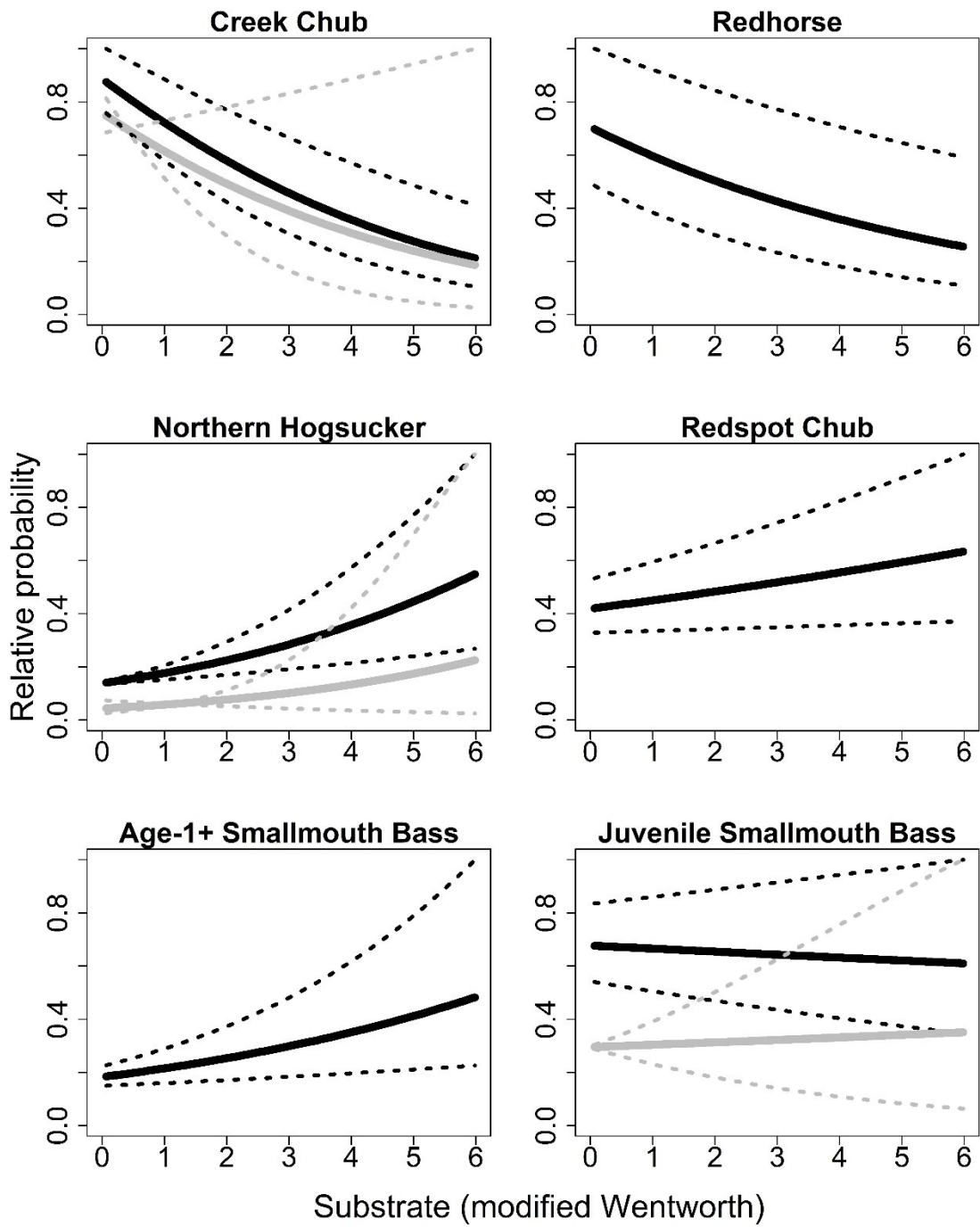


Figure 7.

Figure 7. Relative selection trends of substrate for six species/life stages of stream fishes encountered during microhabitat assessments. All six species had significant relationships with substrate. For three species (Creek Chub, Northern Hogsucker and Juvenile Smallmouth Bass), there were also significant relationships between velocity and the presence of Rainbow Trout (relationships shown as gray lines). In all plots, the estimates are scaled by the highest probability (e.g., $X/\text{highest probability}$) so that the highest predicted probability becomes a value of 1 on the y axis. All plotted relationships are deemed significant using a 95% High Density Interval criteria (dotted lines).

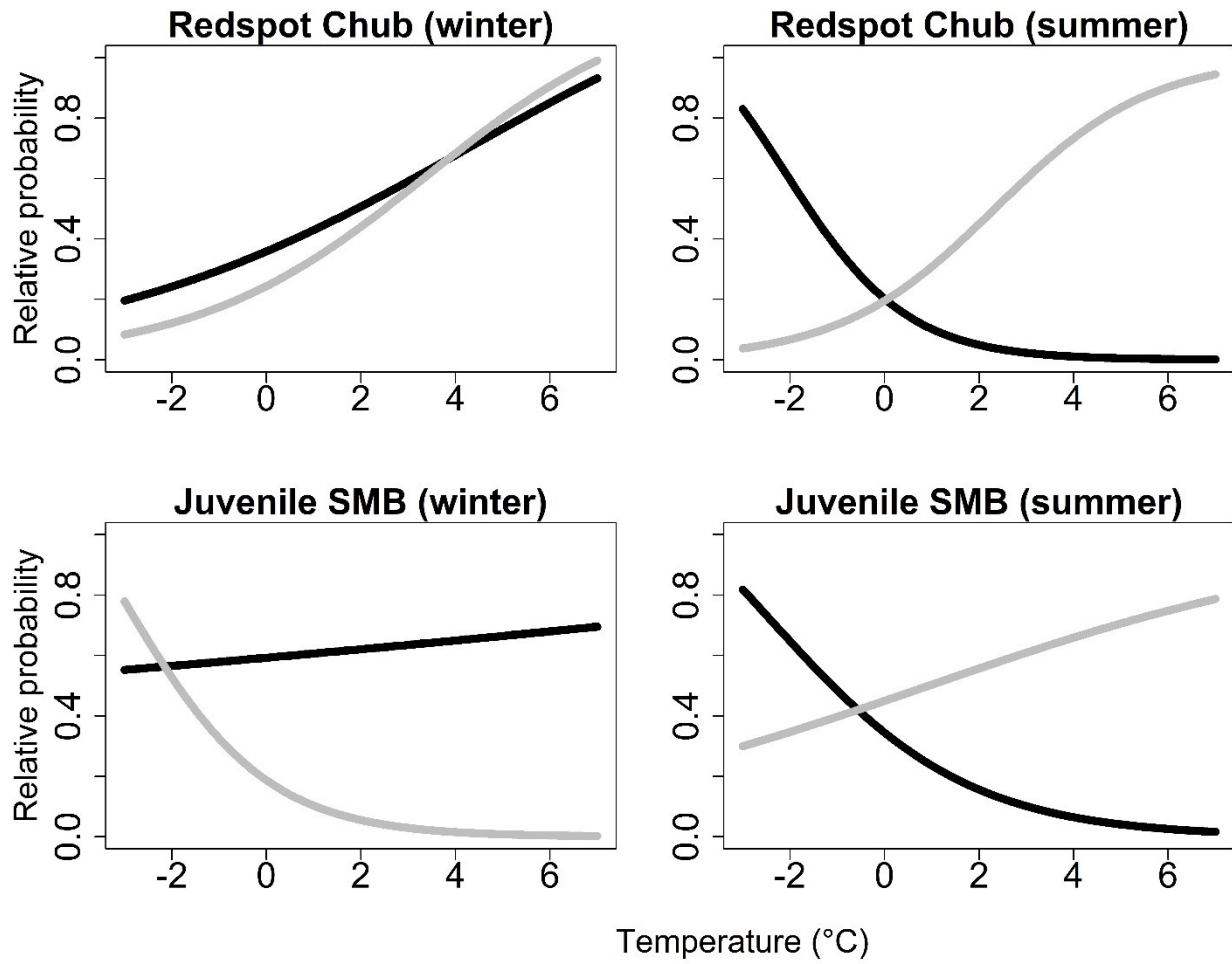


Figure 8.

Figure 8. Temperature selection (deviation from the median site temperature) for Redspot Chub and juvenile Smallmouth Bass during winter (January 31) and summer (June 20). Black lines indicate selection patterns under reference (no trout) conditions and gray lines represent selection patterns with Rainbow Trout present. In all plots, the estimates are scaled by the highest probability (e.g., $X/\text{highest probability}$) so that the highest predicted probability becomes a value of 1 on the y axis. All plotted relationships are deemed significant using a 95% High Density Interval criteria (dotted lines).

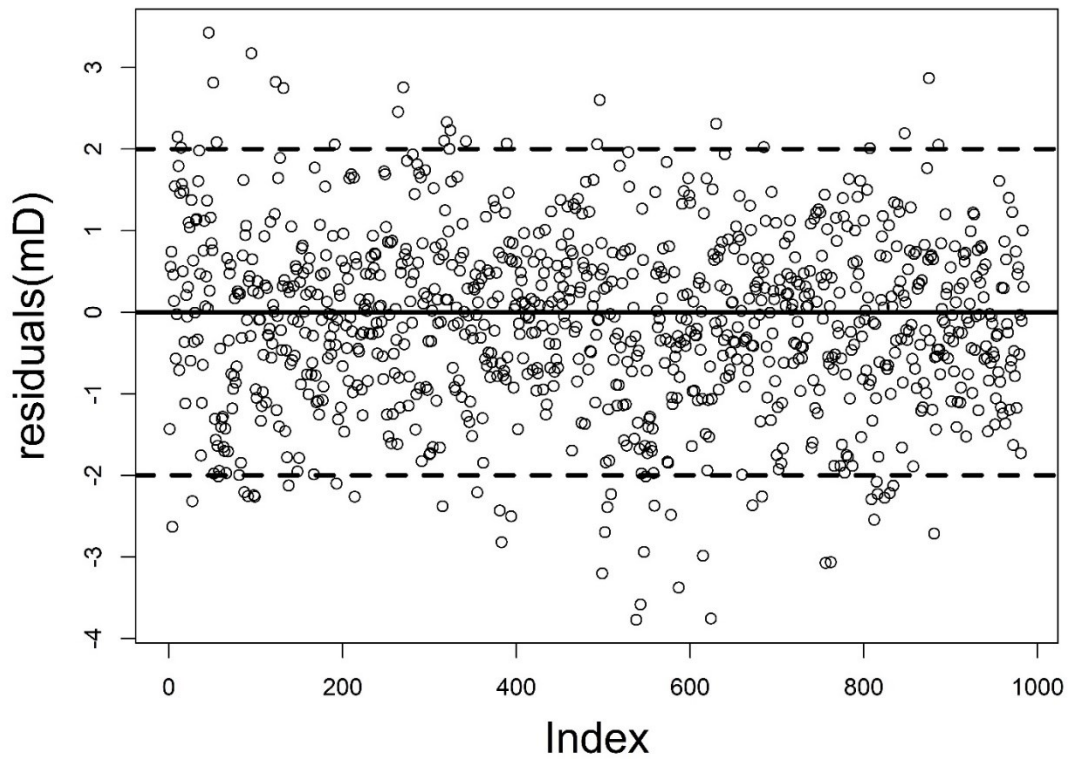


Figure 9. Residual plot of my final reach-scale model (mD) where the x-axis is an index of expected values and the y-axis is the standardized residual values. Standardized residual values should have a mean of 0 and standard deviation of 1; thus, lines at ± 2 indicate approximate 95% error bounds (Gelman and Hill 2007).

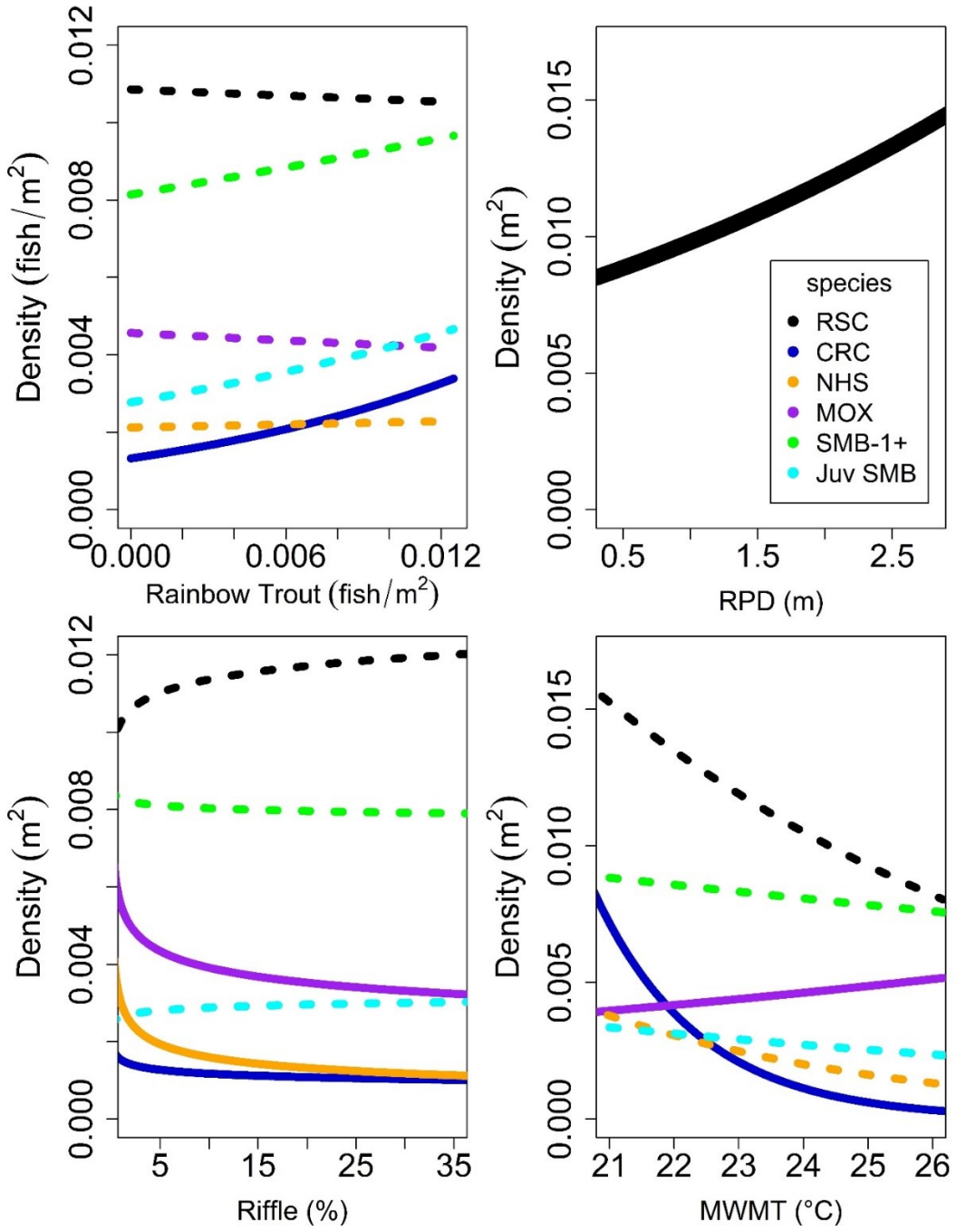


Figure 10.

Figure 10. Relationship between fish density (i.e., fish/m²) of five fish species including two life stages of Smallmouth Bass (juvenile and age-1+) and four continuous reach-scale predictor variables (top left panel to bottom right): Rainbow Trout density, 2) residual pool depth (RPD), 3) percent riffle and 4) maximum weekly maximum temperature (MWMT). Species are: Redspot Chub (RSC), Creek Chub (CRC), Northern Hogsucker (NHS), Redhorse *spp.* (MOX), and Smallmouth Bass (SMB). Redspot Chub served as the reference species for all interactions. Relationships are plotted with all other variables held at mean or reference levels. Solid lines represent significant species-specific differences from the reference (RSC) relationship. RPD was retained only as a main effect during model selection; thus, the plotted line represents the relationship for all species though the actual density (y-axis) would depend on the species-specific intercept (i.e., higher vs lower density species).

CHAPTER III

MOVEMENT AND SURVIVAL OF STOCKED RAINBOW TROUT IN LOWER SPAVINAW CREEK

ABSTRACT

Stocking Rainbow Trout to create additional angling opportunities is not uncommon; however, these fishing opportunities necessitate evaluation in warmwater streams where the spatial and temporal implications of stocking non-native fish are unclear. My objectives were to determine Rainbow Trout dispersal from a stocking location on Spavinaw Creek, Oklahoma and quantify Rainbow Trout apparent survival by two cohorts stocked in autumn 2018 and spring 2019. Rainbow Trout were PIT tagged in November 2018 (n = 495) and February 2019 (n = 605) prior to stocking and actively and passively located following stocking using a floating array and two fixed arrays. Most stocked Rainbow Trout we detected remained within ~1 km of the stocking location but with notable individual variability (up to 4 km observed). Directional movement by stocked Rainbow Trout detected using fixed arrays was evident with upstream movements related to positive changes in daily discharge and downstream movements related to falling daily discharge. Estimated mortality was highest during the first two weeks post stocking. Apparent weekly survival rates for both autumn and spring stocked fish increased through winter and spring when water-temperatures were cool. Rainbow Trout persisted in Spavinaw Creek despite warm water temperatures during the summer; however, the weekly apparent survival rate during summer was reduced when maximum daily water temperatures exceeded 25 °C. My results suggest possible interactions with native warmwater fishes over the first year of initial stocking would be primarily concentrated in 1 km of the stocking location; however, cumulative effects due to repeated stockings and learning by individuals successfully over-summering are unknown. Additionally, warmer and drier conditions than experienced during my 1-year study could alter survival and increase possible interactions with native species, particularly when thermal resources are limiting.

INTRODUCTION

Salmonids are widely stocked to increase angling opportunities, increase license sales, and supplement existing fisheries where salmonids are native (Epifanio et al. 2000). In the United States, trout angling is estimated to provide 8.6 billion dollars in economic benefits each year (USFWS and U.S. Census Bureau 2011); thus, stocking efforts comprise an important component of fisheries management activities for many state and federal agencies. In a single year (2004), Halverson (2008) estimated state and federal agencies stocked 9.96×10^6 kg of Rainbow Trout *Oncorhynchus mykiss*. Forty-six state agencies currently maintain trout stocking programs throughout the country to increase angling opportunities and generate revenue from license sales (Epifanio 2000; Hyman et al. 2016). Trout stockings below impoundments provide valuable tailwater fishing opportunities where extirpation or reduction in native fishes result from human modifications (e.g., Bettinger and Bettoli 2002; Runge et al. 2008; Quinn and Kwak 2011). In addition to agency stockings, private stockings provide angling opportunities and generate additional economic revenue (e.g., angling clubs, see Rasemussen and Petersen 2018). Consequently, salmonid distributions extend well beyond their native range via stocking efforts (Halverson 2010).

Rainbow Trout is perhaps the most commonly-stocked trout in the United States (Halverson 2010) and globally (MacCrimmon 1971; Stankovic et al. 2015); however, possible interactions between Rainbow Trout and native fishes focus primarily on sympatric trout (e.g., Rainbow Trout and Brook Trout *Salvelinus fontinalis*, Larson and Moore 1985; Rainbow Trout and Cutthroat Trout *Clarki lewisi*, Hitt et al. 2003; and Rainbow Trout and Dolly Varden Charr *Salvelinus malma*, Baxter et al. 2004). Rainbow Trout is native to the western United States; however, 39 states currently manage non-native Rainbow Trout fisheries through a combination of hatchery stocking and naturalized populations (Epifanio 2000). In areas where other salmonid species are native, stocking concerns are generally focused on genetic integrity (Hansen and Mensberg 2009; Karlsson et al. 2016; Perrier et al. 2013) and the spread of disease and parasites

(Johnsen and Jensen 1991; Hastein 1991). In non-impounded warmwater systems that lack sympatric trout, concerns expressed about the possible effects on native fishes are less clear (Turek et al. 2013). Possible interactions between introduced Rainbow Trout and native warmwater fishes have been addressed in field (Walsh and Winkelman 2004; Weaver and Kwak 2013) and lab-based studies (Turek 2015; Elkins et al. 2019); however, these examinations have not resulted in a scientific consensus that would help guide agency policies. Consequently, additional studies examining the behavior and survival of Rainbow Trout introduced into warmwater streams would be a useful step to understanding possible ecological implications.

Stocked salmonid survival rates are variable and influenced by habitat, environmental conditions, genetic characteristics of the population stocked, and harvest by anglers. In some cases, low survival is reported in stocked Rainbow Trout populations outside the native range. Bettinger and Bettoli (2002) found < 10% of catchable-size Rainbow Trout survived more than six weeks in a Tennessee dam tailwater. Similarly, Baird et al. (2006) reported no persistence of Rainbow Trout after several years of stocking in a New York stream due to presumed poor habitat quality. In ecosystems that more closely match the natural habitat of Rainbow Trout, survival rates may be higher (Fausch 2008). For example, seasonal survival of Rainbow Trout stocked in the Bluestone River, WV ranged 35 – 90% depending on stocking season (Hartman et al. 2012). Similarly, Flowers et al. (2019) reported high survival rates (> 90%) for Rainbow Trout and other salmonid species stocked in several NC streams. The distinct population characteristics (i.e., strains) of Rainbow Trout stocked may also influence survival due to differences in growth (Brauhn and Kincaid 1982), disease resistance (Hedrick et al. 2003), and thermal tolerances (Rodnick et al. 2004; Hartman and Porto 2014). In systems where Rainbow Trout are stocked under high fishing pressure, survival is reduced through harvest (e.g., Fay and Pardue 1986; Bettinger and Bettoli 2002; Hyman et al. 2016). In addition to survival, other factors including movement may relate to interactions with native species.

Studying movement patterns of stocked salmonids provides key information on their use of critical habitat (e.g., thermal refuge, Torgersen et al. 1999), overlap and subsequent ability to hybridize with native species (Muhlfeld et al. 2009) and allows us to draw inferences on possible reproductive success and subsequent dispersal into new areas of a catchment (Larson and Moore 1985; Fausch 2008; Seiler and Keeley 2009). Thirty-eight state agencies responding to a survey indicated habitat-related factors were the greatest limitation in managing cold-water fisheries including Rainbow Trout (Epifano 2000). Spawning movements to key habitats are common among both anadromous salmon (Robards and Quinn 2002) and freshwater (i.e., landlocked) populations (e.g., Rainbow Trout, James and Kelso 1995). Additionally, understanding movement patterns may help guide stocking decisions by identifying the spatial extent of possible interactions with native species. For example, declines in Cutthroat Trout resulted from movement of non-native Brook Trout into Rocky Mountain headwater streams (Peterson and Fausch 2003). Movement patterns are also useful in determining if stocked fishes remain in areas accessible to anglers if creating a trout fishery is a management objective. For example, Hartman et al. (2012) evaluated site fidelity (i.e., the proportion of fish that remained within the study reach) and survival of Rainbow Trout in an Appalachian river to determine the effectiveness of stocking Rainbow Trout to increase angling opportunities. In some cases, emigration by stocked fish may account for a greater loss of individuals from an accessible population to anglers than actual mortality (e.g., Rainbow Trout, Flowers et al. 2019).

Understanding directional movements from stocking locations and movement distance have important implications for managing stocked fish populations. Most evaluations of stocked Rainbow Trout report downstream movement patterns (Cresswell 1981; Helfrich and Kendall 1982) often related to high discharge events (e.g., hydroelectric power generation, Bettinger and Bettoli 2002; Cocherell et al. 2010). However, upstream movements are also reported and hypothesized to relate to environmental factors other than discharge (e.g., cooler upstream water temperatures, Runge et al. 2008). Like dispersal direction, movement distances by stocked

Rainbow Trout appear conditional with some populations being relatively sedentary (e.g., 1 – 3 km of their stocking location, High and Meyer 2009; Hartman and Logan 2010; Flowers et al. 2019), whereas others show greater dispersal potential over time. For example, a subset of stocked Rainbow Trout was reported to move > 100 km downstream in the Portneuf River, Idaho (Heimer et al. 1985). Although the management implications of dispersal vary depending on the stocking goal, dispersal may limit possible angling opportunities or altered densities spatially, allowing for different interactions (i.e., increased or decreased) with native fishes.

The objectives of my third chapter were to determine Rainbow Trout dispersal and movement direction and quantify Rainbow Trout apparent survival by two cohorts stocked in autumn 2018 and spring 2019 in Spavinaw Creek, OK. Quantifying these parameters provides information on how Rainbow Trout survived and dispersed in an unregulated, warmwater stream where harvest rates were not expected to substantially influence either survival or movement. The underlying karst geology and associated groundwater contribution in Spavinaw Creek creates patchy thermal habitats; therefore, I hypothesized Rainbow Trout summer survival rates would be higher than many other warmwater streams. Understanding the spatial (dispersal) and temporal (survival) dynamics of stocked Rainbow Trout in Spavinaw Creek are useful for guiding future stocking decisions given the native fish assemblage is diverse and includes other popular sportfish and species of conservation.

METHODS

Field methods

Study segment and fixed antenna arrays. – I installed two fixed Passive Integrative Transponder (PIT) tag antenna arrays (hereafter, “fixed arrays”) near the upstream and downstream end of my ~ 6-km study segment to determine directional movement and emigration by stocked Rainbow Trout (Figure 1). Each fixed array consisted of two antennas spaced ~2-m apart to determine the movement direction of tagged fish as they passed through. I constructed each antenna to form a

loop across the stream using 12 American Wire Gauge stranded wire that I strung through PVC along the stream bottom and back above the water column using t-posts (Figure 2). Each antenna was connected to a tuning box and then a multi-antenna reader box (Oregon RFID, Portland, Oregon) using 20 American Wire Gauge stranded wire. I housed the reader box in a bank-located plastic container. I powered the reader using a combination of two, 12-volt deep-cycle batteries and a solar panel. I attempted to switch reader batteries once every 2 wk to maintain constant operation. However, this was not always possible due to flooding events (e.g., flows above 28 m³/s typically disabled arrays) and resulted in several outage periods.

Tagging and stocking. – I used PIT tags to individually mark a subset of Rainbow Trout prior to each stocking occasion in Spavinaw Creek. PIT tags are useful because of their small size, high retention rate, and negligible effects on survival or growth for many species (Cooke et al. 2011; Musselman et al. 2017) including salmonids (95% to 99% post-tagging survival, Gries and Letcher 2002; Dare 2003). I used large, half-duplex tags because of their greater detection distance (O'Donnell et al. 2010; Featherman et al. 2014; Hodge et al. 2015) and reduced susceptibility to environmental noise compared to full-duplex PIT tags (Oregon RFID, <https://www.oregonrfid.com/resources/hdx-fdx/>, accessed September 16, 2019). The size of the PIT tag (23 mm or 32 mm) used in my study was determined by the total length (TL, 1 mm) of each tagged fish. The smallest fish tagged with a 32 mm tag was 230 mm TL.

I tagged each cohort of Rainbow Trout during a single day at the hatchery (Crystal Lake Fisheries, Ava, MO) approximately 1 wk prior to each stocking date. A team of four people (the project PI, Oklahoma Department of Wildlife Conservation biologists, field technicians, and myself) carried out all tagging activities during each tagging occasion. Two people were responsible for netting and transporting each fish to and from the raceway. Two additional people injected PIT tags into the peritoneal cavity of each fish using a 3.9 mm diameter needle to make a small incision (Cooke et al. 2011). In addition, the tagging team measured and recorded the fish

total length (TL, 1 mm). Once tagged, fish were immediately placed back in raceway to recover. Tagged individuals were held at the hatchery for 1 wk after tagging to monitor survival prior to stocking.

Tagged and untagged Rainbow Trout (Emmerson strain) were stocked on November 6, 2018 (autumn stocking cohort) and February 26, 2019 (spring stocking cohort) in the same reach of Spavinaw Creek, OK (Figure 1). Fish mortalities were inspected at the hatchery prior to loading fish on the hatchery truck. Fish were transported to the stocking site by hatchery personnel (Crystal Lake Fisheries, Ava, MO). During the autumn stocking, fish were distributed throughout the entire site (~1 km) using small transport containers and all-terrain vehicles. During the spring stocking, Rainbow Trout were stocked in a single pool using a tube attached to the stocking truck. During each stocking occasion, the project Principle Investigator and Oklahoma Department of Wildlife Conservation biologists checked fish condition and ensured tagged fish were distributed evenly among untagged fish.

Detection of tagged fish. – I began actively tracking tagged Rainbow Trout approximately 3 wk after the autumn stocking in Spavinaw Creek. I actively tracked at 2 – 3-wk intervals throughout winter 2018 and spring 2019 as safe discharge conditions allowed (Table 1). From early May through early June 2019, excessive flooding prevented active tracking (Figure 4). Active tracking resumed at monthly intervals beginning in late June. Hereafter, I refer to tracking occasions prior to May flooding (tracking occasions 1 – 10) as the first tracking period and tracking occasions post flooding (tracking occasions 11 – 13) as the second tracking period.

I used two floating PIT-tag antennas (hereafter “floating array”) to actively located tagged Rainbow Trout throughout my study segment. My floating array design was similar to the raft-based design outlined in Fetherman et al. (2014) except I towed my floating array using kayaks. Briefly, my floating array consisted of two antennas made using 12 American Wire Gauge stranded wire that I ran through an approximately 1 x 1.5 m² PVC frame (Figure 2). Each

antenna was connected to the same multi-antenna reader (Oregon RFID, Portland, Oregon) housed in one of the two kayaks along with a 12-volt deep-cycle battery to provide power to the reader box. A floating array was advantageous in Spavinaw Creek because sampling substantial stream distances using other gears (i.e., electrofishing) would be difficult due to heterogeneous habitat characteristics (e.g., alternating deep bluff pools and shallow riffles). In addition, I was able to tow my floating array across the entire study segment under varying discharge conditions which would not have been possible using other gears. I attempted to cover the entire width of Spavinaw Creek using my floating array on each tracking occasion. In wider areas, I focused on each bank separately (i.e., would do repeat passes in wider pools) and prioritized time in areas of structure (e.g., boulders, rootwads, and logs).

Analysis

Apparent survival analysis. – I considered two model designs to estimate apparent survival of Rainbow Trout in Spavinaw Creek. I considered both the Robust Design (Pollock 1982) and the Cormack-Jolly-Seber (CJS) model to analyze my mark-recapture data. I chose to use the CJS model (i.e., only the open-population component of the Robust Design) because survival of each stocking cohort was my primary interest (i.e., births and immigration did not contribute to the study population). Consequently, abundance estimates could be derived from survival rates without estimating additional model parameters (O'Donnell et al. 2010). Using a Robust Design can help partition apparent survival into mortality and emigration but only with extension of the model using additional data like dead-tag recoveries (Kendall 2007). These data were not available during my study; thus, I proceeded with the CJS model.

I used a CJS Model (Cormack 1964; Jolly 1965; Seber 1965) with both time-varying (i.e., changing environmental conditions) and individual-level (i.e., fish TL) covariates (Lebreton et al 1992; Pledger et al. 2003) to estimate weekly apparent survival rates of Rainbow Trout stocked in Spavinaw Creek. The CJS model is commonly used to estimate apparent survival and detection

probability of animals under the open population assumptions. The model framework is robust to bias via random temporary emigration (Kendall et al. 1997) but true mortality and permanent emigration are confounded; thus, estimates are subsequently reported as apparent survival.

I estimated emigration effects on apparent survival during the first tracking period using the both a fixed array installed at the upstream end of my study segment and additional tracking efforts upstream of my study segment. Using my fixed array, I classified individuals as permanent emigrants if they were detected leaving the study segment (i.e., moving upstream through the antennas) and were not detected again in any subsequent active tracking occasion. I followed methods in Spurgeon et al. (2015) to account for fish permanently leaving the study area and adjusted apparent survival rates accordingly. I calculated the number of tagged fish estimated living on each tracking occasion by multiplying the previous occasion's estimate by the weekly survival rate for the following time interval, raised to the exponent of the interval length. I then removed the number of emigrated fish from my estimate of remaining stocked fish. Lastly, adjusted survival rates were calculated using the following equation:

$$\left(\text{predicted No. at occasion}(x)\right) / \left(\text{predicted No. at occasion}(x-1) - \text{No. leaving}\right)^{\wedge (1 / \text{interval length})}$$

I did not use detections from the downstream fixed array to adjust my survival estimates because this array was installed only for the collection of movement data (i.e., was not installed at the downstream extent of the tracking segment). In addition to accounting for emigration using detections at my upstream fixed array, I investigated upstream dispersal by conducting additional active tracking efforts in an upstream portion of Spavinaw Creek, Arkansas. I actively tracked July 1st – 3rd, 2019 on an additional ~2.5-km segment located 9 km upstream of the stocking location.

The CJS model has six assumptions:

- 1) *each marked individual in the segment at time i has the same probability of being detected,*
- 2) *each marked individual at time i has the same chance of survival to time $i + 1$,*
- 3) *marks are neither lost nor overlooked and are recorded correctly,*

- 4) *sampling periods are instantaneous, relative to the sampling intervals,*
- 5) *all emigration from the segment area is permanent, and*
- 6) *the fate of each animal (i.e., survival) is independent from any other animal.*

Violation of assumption one was my primary concern given I suspected varying habitat contributed to unequal detectability among individuals during sampling occasions. For example, detection efficiency using my floating array was lower in deeper pools compared to shallow water. Consequently, I hypothesized fish using deeper-water habitat would be less likely to be detected. Like temporary emigration, open models such as the CJS are robust to random unequal detectability (Pollock 1982; Kendall 2007). I included a “trap-happy effect” (hereafter, trap effect) to account for possible unequal detection probability among individuals that had and had not been detected on the previous tracking occasion (Pledger and Efford 1998). I hypothesized that if heterogeneous habitat influenced individual fish detections, then an individual detected on occasion t would have a higher detection probability on occasion $t+1$ if continuing to use the same habitat (e.g., using shallow water where array detection efficiency was high). My trap effect was treated as a dummy variable (i.e., indicator variable) where a 1 assigned at tracking occasion X for fish i reflected an individual detected on the previous occasion (Laake and Rexstad 2017).

In addition to a trap happy effect, I hypothesized three additional variables related to variable detection during different tracking occasions (Table 2). I considered “effort” in my model as a measure of the number of days (range 2 – 4) that contributed to each tracking occasion. I also used hourly discharge data from the nearest USGS gauge (USGS stream gauge 071912213, Colcord, OK) to calculate the average discharge during each tracking occasion. I used hourly discharge data from 12:00 am on the first day of tracking through 11:00 pm on the last day of tracking to estimate average discharge on each tracking occasion. Discharge may influence tag detection when using floating arrays (O’Donnell et al. 2010). I also allowed detection to vary over time by treating time as a factor with ten levels for the first survival model and three levels for the second survival model (see below). My hypothesis was the relationship

between time and detection was not linear; instead, I treated time as an indicator variable where each level was interpreted with respect to the reference (i.e., the first detection event for each tracking period). Lastly, I included a fixed parameter (i.e., non-varying detection) that allowed me to test if detection changed over each tracking occasion or remained constant.

The inclusion of predictor variables for survival is an important consideration when designing mark-recapture models (Table 2). The variables I hypothesized would be relevant to Rainbow Trout survival were stocking cohort (i.e., season when fish were stocked), TL, and time since stocking (tracking occasion). The timing (i.e., season) of fish stocking is often an important consideration when examining post-stocking survival because conditions may be variable among seasons (e.g., Carlson and Letcher 2003; Hartman et al. 2012). In addition, individual variation such as TL may contribute to differences in post-stocking survival. For example, Carlson and Letcher (2003) found larger, recently stocked Rainbow Trout had greater survival during winter months when compared to smaller Rainbow Trout. Lastly, survival rates may vary with time so I included time as a continuous variable where I hypothesized the relationship would be linear and survival would increase or decrease over time. Bettinger and Bettoli (2002) found survival rates of stocked Rainbow Trout were lowest immediately following stocking in the Clinch River, Tennessee, and generally increased thereafter. Like detection, I also considered a fixed survival coefficient in my parameter set to determine if survival rates were constant during my study. I created parameter sets using all variable combinations for each tracking period (Table 3).

I developed two CJS models to quantify weekly Rainbow Trout survival. The two models were developed to quantify survival during the two tracking periods (i.e., tracking periods 1 and 2). I constructed separate CJS models for the two tracking periods because I hypothesized apparent survival would increase through the first period following autumn stocking but decrease through time during the second tracking period as summer water temperatures increased. Additionally, the flooding during May and June presented a logical breakpoint in the dataset. I was able to maintain separate apparent survival estimates of the two stocking cohorts (autumn

and spring) within each of the two models. For both models, I adjusted time intervals appropriately between sampling occasions following guidelines outlined in Cooch and White (2007) and Laake and Rexstad (2017) so that model estimates represented weekly survival rates.

I fitted each model using program MARK (White and Burnham 1999) through the Rmark interface (version 2.2.6, Laake 2013) in the statistical program R (version 3.6.0, R core team 2019). I standardized all continuous variables to a mean of zero and a standard deviation of one for easier interpretation of model estimates. I used all possible combinations of my parameters (Table 3) to generate my candidate model set ($N = 81$) because sub-setting variables can bias the relative importance of specific predictors (Doherty et al. 2012). I used Akaike's Information Criterion adjusted for small sample size (AICc, Burnham and Anderson 2002) to rank my candidate models. I accounted for over dispersion in my data by calculating Fletcher's c -hat (Fletcher 2012) for the most parameterized model. Fletcher's c -hat is better-suited for mark-recapture data because it allows for dispersion of observations across a large number of encounter histories like those generated in mark-recapture studies (Cooch and White 2007; Laake and Rexstad 2017; Bond et al. 2019). I determined over dispersion to be 1.05 and 2.74 for the first and second tracking dataset, respectively. I applied the c -hat value to the entire candidate model set (i.e., applied to each model AICc). Consequently, I determined the model with the most support using QAICc which accounts for the effect of over dispersion by adjusting the AICc values associated with each model.

Directional movement analysis. – I characterized daily directional movement using data collected at my two fixed arrays throughout my study duration. These data represent point-in-time detections of tagged Rainbow Trout as they passed through each array location. Directionality was determined by the order a fish passed through the two antennas at each array during a 24-h period. Based on an initial evaluation of my data, I found that Rainbow Trout movements were most common from dusk to dawn. Consequently, I defined a 24-h period as 12:00 pm to 11:59

am of the following day so that the period of highest movement was encompassed in the same 24-h interval. I coded detections over each 24-h period as one of the following 1) an upstream movement, 2) a downstream movement, 3) a non-directional movement (i.e., detected at both antennas but with the first and last detection by the same antenna), and 4) single detections (detected at only one antenna). However, I did not incorporate single detections into my dataset because I could not determine if these were directional movements not captured due antenna malfunction or tag interference (i.e., multiple tagged fish crossing the antenna at the same time).

I developed separate generalized linear mixed models (GLMM) for upstream and downstream movement because these models assume each variable is linearly related to the response variable. For example, some predictor variables may drive increased movement probability in either direction (i.e., upstream or downstream) and this relationship would not be captured using a single model. I coded movements as a binary response where movement in the direction of interest was coded as one and movement in either the opposite direction or a non-directional movement was coded as zero (Spurgeon et al. 2015). The resulting models estimated the probability of an upstream or downstream movement related to several predictor variables I hypothesized related to directional movement.

I considered temperature, discharge, and TL as fixed effects and fish identification (PIT tag number) and array location as random effects in both GLMMs examining directional movement. I included both stream temperature and stream discharge as environmental predictors given their influence on fish movement patterns (Hartman et al. 2012). For example, both seasonally increasing discharge (Bettinger and Bettoli 2002; Mellina et al. 2005) and daily discharge fluctuation (Ovidio et al. 1998; Heim et al. 2016) drive directional movement in stream fishes including salmonids. I averaged hourly discharge (USGS stream gauge 071912213, Colcord, OK) over each 24-h period (i.e., average discharge), and calculated discharge change over each 24-h period. Discharge change represented either a decrease (i.e., negative values) or increase (i.e., positive values) in discharge over 24 h. I also calculated the discharge change for

the 24-h period following each fish detection (discharge change_{t+1}) because fishes may move prior to discharge fluctuation by responding to changes in barometric pressure and rainfall (Guy et al. 1992; Dedual and Jowett 1999). Temperature also drives fish movement patterns, particularly in marginally suitable habitat where water temperature may approach lethal thresholds (Baird et al. 2006; Runge et al. 2008). I calculated maximum water temperature (temp_{MAX}) for each 24-h period because maximum temperature, rather than average temperature, may better explain movement and survival in warmwater streams where diel temperature fluctuation is highly variable (Shelton et al. 2018). All environmental predictors were calculated using hourly data from 12:00 pm to 11:00 am of the following day. Lastly, I included TL as an individual-level covariate because fish size can be positively correlated with salmonid movements (e.g., Brown Trout, Quinn and Kwak 2011). I included fish (i.e., PIT tag number) and the location of the fixed array (upstream or downstream) as random effects in each movement model to control for unexplained variation and the effects of nested observations (Wagner et al. 2006; Gelman and Hill 2007). The random effect of fish accounted for multiple observations on the same individual over time (i.e., temporal pseudoreplication), and the array location accounted for site-specific differences at the two arrays that may have contributed to directional movements.

I fitted two GLMMs (upstream and downstream movement) with a logit link and binomial error distribution using the package lme4 (Bates et al. 2015) in the statistical software R (version 3.6.0, R Core Team 2019). The models predicted the probability of upstream or downstream movement. I standardized all continuous predictor variables to a mean of zero and standard deviation of one prior to analysis to facilitate model convergence and interpretation (Gelman and Hill 2007). I tested for correlation among all predictor variables using Pearson's correlation coefficient and omitted multicollinear predictor variables ($r > |0.28|$; Graham 2003) from the same model (Appendix C, Table 1). I generated an *a priori* candidate set of models using combinations of the remaining uncorrelated predictor variables (N=16 for each model, Table 4).

Once I fit each candidate model set, I ranked my models and used binned residuals to assess top model fit. I ranked models using AICc and selected my top model based on the lowest AICc value (Burnham and Anderson 2002). I used binned residuals generated with the R package Arm (Gelman and Su 2016) to assess the fit of my top-ranked model. I expected approximately 95% of generated points to fall within the theoretical error bounds if model fit was appropriate using a binomial distribution (Gelman and Hill 2007). I calculated both the conditional R^2 (variation explained by both predictor variables and random intercepts) and marginal R^2 (variation explained by predictor variables; Nakagawa and Schielzeth 2013) for my final model using the R package MuMIn (Barton 2018).

Movement distance and dispersal. – I characterized the coarse distances moved by tagged Rainbow Trout and overall dispersal of each stocked Rainbow Trout cohort. I established GPS points along the thalweg of my study segment at 100-m increments (i.e., bins) and recorded the time (1 sec) each bin was passed during active tracking occasions (Fetherman et al. 2014). I spaced the GPS locations 100-m apart to characterized coarse movement patterns while avoiding movements due to a behavioral response to my tracking activities (e.g., displacement within the same pool). I related the detection times of tagged fish obtained during my active tracking occasions to the times associated with the GPS points taken at each 100-m bin to place detected fish within the appropriate bin. Detection times associated with each tagged fish (1 sec) were recorded by the multi-antenna reader I used during each active tracking occasion. I used the bin location of each fish's first detection rather than the stocking bin location as a starting point for movement and dispersal estimates because fish were stocked in different channel units across ~1 km of stream during autumn. I used the first fish detection on each tracking occasion for my movement analysis because it was possible to detect the same fish over consecutive days during each occasion. I scaled movements between detections so that distances were comparable between tracking occasions. Most tracking occasions occurred at 2-wk intervals, but some

intervals were longer (e.g., tracking occasions during the second tracking period were at monthly intervals). To facilitate comparisons of movement distance between tracking occasions during my entire study period, I scaled movements to a rate of 2-week intervals (i.e., distances moved between detections during the second tracking period were divided by two). Using these data, I calculated the following metrics for each stocking cohort and each tracking occasion: 1) the percent of detected fish that moved up, down, or remained in the same bin, 2) the average bin movement (100 m) in each direction and 3) the maximum bin movement in each direction (100 m).

RESULTS

Tagging and stocking. – I PIT tagged a subset of Rainbow Trout from the autumn and spring stocking cohorts, and there were differences in the overall size structure and condition of the two stocked cohorts. There were 1,360 kg of Rainbow Trout stocked in both autumn and spring. I tagged 495 Rainbow Trout in autumn and 605 in spring. The average TL of fish tagged during the spring was larger than those fish tagged in autumn (Figure 3); consequently, 32-mm tags were used almost exclusively for marking fish during the spring. I used 200 23-mm tags and 295 32-mm tags to tag the autumn stocking cohort. I used five 23-mm tags and 600 32-mm tags to tag the spring stocking cohort. The average TL of the autumn stocking cohort was 292 mm (minimum – maximum: 100 mm – 530 mm). The average TL of the spring stocking cohort was 380 mm (minimum – maximum: 220 mm – 490 mm). Based on the size distribution of each stocking cohort, the estimated number of fish stocked was 4,492 during autumn and 2,000 during spring. Consequently, PIT-tagged fish represented 10% and 30% of the estimated total number of fish stocked in both autumn and spring, respectively. Tagged Rainbow Trout stocked in autumn appeared in better condition than those tagged and stocked in the spring (i.e., more instances of fin rot and missing fins in spring cohort fish).

I had low mortalities associated with my PIT tagged Rainbow Trout. Both tagged cohorts were held at the hatchery 1-week post tagging. There were two mortalities associated with my autumn fish tagging. No mortalities of tagged Rainbow Trout were found following spring tagging.

Detection of tagged fish. – I detected 715 tagged fish at least once over 13 active tracking occasions (Table 5). For each cohort, the number of detections was highest immediately following each stocking date. During the first tracking period (occasions 1 – 10), I detected 313 (63%) of the autumn stocking cohort and 284 (54%) of the spring stocking cohort at least one time. During the second tracking period (occasions 11 – 13), I detected 82 and 169 individuals from the autumn and spring stocking cohorts, respectively. Of fish detected in the second tracking period, nine autumn-stocked fish and 65 spring-stocked fish were not previously detected in the first tracking period.

Several tagged fish emigrated from my study segment but none of these tagged fish were detected in Arkansas. I detected 134 uniquely tagged fish using my fixed arrays (~late December 2018 through August 2019). Of these fish, 28 individuals were not detected on any active tracking occasions. Prolonged periods of flooding limited the temporal coverage of my fixed arrays (Appendix C, Table 2). At the upstream array, 40 fish from the autumn cohort and 15 fish from the spring cohort were last detected moving upstream (i.e., out of the study segment) and were not detected again during subsequent active tracking. These fish were considered permanently emigrated from the study segment and were not included in my analyses. I did not detect any tagged Rainbow Trout in Arkansas during the additional active tracking effort in July.

Apparent survival analysis. – Covariates for the best-fit model describing apparent survival differed between the first and second tracking period. The top model for the first tracking period (*model weight* = 0.64; Table 6) had interactive survival terms for $\Phi_{(Time)}$ and $\Phi_{(cohort)}$ and for

$\Phi_{(cohort)}$ and $\Phi_{(TL)}$ and for the respective main effects (Table 7). Detection coefficients were $p_{(time)}$ and the trap effect $p_{(D)}$ (Table 7). For the second tracking period, the top model (*model weight* = 0.15; Table 6) had the fixed parameters $\Phi_{(t)}$ and $p_{(t)}$ for survival and detection, respectively.

The trend in apparent survival rates over the first tracking period were similar among stocking cohorts and were close to adjusted survival estimates that accounted for emigrated individuals. Weekly-survival rates for both stocking cohorts were lowest following stocking and increased steadily over time (Figures 5 and 6). However, the initial apparent survival rate was lower for the spring stocking cohort (0.77 weekly survival rate, 0.68 – 0.84 95% CI) compared to the autumn stocking cohort (0.90 weekly survival rate, 0.88 – 0.92 95% CI). Increasing TL was positively related to higher apparent survival though only for the spring stocking cohort (i.e., weekly survival was essentially the same regardless of fish TL in the autumn stocking cohort). Detections using the fixed arrays indicated emigration did not substantially contribute to apparent mortality for either the autumn or spring stocking cohorts during the first tracking period (Table 8). All adjusted survival rates fell within the 95% CI intervals of survival rates from the unadjusted CJS model. Using apparent survival rates from my CJS model, I calculated 44% and 56% Rainbow Trout from the autumn and spring cohorts, respectively, were still alive within my study segment at the end of the first tracking period (end of April).

During the second tracking period, apparent survival rates were constant over time and did not vary by stocking cohort or TL. The top model indicated a fixed weekly survival rate of 0.93 (95% CI: 0.89 – 0.95) over the second tracking period (June 30th through September 22nd, 2019). This suggests that cumulative summer survival was 39% and did not differ by cohort. Detection was also estimated to be constant during this period (0.70, 95% CI: 0.55 – 0.83).

Directional movement. – The top models examining both upstream and downstream movements by Rainbow Trout had an interaction between average discharge and the discharge change during

the same 24-h period (Table 4 and Table 9). The following 24-h discharge change (discharge change_{t+1}) was not included in either model. As expected, the response to each variable (increased or decreased probability) differed between upstream and downstream movement with the interaction effect having the strongest relationship with movement in both models (Table 9 and Figure 7). The upstream movement probability increased with increasing 24 h discharge change at all by the highest average 24 h discharge levels (Figure 7). Conversely, the downstream movement probably increased with decreasing 24 h discharge change (Figure 7). Despite these relationships, both models explained little variation in directional movement (marginal R²: 0.07 and 0.08 for downstream and upstream, respectively). The inclusion of random effects in each model increased model fit (conditional R²: 0.11 and 0.21 for downstream and upstream, respectively). I evaluated the residuals of each model and determined the fit was reasonable using a binned plot and theoretical error bounds (Appendix C, Figure 1).

Movement distance and dispersal. – Movement distances by the majority of tagged Rainbow Trout were limited and consistent throughout my study period. Most Rainbow Trout remained within the same bin between tracking occasions (Table 10). Of individuals that did move between bins, movement distances ranged 1 to 3 bins (i.e., 100 to 300 m) when scaled to a rate of 2-week intervals (Table 10). Average downstream movements between bins were slightly greater than average upstream movements and maximum downstream movements were on average, much higher than upstream movements. The maximum downstream movement rate was 27 bins (i.e., 2,700 m) per 2 weeks, and the maximum upstream movement rate was 8 bins (i.e., 800 m) per 2 weeks.

Binned detection results indicated overall dispersal from the stocking location was minimal over time but with much individual variation. By the end of the first tracking period (i.e., end of April), most remaining tagged fish (93%) still occurred within ~ 1 km of the stocking site (Figure 8). Even after the prolonged period of high flows in May and June, clustering around the

stocking location was still apparent (Figure 8). During my active tracking, the greatest downstream detection distances were 4.1 km (autumn stocking cohort, 4/10/2019) and 4.3 km (spring stocking cohort, 8/5/2019) from the stocking location.

DISCUSSION

I found Rainbow Trout had relatively high survival throughout the summer in a relatively unaltered warmwater stream with patchy groundwater contribution. Summer survival rates of stocked salmonids are often improved through their use of resources like groundwater seeps or springs in lotic systems (Baird and Krueger 2006; Runge et al. 2008) and thermal stratification in lentic systems (Barwick et al. 2004). Summer survival rates may be reduced for Rainbow Trout stocked in warmwater streams at similar latitudes but with minimal or no groundwater contribution (Ray et al. 2012; Erskine et al. 2017; Flowers et al. 2019), highlighting the importance of these resources for coldwater species stocked in warmwater environments (Ebersole et al. 2003). Additionally, high rainfall in spring and summer during my study would result in higher than average groundwater contributions to Spavinaw Creek throughout the summer. Years with higher groundwater contributions would be expected to relate to higher survival rates of Rainbow Trout compared to years of average or below-average rainfall.

Lower survival rates are common for recently stocked salmonids and may be related to predation and lack of adaptation to natural stream conditions. I found apparent survival was lower in Spavinaw Creek following stocking but was relatively high thereafter. Bettinger and Bettoli (2002) reported high mortality rates in the 2-wk period following Rainbow Trout stocking in a Tennessee tailwater. Similarly, High and Meyer (2009) observed high mortality for catchable size Rainbow Trout following stocking in an Idaho stream. Similar patterns of low post-stocking survival among other salmonid species are common (e.g., Brook Trout, Ersbak and Haase 1983; Brown Trout *Salmo trutta*, Berg and Jorgensen 1991). Predation from birds often contributes to mortality of both stocked and wild salmonids (Kennedy and Greek 1988; Evans et al. 2016;

Evans et al. 2019) and may have contributed to increased mortality following my stocking events. Rainbow Trout are more susceptible to bird predation than many other salmonid species (e.g., Brook Trout and Splake *Salvelinus fontinalis* × *Salvelinus namaycush*, Matkowski 1989). Evans et al. (2019) estimated avian predation accounted for 42 – 70% of total mortality in Steelhead (i.e., anadromous Rainbow Trout) released in the Columbia River and Modde et al. (1996) reported that up to 32% of recently stocked Rainbow Trout were consumed by Cormorants *Phalacrocorax auritus* and Grebes *Aechmophorus occidentalis* in southern Utah. Large numbers of Bald Eagles *Haliaeetus leucocephalus* overwinter in eastern Oklahoma including Spavinaw Creek where they target prey including fishes (Lish 1973; Oklahoma Department of Wildlife Conservation). Additional species in this region may also consume stocked trout (e.g., Great Blue Heron *Ardea Herodias*, Hodgens et al. 2004 and River Otter *Lontra Canadensis*, Harvey et al. 2005). In addition to predation, delays in transitioning from hatchery to natural food (Ebert and Filipek 1991; Fenner et al. 2005) and a lack of natural stream-fish behavior (e.g., not using cover and velocity refuge) may decrease survival of Rainbow Trout and other salmonids immediately following stocking (Dickson and McCrimmon 1982; Brown and Laland 2001; Weber and Fausch 2003; Orlov et al. 2006). Recently stocked salmonids may occupy unfavorable microhabitats (Pollard and Bjornn 1973), feed less (Bachman 1984) and avoid cover (Mesa 1991), resulting in reduced survival. In addition, Ebert and Filipek (1991) noted the relationship between low post-stocking survival and a lack of natural prey in the diets of Rainbow Trout. Consequently, higher post-stocking mortality was expected due to predation risk and ability of newly stocked fish to successfully navigate the stream environment.

Increased apparent survival over time by both stocking cohorts may relate to adaptation of habitat use and natural feeding and to reduced competition among trout as fish densities decreased. Hatchery-raised fishes are typically not well adjusted to feeding or antipredator behaviors (Ebert and Filipek 1991; Brown and Laland 2001) and it is possible stocked Rainbow Trout became better adapted to the natural stream environment over time. Orlov et al. (2006)

found stocked Atlantic Salmon *Salmo salar* transitioned to natural feeding behaviors and had diet compositions similar to wild Atlantic Salmon after approximately one month. Hatchery rearing is related to behavioral changes in fishes (Berejikian et al. 1996). Interjecting predatory experience in the hatchery can quickly improve a fish's response (Olla and Davis 1989; Olla et al. 1998); however, fish were not conditioned at the hatchery during my study. Possible density-driven competition over food and habitat resources may also decline after the initial high mortality rate and dispersal of stocked Rainbow Trout (Ellis et al. 2005; Flowers et al. 2019). I speculate suitable water temperatures ($< 25^{\circ} \text{C}$, Matthews and Berg 1997) and time to adjust to living in a lotic environment (Mesa 1991) contributed to higher survival of stocked Rainbow Trout over time.

Weekly survival rates varied among stocking cohorts (autumn and spring) after initial stocking and may relate to fish condition, physicochemical conditions, stocking protocol, or individual heterogeneity. The first weekly survival estimate was higher for Rainbow Trout stocked in autumn compared to those stocked in the spring. The general condition of individuals in the spring cohort was poor compared to those stocked in autumn. I observed fish in the spring cohort with lesions, missing or eroded fins, and other signs of stress at the hatchery. The general condition of stocked fish relates to initial survival following stocking (Heimer et al. 1985; Cowx 1994; Hyvarin et al. 2004). Fish hauled in tanks and immediately released in their new environment are already stressed, increasing fish vulnerability to changes in physicochemical conditions (Strange et al. 1978; Mock and Peters 1990). Specifically, stress can alter social behaviors (Cresswell and Williams 1983; Olla et al. 1992) and make fish more vulnerable to infection (Shepherd and Bromoage 1992). Stocking protocol is also a factor that relates to trout survival (Dexter and O'Neal 2004). The Rainbow Trout stocked in autumn were distributed throughout ~ 1 km of stream, whereas Rainbow Trout stocked in the spring were introduced to a single large pool. It is possible that stocking in a single location increased susceptibility to avian predators (see previous paragraph) and higher fish densities increased fish stress and aggression

(Olla et al. 1992). It is also possible autumn-stocked Rainbow Trout experienced a period of learning to acquire stream resources and were competing with the newly introduced fish (Dickson and McCrimmon 1982; Weber and Fausch 2003; Orlov et al. 2006). Mesa (1991) showed lower survival rates in recently stocked Cutthroat Trout via wasted energy through aggressions towards resident Cutthroat Trout and were often displaced to higher-velocity habitat. Interestingly, larger Rainbow Trout in the spring cohort (> 450 mm TL) had similar post-stocking survival rates compared to fish in the autumn cohort. If intraspecific habitat interactions were a contributing factor for spring stocked fish (e.g., Mesa 1991), then larger fish from the spring cohort may have held higher hierarchical social positions and successfully competed with autumn stocked fish (Abbot et al. 1985; Huntingford et al. 1990; Hughes 1992).

Summer survival rates were relatively low and constant across both cohorts of Rainbow Trout and may have resulted from increased water temperature during the second tracking period (Dickerson and Vinyard. 1999; Xu et al. 2010). The average water temperature during the second tracking period was 22 °C and maximum daily water temperatures commonly exceeded 25 °C. General guidelines for Rainbow Trout management and conservation indicate 19 °C and 24 °C as chronic and acute thermal thresholds, respectfully (Nevada Department of Environmental Protection; Shelton et al. 2018). Despite the reduced survival rates, apparent summer survival remained surprisingly high given available water temperatures in Spavinaw Creek. Thermal tolerances vary with strain of Rainbow Trout and can improve summer survival in warmwater streams (Hartman and Porto 2014). The Emmerson strain of Rainbow Trout has a higher thermal tolerance compared to many other strains (Brewer, *unpublished data*), making it popular for stocking at southern latitudes. In addition, selected habitat that serves as thermal refuge is common among salmonids in warmer climates (e.g., Torgersen et al. 1999; Ebersole et al. 2003; Brewitt et al. 2014, see also Chapter 2) and may have increased summer Rainbow Trout survival in Spavinaw Creek. The Ozark Highlands ecoregion is emblematic of karst topography and has various levels of groundwater contribution (Gore 1952; Czarnecki et al. 2009; Zhou et al. 2019).

Groundwater contribution likely created thermal refugia for Rainbow Trout and native warmwater species during summer (see Chapter 2). Thermal refugia available during the wet-year conditions encountered during my study (195 cm of rainfall since Jan. 1, 2019, Oklahoma Climatological Survey, https://climate.ok.gov/index.php/climate/rainfall_table/local_data, accessed 10/31/2019) would be expected to be higher than average; consequently, the Rainbow Trout summer survival rates I reported may be higher-than-average for even this study system. Future efforts would benefit from examining survival across multiple years to determine cyclical patterns of survival.

Angler harvest was likely not a substantial contributor to mortality of stocked Rainbow Trout in Spavinaw Creek. In most warmwater streams, Rainbow Trout are stocked as put-and-take fisheries where harvest is high (Patterson et al. 2016; Hyman et al. 2016) and subsequent survival (i.e., persistence) is low (Bettinger and Bettoli 2002; Flowers et al. 2019). For example, harvest contributed substantially to the total mortality rate across a range of environmental conditions (e.g., Heimer et al. 1985; Bettinger and Bettoli 2002; Flowers et al. 2019). Fishing within the immediate stocking area of Spavinaw Creek was restricted to catch and release (per angling group regulations). Additionally, private land ownership outside the immediate stocking area limited public angling. Although it is unlikely many Rainbow Trout were removed from the study segment via angling, catch and release efforts may have reduced survival rates via hooking and handling mortality. Schisler and Bergersen (1996) reported an average mortality rate of 3.9% for released Rainbow Trout caught with artificial flies. Angling related mortality may also relate to other factors I did not consider including bait type (Schill 1992), angler experience (Meka 2004), fish size (Huhfer and Alexander 1989; Meka 2004), and hook type (Schisler and Bergersen 1996; Meka 2004).

I found a time effect and a trap effect contributed to variable detection between tracking occasions and among individuals during my first tracking period. I hypothesize that the majority of detection variation over time was due to discharge fluctuation between tracking occasions

(O'Donnell et al. 2010); however, a time effect was indicated as a better predictor of detection compared to discharge alone using my model ranking approach and likely accounted for additional detection variation beyond discharge. For example, high concentrations of fish near the stocking location after initial stocking may have increased detection probability during initial tracking occasions (Ivasauskas and Bettoli 2011). The retention of the trap effect was interesting and suggests that fish detected on a previous tracking occasions had a greater detection probability on the subsequent tracking occasion. Differing water depths influences PIT-tag detections using floating arrays (O'Donnell et al. 2010; Zentner and Wolf *unpublished data*); thus, fish that occupied deeper habitats (e.g., bluff pools 2 – 3-m deep) were likely not detected. Fish associated with shallower habitat may have been easier to detect on initial occasions and on subsequent tracking occasions if they remained in the same area.

The effect of emigration should be considered in open population models where apparent survival is reported (Pledger et al. 2003). Emigration can affect apparent survival estimates (e.g., Pine et al. 2003; Spurgeon et al. 2015), though my analysis did not suggest substantial emigration to be a major contributor to perceived mortality. Without continuous operation of either fixed array or estimates of downstream emigration from my study segment, I cannot report survival estimates as true survival. Instead, I suggest that unadjusted estimates from apparent survival analysis are good approximates of true survival in Spavinaw Creek.

Tag fate is also an important consideration when analyzing mark-recapture data relying on tag detections. Tags lost from a fish (i.e., sheds) that remain in the study system are problematic because they may continue to be detected and incorrectly classified as living fish (O'Donnell et al. 2010). Shed tags are most likely to occur immediately following tagging or during spawning activities (Bateman et al. 2011). High tag retention rates for salmonids are well established (e.g., 99% retention in Rainbow Trout, Meyer et al. 2011; Flowers et al. 2019) and other coldwater species (Cutthroat Trout, Bateman and Gresswell 2009; Brook Trout and Brown Trout, Dieterman and Hoxmeier 2009). I did not observe any spawning activity among Rainbow

Trout; thus, spawning activity is unlikely to be a contributing factor to lost tags. However, tags may accumulate in the study segment as fish die (i.e., “ghost tags”, see Bond et al. 2019). In some systems, it may be possible to actively check each detection while tracking and recover shed or ghost tags (O’Donnel et al. 2010; Hodge et al. 2015). Given the size of my floating array, width and depth of Spavinaw Creek, and the behavior and density of Rainbow Trout (i.e., multiple detections occurring simultaneously), it was not possible to pinpoint ghost tags in the substrate. In rare instances (< 5) where a detection could be attributed to a lost tag (e.g., detection in a clear, shallow riffle without cover), the tag ID was removed from the entire dataset because the fate of the fish was unknown. Additionally, all detections were indicated by a Piezo Buzzer (Oregon RFID, Portland, Oregon), and I was often able to visually confirm the presence of trout (but not necessarily individuals in groups) during detections. Based on the habitats selected (see Chapter 2), shed tags within the stream would be most likely in deeper pools out of my detection range. Because I speculated avian predation was relatively high, it is also likely that shed tags were deposited outside of the stream channel (Frechette et al. 2012; Teuscher et al. 2015).

Upstream and downstream movements were related to discharge changes during my study, but additional factors I did not consider may also affect fish movement. Upstream movements may result from spawning cues in more-natural systems (Dedual and Jowett 1999; Venman and Dedual 2005); thus, Rainbow Trout in my study may have had some evolutionary trait to move upstream in response to increasing flows. More often, movements of stocked salmonids are in the downstream direction (Cresswell 1981; Helfrich and Kendall 1982; Bettinger and Bettoli 2002, Flowers et al. 2019). For example, a synthesis of post-stocking movements of Brook Trout and Rainbow Trout showed overall downstream movements (Cresswell 1981). Many studies only examine stocked fish over larger temporal scales (e.g., weekly or monthly, Helfrich and Kendall 1982; Bettinger and Bettoli 2002) and are unable to capture event-specific phenomena that my fixed arrays allowed. Some fish were detected moving both upstream and downstream during my study. Consequently, it is possible that stocked Rainbow Trout typically

move and disperse in a downstream direction (Cresswell 1981) but move upstream due to key environmental cues (e.g., changing discharge). Given the low amount of variation my data explained (marginal R^2), it is possible that other unmeasured environmental drivers (e.g., seasonal cues outside of temperature like photoperiod, Mellina et al. 2005; Falke et al. 2017) also contributed to directional movements. It is also possible that individual heterogeneity contributed to movement patterns with some fish moving upstream and some moving downstream irrespective of environmental conditions. Future studies that include additional fixed arrays to increase detections may provide additional information of factors related to directional movement.

Movement distance and subsequent dispersal patterns of Rainbow Trout from the stocking location were typically minimal with some individual heterogeneity. Flowers et al. (2019) reported movement rates of 0.03 – 0.13 km/day for Rainbow Trout in three unregulated North Carolina streams. When scaled to the interval length of my study, their reported movement rates were similar to my findings (42 m – 182 m over two weeks). Little to no movement in salmonid populations is not uncommon (e.g., Bettinger and Bettoli 2002; High and Meyer 2011) and hatchery-reared fishes may not be conditioned to move substantial distances (Helfrich and Kendall 1982). Minimal movements over each two-week period resulted in the majority of my fish remaining within 1 km of the stocking location during the entire study. However, greater dispersal distances by some individuals during my study (> 14 km) and other studies (> 12 km, Bettinger and Bettoli 2002; > 10 km, High and Meyer 2009; > 11 km Flowers et al. 2019) highlights individual heterogeneity in dispersing populations and supports the idea of leptokurtic dispersal patterns (Radinger and Wolter 2013). Continued monitoring at a greater spatial scale would benefit our understanding of how dispersing individuals interact with native species outside of the immediate stocking area. The temporal scale of tracking efforts should also be considered as small, frequent movements (e.g., daily movements within a fish's home range) may not be captured over greater (e.g., weekly) monitoring intervals. For example, Bunnell et al.

(1998) used hourly measurements and found Brown Trout moved over 80 m each day but displacement between the start and end of each 24-h period was typically less than 10 m. Consequently, inferences on movement distance are limited by the tracking intervals during my study and highlight how movement distance may differ from overall dispersal over time.

Management implications. – If a management objective is to protect native species in Spavinaw Creek, then managers may consider the implications of potential interactions between Rainbow Trout and native species over thermal resources. My results suggest that under the environmental conditions encountered in my approximately 1-year study, Rainbow Trout had the ability to persist throughout warm summer months. Their persistence may relate to use of distinct habitat resources (i.e., groundwater seepage areas) to survive these warm periods (see Chapter 2). Several native fishes of the Ozark Highlands seek similar thermal resources during the summer (Wolf, *unpublished data*; Whitley et al. 2006; Walker et al. 2013). For example, the growth scope of Smallmouth Bass is optimal at 22° C (Shuter and Post 1990; Whitley et al. 2006). During most summers, this is exceeded, and fish are likely to seek cooler refuges (Whitley et al. 2002; Brewer 2013). Other fishes occupying Spavinaw Creek are considered spring associates and tend to seek cooler waters (e.g., Southern Redbelly Dace, Walker et al. 2013). Use of similar resources due to weather patterns may increase the likelihood of species interactions (see Chapter 2). If conservation of native species is a goal, one management consideration may be to limit stocking to autumn. Despite relatively high survival rates throughout the winter and early spring, approximately half (56%) the autumn-stocked Rainbow Trout died by the beginning of the second (i.e., summer) tracking period. However, more work is needed to quantify behavior and diets by stocked Rainbow Trout during winter and early spring when native fish are less active or preparing for the critical spawning period.

My findings from two seasons during a wet year suggest most potential interactions with native fishes would occur within about 1 km of the stocking site. Although a single trout can

show aggressive behaviors toward and consume native species (Turek et al. 2015; Hitt et al. 2017; Elkins et al. 2019), it is unknown what densities are needed to create a population-level effect. The Arkansas portion of Spavinaw Creek has cooler water temperatures and is more likely to favor some reproduction (Bowman 1995; Williams et al. 2011); however, recent surveys suggest persistence at these locations without stocking is also unlikely given the greatly reduced numbers of fish observed over time (Brewer, *unpublished data*). My data suggests over-summer survival is likely during some years (i.e., high groundwater due to excess rainfall) but it is unlikely that persistence over many years would be supported without additional stockings given the frequency of hot and dry years within this basin (5 of the 10 most-recent years received below-average rainfall, Oklahoma Mesonet, https://www.mesonet.org/index.php/weather/monthly_rainfall_table/jayx, accessed 11/1/2019). Future studies would benefit from long-term survival estimates (e.g., multiple years to capture wet and dry cycles)

TABLES

Table 1. Active tracking occasions throughout my study period. Rainbow Trout were stocked prior to tracking occasion one (autumn stocking cohort, 11/6/2018) and tracking occasion six (spring stocking cohort, 2/26/2019). Effort represents the number of days spent attempting to detect tagged fish on each tracking occasion. Discharge was calculated by averaging hourly discharge data over the time interval of each tracking occasion (i.e., 12:00 am on day one through 11:00 pm on last day). Discharge data were obtained by the U.S. Geological Survey stream gauge located nearest to the stocking site (USGS stream gauge 071912213, Colcord, OK).

Tracking occasion	Dates	Effort (days)	Discharge (m ³ /s)
Occasion 1	11/29/2019 – 12/2/2019	4	1.02
Occasion 2	12/17/2019 – 12/19/2019	3	1.16
Occasion 3	1/9/2019 – 1/11/2019	3	5.21
Occasion 4	1/24/2019 – 1/26/2019	3	6.17
Occasion 5	2/8/2019 – 2/10/2019	3	5.13
Occasion 6	2/27/2019 – 3/1/2019	3	4.70
Occasion 7	3/14/2019 – 3/16/2019	3	6.51
Occasion 8	3/27/2019 – 3/29/2019	3	5.38
Occasion 9	4/10/2019 – 4/12/2019	3	5.10
Occasion 10	4/24/2019 – 4/25/2019	2	5.32
Occasion 11	6/28/2019 – 6/30/2019	3	8.46
Occasion 12	8/5/2019 – 8/7/2019	3	4.33
Occasion 13	9/21/2019 – 9/22/2019	2	2.41

Table 2. Predictor variables used for apparent survival (*Phi*) and detection (*p*) components of the Cormack-Jolly-Seber apparent survival model.

Abbreviation	Explanation
Survival	
$\sim \Phi_{(.)}$	Fixed parameter (survival rate constant across time).
$\sim \Phi_{(Time)}$	Continuous variable where survival increased, decreased, or was constant across each tracking occasion.
$\sim \Phi_{(TL)}$	Standardized continuous variable (mean of zero, standard deviation of one) for total length of each fish (mm).
$\sim \Phi_{(cohort)}$	Grouping factor for each stocked cohort, autumn and spring.
Detection	
$\sim p_{(.)}$	Fixed parameter (detection was constant across time).
$\sim p_{(time)}$	Factored variable allowing detection to vary as a unique intercept for each tracking occasion (i.e., N = 10 for first tracking period, N = 2 for second tracking period).
$\sim p_{(effort)}$	Standardized continuous variable (mean of zero, standard deviation of one) for effort (range 2 – 4 days) associated with each tracking occasion.
$\sim p_{(discharge)}$	Standardized continuous variable (mean of zero, standard deviation of one) for discharge associated with each tracking occasion.
$\sim p_{(D)}$	Coded "trap effect" (1 or 0) where 1 represented a detection on the most-previous tracking occasion.

Table 3. Combinations (i.e., parameter lists) of survival (Φ) and detection (p) parameters used for two Cormack-Jolly-Seber apparent survival models used in my analysis. The survival parameter lists differed between the first (top) and second (bottom) tracking period models. All possible combinations of the survival and detection parameter lists were evaluated which resulted in 81 candidate models for each tracking period.

Name	Formula
Survival (first tracking period)	
Phi.dot	$\sim \Phi_{(.)}$
Phi.1	$\sim \Phi_{(cohort)}$
Phi.2	$\sim \Phi_{(cohort)} + \Phi_{(TL)}$
Phi.3	$\sim \Phi_{(cohort)} + \Phi_{(Time)}$
Phi.4	$\sim \Phi_{(cohort)} + \Phi_{(TL)} + \Phi_{(Time)}$
Phi.5	$\sim \Phi_{(Cohort)} * \Phi_{(time)}$
Phi.6	$\sim (\Phi_{(cohort)} * \Phi_{(Time)}) + (\Phi_{(cohort)} * \Phi_{(TL)})$
Phi.7	$\sim \Phi_{(cohort)} * \Phi_{(Time)} + \Phi_{(TL)}$
Phi.8	$\sim \Phi_{(cohort)} * \Phi_{(TL)} * \Phi_{(Time)}$
Survival (second tracking period)	
Phi.dot	$\sim \Phi_{(.)}$
Phi.1	$\sim \Phi_{(Time)}$
Phi.2	$\sim \Phi_{(Time)} + \Phi_{(TL)}$
Phi.3	$\sim \Phi_{(Time)} + \Phi_{(cohort)}$
Phi.4	$\sim \Phi_{(cohort)}$
Phi.5	$\sim \Phi_{(TL)}$
Phi.6	$\sim \Phi_{(cohort)} + \Phi_{(TL)}$
Phi.7	$\sim \Phi_{(Time)} + \Phi_{(cohort)} + \Phi_{(TL)}$
Phi.8	$\sim \Phi_{(cohort)} * \Phi_{(TL)}$
Detection	
p.dot	$\sim p_{(.)}$
p.1	$\sim p_{(time)}$

p.2	$\sim \mathcal{P}(\text{time}) + \mathcal{P}(\text{effort})$
p.3	$\sim \mathcal{P}(\text{discharge})$
p.4	$\sim \mathcal{P}(\text{discharge}) + \mathcal{P}(\text{effort})$
p.5	$\sim \mathcal{P}(\text{discharge}) + \mathcal{P}(D)$
p.6	$\sim \mathcal{P}(\text{time}) + \mathcal{P}(D)$
p.7	$\sim \mathcal{P}(\text{time}) + \mathcal{P}(D) + \mathcal{P}(\text{effort})$
p.8	$\sim \mathcal{P}(\text{discharge}) + \mathcal{P}(\text{effort}) + \mathcal{P}(D)$

Table 4. Results from 16 candidate generalized linear mixed models of upstream and downstream directional movement where $Y_{(ij)}$ is the relative probability of a directional movement, β_0 is the grand intercept, β_1 to β_x are slopes associated with the predictor variables average discharge over 24 h ($\text{Discharge}_{\text{avg}}$; m^3/s), discharge change over 24 h ($\text{Discharge}_{\text{change}}$; m^3/s), the next day (i.e., following 24 h) discharge change ($\text{Discharge}_{\text{changeT1}}$; m^3/s), fish total length (TL; mm), and the daily maximum temperature (Temp_{max} ; °C). All discharge and temperature metrics were calculated from 12:00 pm to 11:00 am of the following day to match of interval length that fish movements were investigated. Two random effects were included for each model, array location (ρ) for location j , and fish ID (ϵ) for fish l . The number of parameters (K) is reported for each model considered. Models were ranked using Akaike’s information criterion adjusted for small sample size (AIC_c) and ΔAIC_c represents the difference between the given model and the top model in terms of AIC_c . Likelihood and Akaike weight (w_i) indicate the relative support for each model. For models with ($\Delta\text{AIC}_c < 2$), the marginal (R^2_m ; variance explained by fixed effects) and condition (R^2_c ; variance explained by fixed and random effects) R^2 are reported.

Model	K	AIC_c	ΔAIC_c	Likelihood	W_i	R^2_m	R^2_c
Upstream							
$Y_{(ijl)} = \beta_0 + \beta_1\text{Discharge}_{\text{avg}(i)} * \beta_2\text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \epsilon_{(l)}$	4	474.78	0.00	1.00	0.32	0.08	0.21
$Y_{(ijl)} = \beta_0 + \beta_1\text{Discharge}_{\text{avg}(i)} * \beta_2\text{Discharge}_{\text{change}(i)} + \beta_3\text{Discharge}_{\text{change}^2(i)} + \rho_{(j)} + \epsilon_{(l)}$	6	475.15	0.37	0.83	0.26	0.09	0.21
$Y_{(ijl)} = \beta_0 + \beta_1\text{Discharge}_{\text{avg}(i)} * \beta_2\text{Discharge}_{\text{changeT1}(i)} + \beta_3\text{Discharge}_{\text{changeT1}^2(i)} + \rho_{(j)} + \epsilon_{(l)}$	6	476.91	2.14	0.34	0.11		
$Y_{(ijl)} = \beta_0 + \beta_1\text{TL}(i) + \rho_{(j)} + \epsilon_{(l)}$	2	477.86	3.09	0.21	0.07		
$Y_{(ijl)} = \beta_0 + \beta_1\text{Discharge}_{\text{change}(i)} + \beta_2\text{Discharge}_{\text{change}^2(i)} + \rho_{(j)} + \epsilon_{(l)}$	3	479.16	4.38	0.11	0.04		
$Y_{(ijl)} = \beta_0 + \beta_1\text{Discharge}_{\text{avg}(i)} + \rho_{(j)} + \epsilon_{(l)}$	2	479.35	4.57	0.10	0.03		

$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{changeT1}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	479.35	4.57	0.10	0.03
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Temp}_{\text{max}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	479.61	4.83	0.09	0.03
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	479.71	4.93	0.08	0.03
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{changeT1}(i)} + \beta_2 \text{Discharge}_{\text{changeT1}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	480.66	5.88	0.05	0.02
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \beta_3 \text{Discharge}_{\text{change}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	4	481.24	6.46	0.04	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Temp}_{\text{max}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	481.29	6.51	0.04	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Temp}_{\text{max}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	481.31	6.53	0.04	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	481.4	6.62	0.04	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Temp}_{\text{max}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	481.68	6.9	0.03	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Discharge}_{\text{changeT1}(i)} + \beta_3 \text{Discharge}_{\text{changeT1}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	4	482.38	7.6	0.02	0.01

Downstream

$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} * \beta_2 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	4	390.56	0.00	1.00	0.51	0.07	0.11
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} * \beta_2 \text{Discharge}_{\text{changeT1}(i)} + \beta_3 \text{Discharge}_{\text{changeT1}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	6	393.46	2.90	0.23	0.12		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} * \beta_2 \text{Discharge}_{\text{change}(i)} + \beta_3 \text{Discharge}_{\text{change}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	6	394.72	4.17	0.12	0.06		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{change}(i)} + \beta_2 \text{Discharge}_{\text{change}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	394.79	4.23	0.12	0.06		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	394.82	4.26	0.12	0.06		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \beta_3 \text{Discharge}_{\text{change}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	4	396.18	5.62	0.06	0.03		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{changeT1}(i)} + \beta_2 \text{Discharge}_{\text{changeT1}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	396.21	5.65	0.06	0.03		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Temp}_{\text{max}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	396.59	6.04	0.05	0.02		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	396.69	6.14	0.05	0.02		
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{avg}(i)} + \beta_2 \text{Discharge}_{\text{changeT1}(i)} + \beta_3 \text{Discharge}_{\text{changeT1}^2(i)} + \rho_{(j)} + \varepsilon_{(l)}$	4	396.94	6.39	0.04	0.02		

$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	397.54	6.99	0.03	0.02
$Y_{(ijl)} = \beta_0 + \beta_1 \text{TL}_{(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	397.82	7.27	0.03	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Temp}_{\text{max}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	398.32	7.76	0.02	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Discharge}_{\text{changeT1}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	2	398.39	7.83	0.02	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Temp}_{\text{max}(i)} + \beta_2 \text{Discharge}_{\text{change}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	399.56	9.01	0.01	0.01
$Y_{(ijl)} = \beta_0 + \beta_1 \text{Temp}_{\text{max}(i)} + \beta_2 \text{Discharge}_{\text{changeT1}(i)} + \rho_{(j)} + \varepsilon_{(l)}$	3	400.37	9.82	0.01	0.00

Table 5. Detections by tracking occasion and date for autumn 2018 and spring 2019 stocking cohorts of tagged Rainbow Trout. The number (No.) detected represents the total number of Rainbow Trout from each cohort that were detected on each tracking occasion. Cumulative indicates the number of Rainbow Trout from each cohort that were detected at least one time up until that tracking occasion. New column represents Rainbow Trout from each cohort that were not previously detected but were detected on that tracking occasion.

Tracking occasion	Dates	<u>Autumn cohort</u>			<u>Spring cohort</u>		
		No. detected	Cumulative	New	No. detected	Cumulative	New
Occasion 1	11/29/2018 – 12/2/2018	213	213	213	NA	NA	NA
Occasion 2	12/17/2018 – 12/19/2018	213	246	33	NA	NA	NA
Occasion 3	1/9/2019 – 1/11/2019	47	260	14	NA	NA	NA
Occasion 4	1/24/2019 – 1/26/2019	61	272	16	NA	NA	NA
Occasion 5	2/8/2019 – 2/10/2019	77	280	8	NA	NA	NA
Occasion 6	2/27/2019 – 3/1/2019	129	297	17	167	167	167
Occasion 7	3/14/2019 – 3/16/2019	73	298	1	114	214	47
Occasion 8	3/27/2019 – 3/29/2019	96	305	7	134	252	38
Occasion 9	4/10/2019 – 4/12/2019	106	311	6	157	293	41
Occasion 10	4/24/2019 – 4/25/2019	84	313	2	153	328	35
Occasion 11	6/28/2019 – 6/30/2019	23	317	4	62	351	23
Occasion 12	8/5/2019 – 8/7/2019	29	321	4	115	382	31
Occasion 13	9/21/2019 – 9/22/2019	25	322	1	79	393	11

Table 6. Comparison of top-ranked Cormack-Jolly-Seber models (i.e., a subset of all models) for apparent survival of Rainbow Trout during the first (top) and second (bottom) tracking periods in Spavinaw Creek, Oklahoma. QAIC_c is the quasi-Akaike’s information criterion adjusted for small sample size and variation using the inflation factor (c-hat; 1.05 and 2.74 for the first and second tracking period, respectively). ΔQAIC_c is the difference in QAIC_c between the given model and the top-ranked model where values less than two indicate substantial support for the given model (Burnham and Anderson 2002). W_i is the QAIC_c weight and can be considered as the probability that a given model is the best approximating model among those in the candidate model set (Symonds and Moussalli 2011).

Rank	Model	K	QAIC _c	ΔQAIC _c	W_i
First tracking period					
1	$\sim\{[Phi_{(Time)} * Phi_{(cohort)} + Phi_{(cohort)} * Phi_{(TL)}][p_{(time)} + p_{(D)}]\}$	17	5876.01	0.00	0.64
2	$\sim\{[Phi_{(Time)} * Phi_{(cohort)} + Phi_{(cohort)} * Phi_{(TL)}][p_{(time)} + p_{(effort)} + p_{(D)}]\}$	18	5878.00	1.99	0.23
Second tracking period					
1	$\sim\{Phi_{(.)}p_{(.)}\}$	2	135.44	0.00	0.15
2	$\sim\{Phi_{(Time)}p_{(.)}\}$	3	137.11	1.67	0.06
3	$\sim\{Phi_{(.)}p_{(time)}\}$	3	137.11	1.67	0.06
4	$\sim\{Phi_{(.)}p_{(discharge)}\}$	3	137.11	1.67	0.06

Table 7. Coefficient estimates (logit scale) and standard error (SE) for apparent survival (Φ) and detection (p) for top-ranked Cormack-Jolly-Seber models during the first (tracking occasions 1 – 10) and second (occasions 11 – 13) tracking occasions in Spavinaw Creek, Oklahoma.

Beta	Estimate	SE
First tracking period		
Φ (Intercept)	2.25	0.13
Φ (Time)	0.12	0.03
Φ (cohort)	-13.80	6.18
Φ (TL)	0.03	0.10
Φ (Time*cohort)	0.79	0.44
Φ (cohort*TL)	0.50	0.19
p (Intercept)	0.41	0.12
p (time2)	-0.53	0.18
p (time3)	-3.01	0.22
p (time4)	-1.87	0.20
p (time5)	-1.56	0.19
p (time6)	-0.52	0.21
p (time7)	-1.60	0.17
p (time8)	-1.34	0.18
p (time9)	-1.17	0.19
p (time10)	-1.46	0.19
p (D)	1.39	0.10
Second tracking period		
Φ (Intercept)	2.58	0.24
p (Intercept)	0.87	0.39

Table 8. Weekly apparent survival rate and rate adjustments during the first tracking period for the autumn and spring stocking cohorts of Rainbow Trout using both active and fixed array detections at the upstream location. Tracking occasions represent the interval corresponding to each survival rate. Interval start date is the date each interval begins and the interval week (wk) describes the length of each interval. “Predicted No.” represents the number of Rainbow Trout estimated to remain in the segment during each tracking occasion as calculated using the equation $\{predicted\ No.\ at\ occasion(x-1)X(weekly\ survival\ rate(x)^{interval\ length})\}$. To calculate “the adjusted weekly survival rates”, I incorporated emigrating fish “Leaving No.” using the equation $\{[predicted\ No.\ at\ occasion(x) / (predicted\ No.\ at\ occasion(x-1) - No.\ leaving)]^{(1 / interval\ length)}\}$. “Adjusted No.” reflects the remaining Rainbow Trout in the system using the adjusted weekly survival rate.

Tracking occasion	Interval (start date)	Interval (wk)	Weekly survival rate (95% CI)	Predicted No.	Leaving No.	Adjusted weekly survival rate	Adjusted No.
Autumn stocking	11/6/2018			495*			495*
Stocking to occasion 1	11/7/2018	3.1	0.90 (0.88 – 0.92)	361	NA**	NA**	NA**
Occasion 1 to 2	12/3/2018	2	0.93 (0.92 – 0.95)	316	NA**	NA**	NA**
Occasion 2 to 3	12/20/2018	2.9	0.95 (0.94 – 0.96)	273	10	0.96	282
Occasion 3 to 4	1/12/2019	1.7	0.97 (.95 – 0.98)	258	8	0.98	275
Occasion 4 to 5	1/27/2019	1.7	0.97 (0.96 – 0.98)	247	3	0.98	266
Occasion 5 to 6	2/11/2019	2.3	0.98 (0.96 – 0.99)	236	0	0.98	254
Occasion 6 to 7	3/2/2019	1.7	0.99 (0.97 – 0.99)	230	4	1	252
Occasion 7 to 8	3/17/2019	1.4	0.99 (0.98 – 0.99)	226	2	0.99	250

Occasion 8 to 9	3/30/2019	1.6	0.99 (0.98 – 1.00)	223	6	1	250
Occasion 9 to 10	4/13/2019	1.6	0.99 (0.98 – 1.00)	220	6	1	250
Spring stocking	2/26/2019						
				605*			605*
Occasion 6 to 7	3/2/2019	1.7	0.77 (0.68 – 0.84)	388	0	0.77	388
Occasion 7 to 8	3/17/2019	1.4	0.94 (0.80 – 0.98)	354	1	0.94	355
Occasion 8 to 9	3/30/2019	1.6	0.98 (0.80 – 0.99)	343	8	0.99	352
Occasion 9 to 10	4/13/2019	1.6	1.00 (0.79 – 1.00)	341	4	1	352

Table 9. Model parameters (Beta), estimates (Estimate), and standard error (SE) associated with my top-ranked upstream (top) and downstream (bottom) directional-movement models. All estimates are on logit scale. The average discharge ($\text{Discharge}_{\text{avg}}$) was calculated using hourly discharge data (USGS 071912213 Spavinaw Creek near Colcord, OK) over each 24-h period (12:00 pm to 11:00 am of the following day). The change in discharge ($\text{Discharge}_{\text{change}}$) was also calculated over each 24-h period (12:00 pm to 11:00 am of the following day) using data from the same gauging station. Asterisks between terms indicate an interactive effect between the two terms.

Beta	Estimate	SE
Upstream movement		
(Intercept)	-0.29	0.23
$\text{Discharge}_{\text{avg}}$	-0.09	0.14
$\text{Discharge}_{\text{change}}$	0.64	0.25
$\text{Discharge}_{\text{avg}} * \text{discharge}_{\text{change}}$	-0.42	0.17
Downstream movement		
(Intercept)	-1.15	0.33
$\text{Discharge}_{\text{avg}}$	0.17	0.14
$\text{Discharge}_{\text{change}}$	-0.71	0.36
$\text{Discharge}_{\text{avg}} * \text{discharge}_{\text{change}}$	0.36	0.14

Table 10. Summary statistics associated with Rainbow Trout movement in Spavinaw Creek, Oklahoma. From December 2018 through August 2019. Percent values are in reference to all fish detected during that tracking occasion with actual number (N) reported for clarity. Fish that remained within the same bin between detections (i.e., moved less than 100 m) were classified as “non-movement”. For each fish, average (avg) and maximum (max) distance (m) is in reference to the previous detection scaled by two-week increments. Negative values represent downstream movement. Positive values represent upstream movement. All average movements have been rounded to the nearest 100 m to match the spatial scale of the study.

Metric	Dec 17	Jan 9	Jan 24	Feb 8	Feb 27	Mar 14	Mar 27	Apr 10	Apr 24	Jun 28	Aug 5
Autumn stocking cohort											
Non movement percent	35 (63)	42 (14)	53 (26)	59 (41)	45 (46)	49 (35)	67 (99)	66 (65)	65 (53)	26 (0)	24 (6)
Downstream movement percent	6 (11)	39 (13)	43 (21)	23 (16)	15 (15)	44 (32)	29 (42)	11 (11)	14 (11)	16 (3)	72 (18)
Upstream movement percent	59 (106)	18 (6)	4 (2)	17 (12)	40 (41)	7 (5)	4 (6)	23 (23)	21 (17)	58 (11)	4 (1)
Avg. downstream movement(m)	-200	-200	-200	-300	-200	-200	-100	-200	-500	-200	-200
Max. downstream movement(m)	-500	-600	1,200	-1,400	-900	-700	-500	-700	-2,700	-500	-400
Avg. upstream movement (m)	200	100	100	100	100	200	200	100	200	200	100
Max. upstream movement (m)	300	300	100	100	200	400	500	100	500	500	100
Avg. movement (m)	100	0	100	0	0	-100	0	0	0	100	-100

Spring stocking cohort

Non movement percent	NA	NA	NA	NA	NA	22 (14)	49 (46)	34 (38)	42 (50)	18 (7)	24 (7)
Downstream movement percent	NA	NA	NA	NA	NA	75 (47)	33 (31)	10 (11)	41 (48)	51 (20)	64 (20)
Upstream movement percent	NA	NA	NA	NA	NA	3 (2)	18 (17)	57 (64)	17 (20)	31 (12)	12 (12)
Avg. downstream movement (m)	NA	NA	NA	NA	NA	-200	-200	-100	-200	-400	-300
Max. downstream movement (m)	NA	NA	NA	NA	NA	-400	-900	-200	-600	-1,000	-2,100
Avg. upstream movement (m)	NA	NA	NA	NA	NA	200	200	100	200	200	300
Max. upstream movement (m)	NA	NA	NA	NA	NA	400	800	400	500	500	800
Avg. movement (m)	NA	NA	NA	NA	NA	-100	0	100	-100	-100	-100

FIGURES

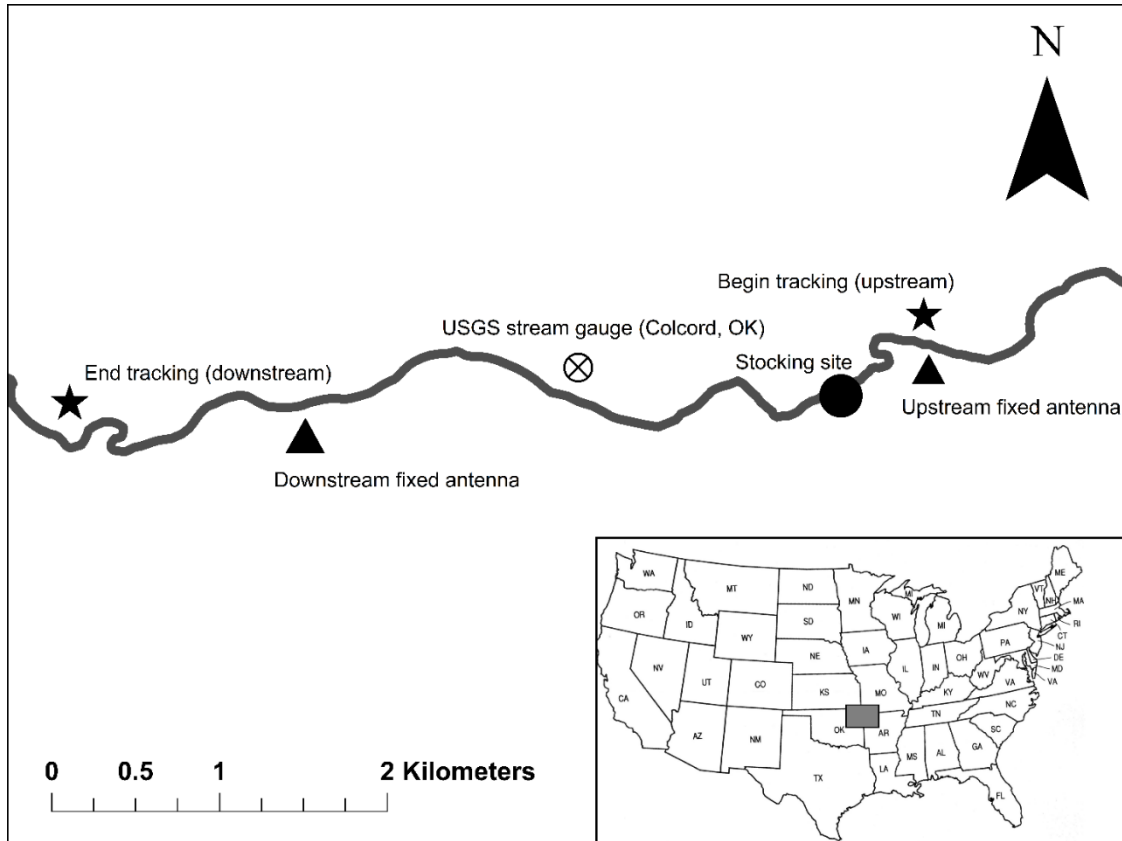


Figure 1. Upstream and downstream tracking extent (stars) of my study segment (gray box) on Spavinaw Creek, Oklahoma. I actively tracked Rainbow Trout tagged with passive integrated transponder tags using floating arrays (see Figure 2). Fixed arrays (triangles) were placed near the upstream and downstream tracking extent to determine Rainbow Trout emigration (see Figure 2). Rainbow Trout were stocked (circle) in autumn 2018 and spring 2019. The U.S. Geological Survey stream gauge (USGS stream gauge 071912213) near Colcord, OK was used to obtain daily discharge data during the study period.



Figure 2. Fixed array constructed at upper end of study segment (left) and floating array used for active tracking (right) in Spavinaw Creek. At fixed array sites, two antennas were placed parallel to one another to determine directional movement of each fish passing through the antenna. The floating array consisted of two antennas housed in floating PVC towed behind kayakers. Both fixed and floating arrays were connected to a multi-antenna reader (Oregon RFID; Portland, Oregon) and powered using a 12-volt deep-cycle battery.

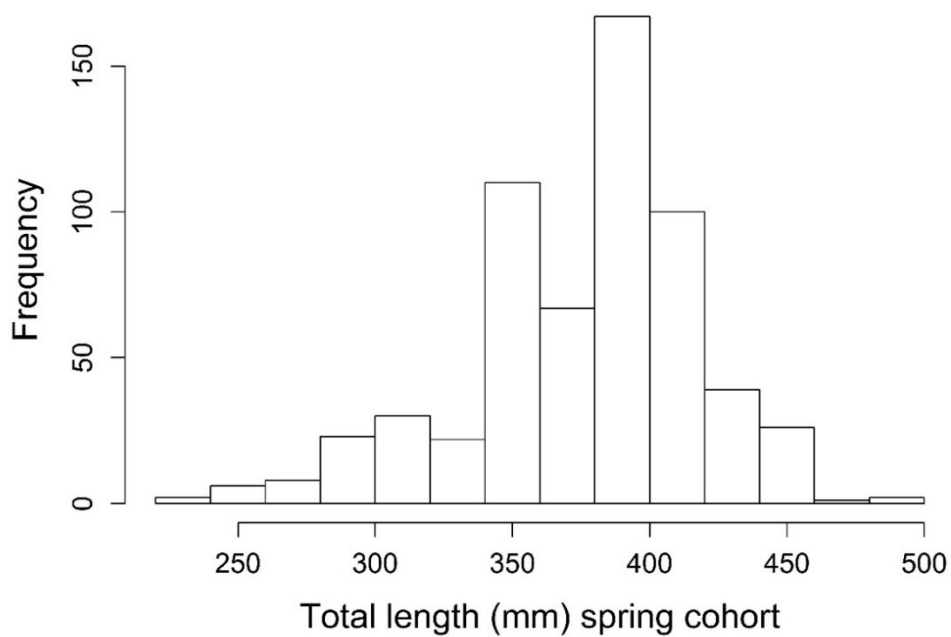
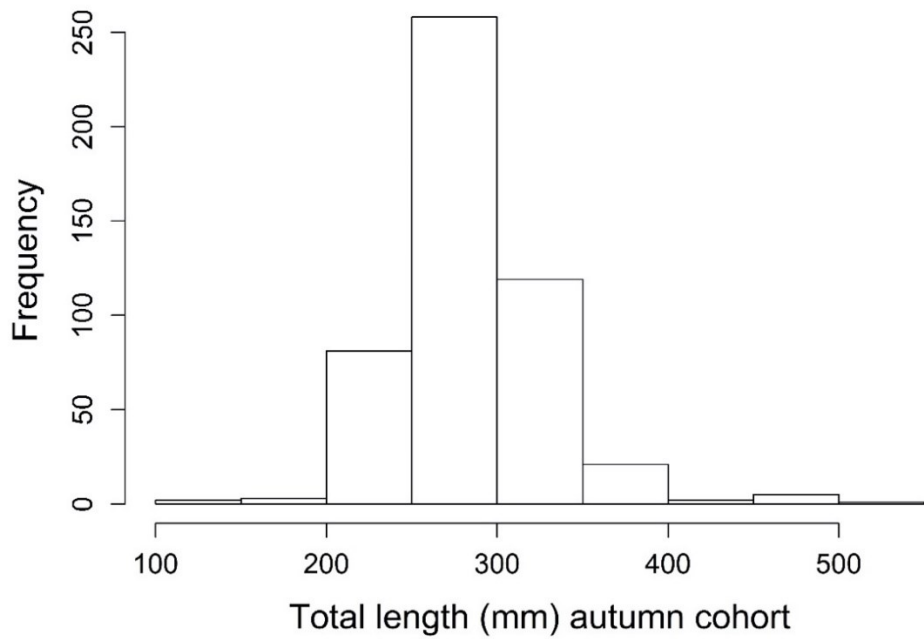


Figure 3. Size distribution (total length of passive integrated transponder (PIT) tagged Rainbow Trout stocked in autumn 2018 (N = 495) and spring 2019 (N = 605). Fish were tagged using 23 mm and 32 mm PIT tags.

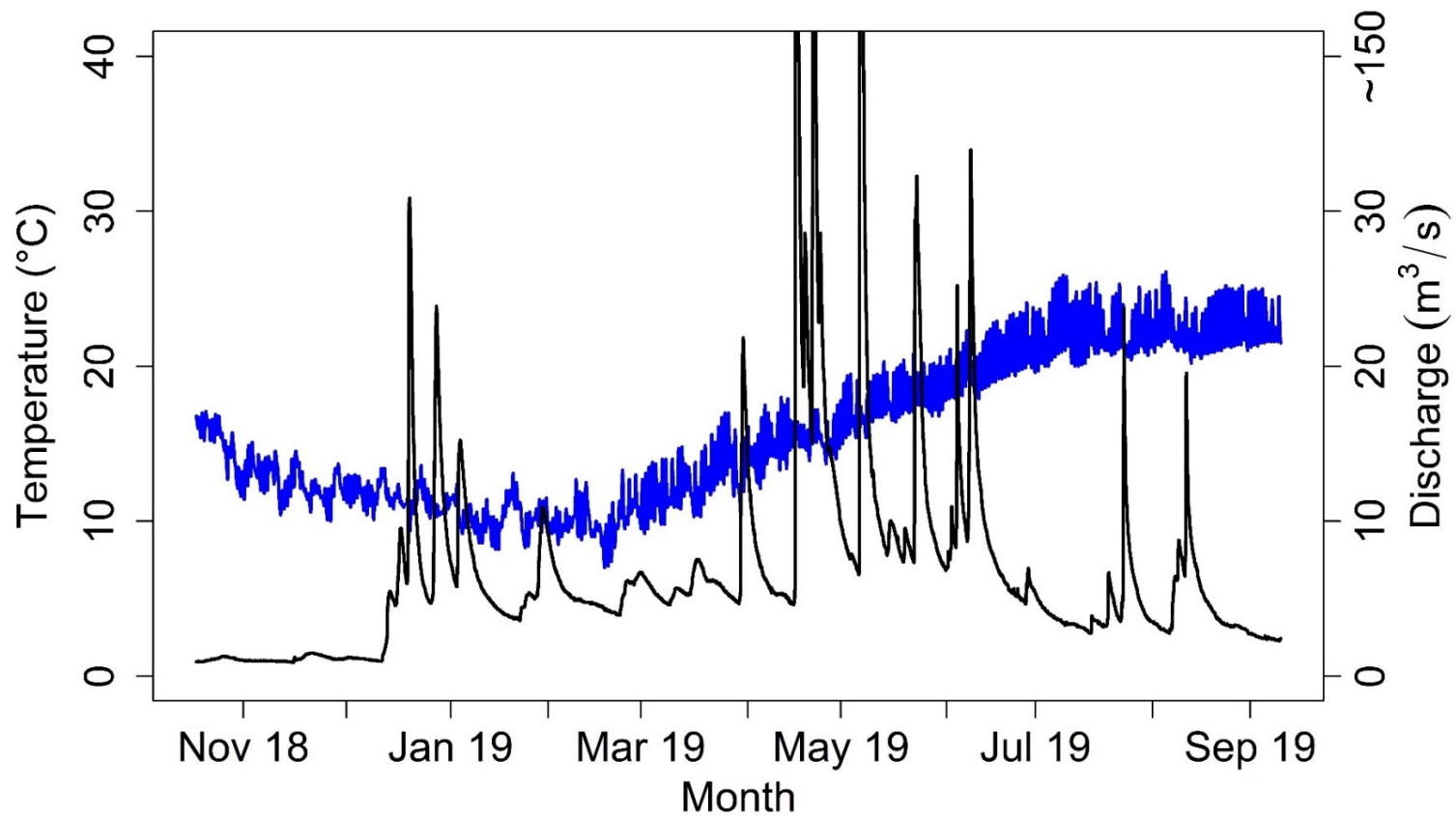


Figure 4. Discharge (black) and water temperature (blue) during my study period on Spavinaw Creek, Oklahoma. High discharge peaks (> 35 m^3/s) are not shown for scaling purposes. Active tracking occasions did not take place during the period of early May to mid-June due to high-flow events. Maximum flows during May and June reached $148 \text{ m}^3/\text{s}$. All data were retrieved from the U.S. Geological Survey stream gauge (USGS stream gauge 071912213) near Colcord, OK.

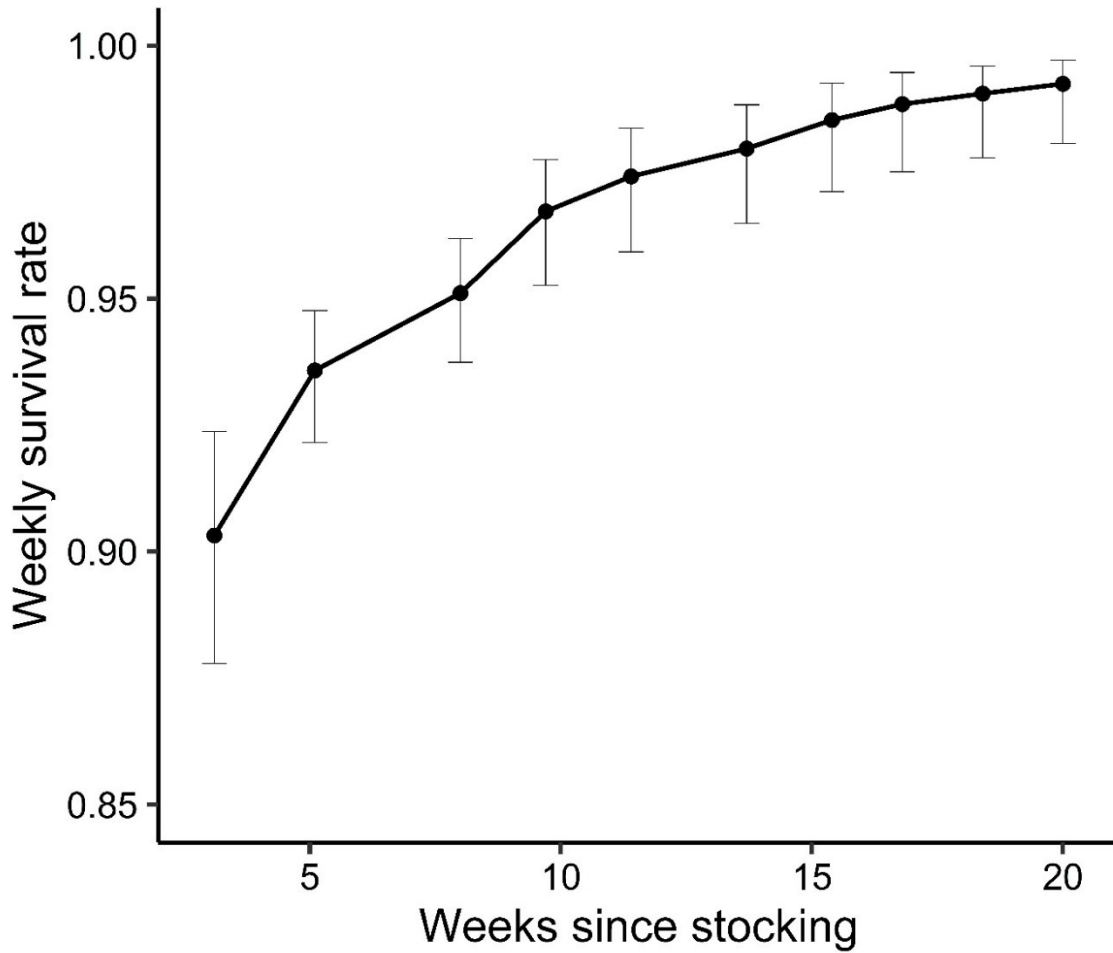


Figure 5. Weekly apparent survival rate estimates (black circles) and 95% confidence intervals (lines) for the autumn cohort of stocked Rainbow Trout in Spavinaw Creek, Oklahoma. Rainbow Trout were stocked on November 6, 2018 (week 0). The x-axis represents weekly intervals from the stocking date. For reference, week 10 is 1/30/2019 and week 20 is 4/30/2019.

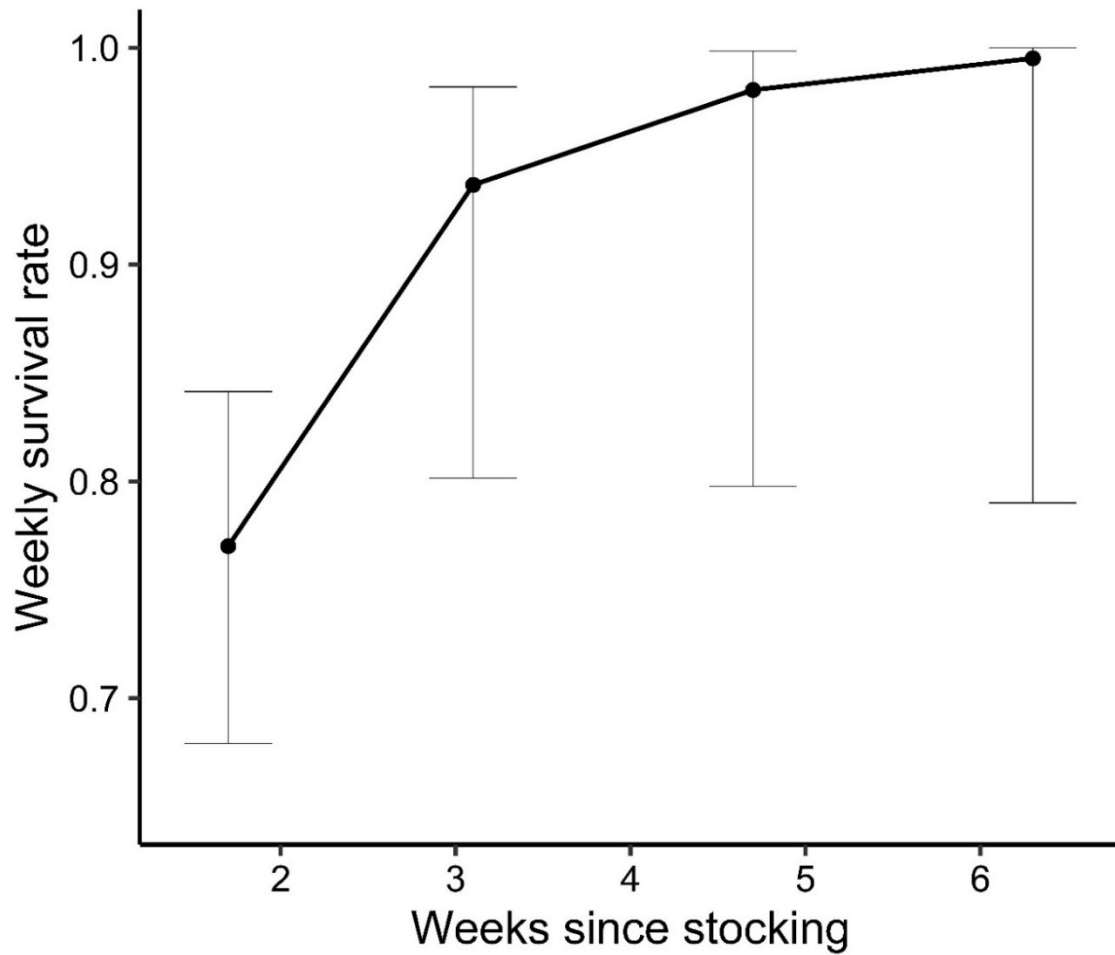


Figure 6. Weekly apparent survival rate estimates (black circles) and 95% confidence intervals (lines) for spring cohort of stocked Rainbow Trout in Spavinaw Creek, Oklahoma. Stocking date for spring cohort was 2/26/2019 (week 0) and x-axis represents weekly intervals from that date. For reference, week six is 4/30/2019.

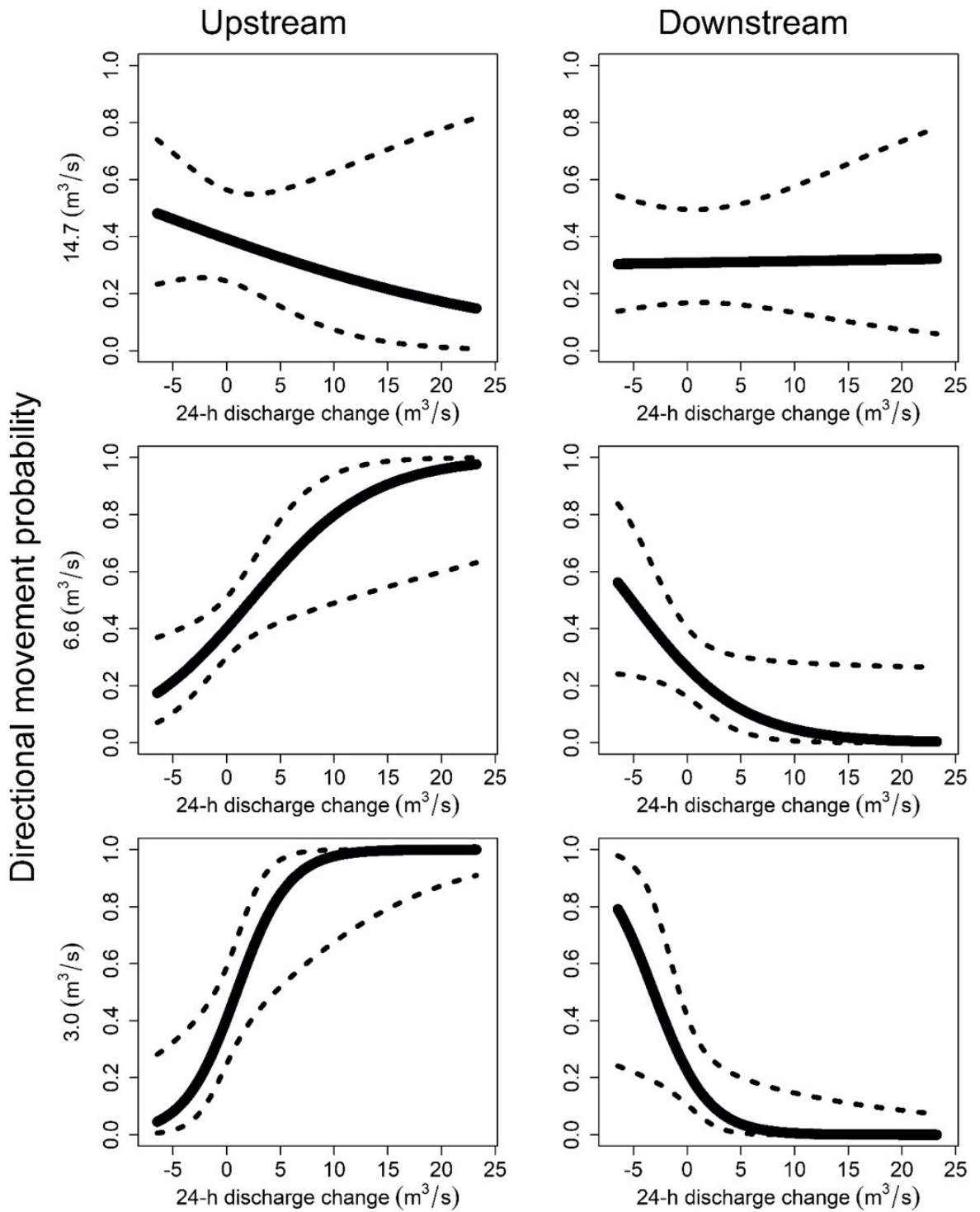


Figure 7 (next page).

Figure 7. Interaction between changes in 24-h discharge (plotted lines) and average 24-h discharge (rows) in relation to upstream (left column) and downstream (right column) movement probability. The x-axis of each plot represents how much discharge changed over each 24-h period where negative values represent decreasing discharge and positive values represent increasing discharge from 12:00 pm to 11:00 am of the following day. The y-axis of each plot represents the movement probability where a probability of 1 indicates all directional movements were in the direction of interest (i.e., upstream or downstream depending on left or right column). The average 24-h discharge is calculated during 12:00 pm to 11:00 am of the following day and each row represents relationships plotted at different levels of average 24-h discharge. The top row is the relationship between the change in 24-h discharge and movement probability at 14.7 m³/s of average discharge, the middle row is relationship between the change in 24-h discharge and movement probability at 6.6 m³/s of average discharge (mean levels) and the bottom row is the relationship between the change in 24-h discharge and movement probability at 3.0 m³/s of average discharge. All data were retrieved from the U.S. Geological Survey stream gauge (USGS stream gauge 071912213) near Colcord, OK.

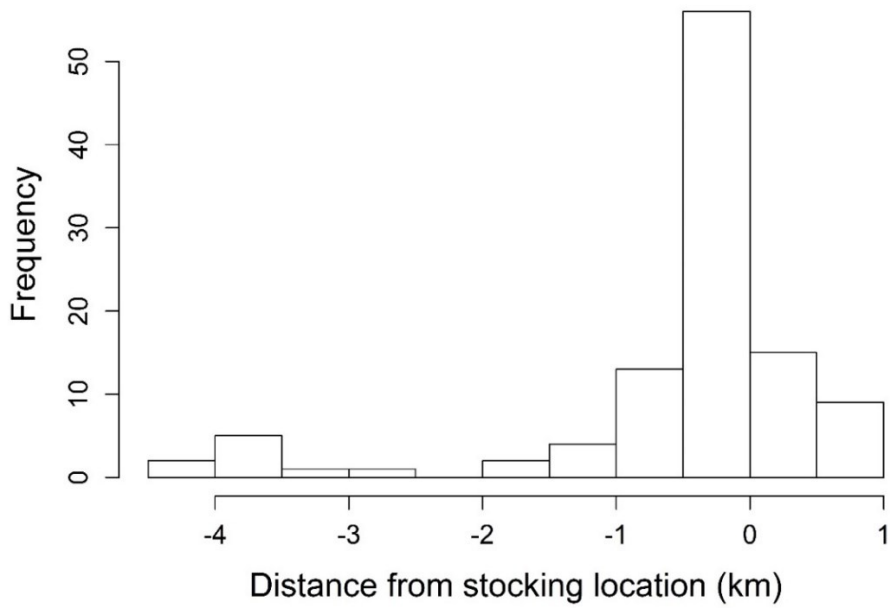
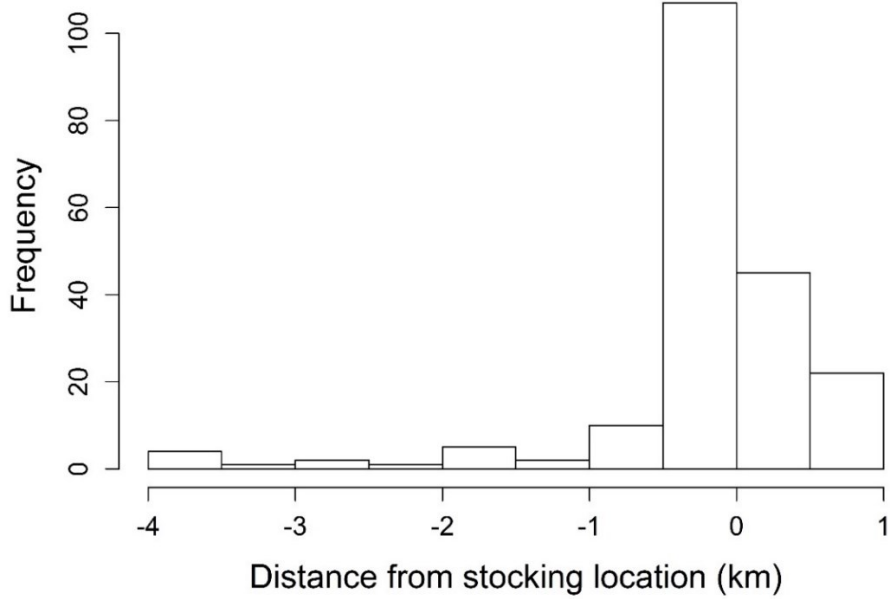


Figure 8. Distribution of tagged Rainbow Trout detections (frequency) on April 30 (top) and August 5 (bottom), 2019 in relation to stocking site. In each plot, 0 (km) represents the stocking location and negative values represent downstream locations from the stocking site while positive locations represent upstream locations from the stocking site.

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APPENDICES

APPENDIX A

Methods

To determine what proportion of available data were needed in my analyses, I examined use-availability data from two of my study species under various use-availability ratios. Smallmouth Bass was the most commonly encountered species, whereas I chose Creek Chub to represent a rarer species. For each species evaluation, I paired all used points with either all or some number of randomly selected availability. This resulted in four datasets which were a full dataset (i.e., all available points), a 1:5 ratio, a 1:3 ratio, and a 1:1 ratio for both Creek Chub (Table 1) and Smallmouth Bass (Table 2). Consequently, the full dataset ratio of used to available points differed between Smallmouth Bass and Creek Chub because Smallmouth Bass were more common (i.e., more used points) whereas the same number of availability points were collected for each species using my transect method in the field (see Chapter 2 methods).

I developed a generalized linear mixed model using the package lme4 (Bates et al. 2015) in the statistical software R (version 3.4.2, R Core Team 2017) for each species-ratio combination (eight models in total). I fit a global model to each dataset using interactions between the species of interest (Smallmouth Bass or Creek Chub), two seasons (autumn and winter) and five habitat variables (cover, depth, velocity, substrate, and temperature).

To understand the effects of various use-availability ratios, I compared model estimates between datasets in terms of significance ($\alpha \leq 0.10$). This was important because it allowed me to investigate if the final model for each dataset (i.e., the variables retained following a model-selection) would differ as a result of the dataset used. For example, non-significant variables (as determined by alpha) are eliminated first at the interaction level followed by main effects using a

backward-selection process (e.g., Wolf et al. 2019). In this particular analysis, I did not complete a formal selection process for each model. I chose, instead, to stop after fitting the global model to each dataset. I did this because it was already clear that the variables retained in the final model after a backward-selection approach would depend on the ratio of data used (see results). Additionally, I felt it important to use the same model to compare trends in predicted values of microhabitat use as opposed to models that differed in complexity as a result of a selection process. I plotted the predicted relative probability values for a continuous significant variable (substrate) and evaluated likelihood ratios of a significant factor variable (cover) using the global model generated from each dataset. I chose substrate as a continuous variable because I knew from a previous analysis that both species showed strong selection patterns for coarse (i.e., larger) substrate size using the full dataset. This provided a meaningful reference for how differing ratios would influence perceived selection patterns. Both substrate and cover were deemed significant ($P \leq 0.10$) in all eight model described above.

Results

Model Comparison. – Significant coefficients varied among models using the four Creek Chub datasets. Using the full dataset (~1:10 use-available ratio), all main effects and interactions were significant. However, the interaction winter x cover occurred near the cutoff ($P = 0.09$) and contained substantial error relative to the coefficient estimate (Table 3). The winter x cover interaction was estimated as non-significant using the 1:5 dataset. Using the 1:3 dataset, the winter x depth and winter x quadratic depth term were dropped in addition to the winter x cover interaction in terms of significance (Table 3). Lastly, the 1:1 dataset resulted in a model that would have dropped the winter x cover interaction and the winter x velocity interaction.

The Smallmouth Bass data resulted in more-robust estimates across varying use-availability ratios relative to the less common Creek Chub. The model that I generated using the full dataset contained the same significant terms as those that I generated using subsets of 1:5 and

1:3 (Table 4). Only in the 1:1 dataset was an additional interaction (winter x velocity) estimated as non-significant (Table 4).

Variable Comparison – Substrate selection trends were relatively consistent regardless of the use-availability ratio used. Both Creek Chub (Figure 1) and Smallmouth Bass (Figure 3) selected coarser substrate during autumn and less so in winter. As expected, the predicted probability of use increases for estimates derived from more-even ratios of use-availability points (see discussion). Regardless, the conclusion that both species were selecting coarse substrate during autumn could be drawn from models I created using the full, 1:5, and 1:3 datasets. However, the selection of coarse substrates using a 1:1 ratio was less evident and differed substantially from other ratios in terms of predicted probabilities and associated error (Figures 2 and 4).

For both species, my analysis using each dataset indicated that there was a shift in selection towards greater association with cover during winter months (Tables 5 and 6). However, the magnitude of this effect was reduced in conjunction with the sampling ratio. I found that the degree of change (differences in estimates) was less between ratios for the more-common Smallmouth Bass.

Discussion

My findings are similar to others (e.g., Northrup et al. 2013; Nad' o and Kanuch 2018) who have suggested that differences in sampling ratios have the potential to influence model estimates and associated ecological inferences on habitat selection. In addition, I noted other differences between ratios like changes in the value of predictions (i.e., relative probability) and variation between ratios that resulted from rare vs common species. For example, it appears that reduced datasets produce higher predicted probabilities of use. Additionally, the number of used points resulting from differences in the relative abundance among different species also influences the robustness of estimates when ratios are changed.

I found that differing ratios of use-availability points may either increase or decrease the predicted probability of use for a given resource. For example, I found that the predicted probability of use for a 1:3 ratio at substrate class 6 (i.e., boulders) was substantially higher than the predicted probability of use at substrate class 6 using the full dataset for both species (Figures 1 and 3). This is logical because as available points are reduced, the species of interest appears to become “more common” in the dataset (i.e., use observations are offset by less available points). This is perhaps only an issue in studies attempting to implement an occupied – unoccupied habitat framework where true probabilities are attempted to be estimated as oppose to only a strength of selection response as in use-availability studies (Nad’o and Kanuch 2018). However, as the ratio of use to available points approaches one, available points are likely also serving as used points (often referred to as contamination, see Johnson et al. 2006). This likely prevents valid inferences of selection and introduces substantial error to estimates (e.g., substrate selection constructed with 1:1 ratio; Figures 2 and 4). Additionally, differing use-availability ratios among species may lead to incorrect interpretation of results during species comparisons if the goal is to compare multiple species using the same model. This is because more-common species would be associated with higher predicted probabilities. If this point was not well understood, the result could be that these estimates would incorrectly be interpreted as greater selection for the resource relative to the less-common species.

Comparing model estimates from the two species I examined suggested that coefficient estimates are more robust to changes in use-availability ratios when a greater number of used observations are included. For example, Smallmouth Bass estimates of cover use were less affected compared to those of Creek Chub under varying use-availability ratios. This suggests that the greater number of used points within the Smallmouth dataset preserved the estimated selection patterns within the reduced datasets. It seems that with less used points to compare with, the reduction in available points creates potential to miss ecological relationships that may be apparent using only a full dataset (e.g., the winter x cover interaction that was estimated as

significant only in the full Creek Chub dataset). However, increased data points beyond a necessary amount can increase computation time immensely. In addition (as mentioned above), it may also confound comparisons between species should their ratios of use-available points differ within the same model. Consequently, a compromise would be beneficial to facilitate meaningful model estimates while allowing for realistic computation time and model interpretation.

I found that a reduced dataset of 1:5 produced essentially the same coefficient estimates as those produced using the full Smallmouth Bass dataset. This was not surprising given the full dataset was near a 1:5 ratio naturally (though differed seasonally as described above). The Creek Chub dataset that was reduced to a 1:5 ratio dropped only a weakly significant interaction term (winter x cover) from what would have been included in the full dataset. Given that Creek Chub are the rarest species within my microhabitat dataset (i.e., fewest used observations relative to available points), I concluded that my other species would be less prone to dropping significant terms using a reduced dataset of 1:5 given my findings of robustness from more used points. Additionally, this preliminary analysis consisted of only two seasons. Consequently, the inclusion of more data (e.g., my final dataset) would add robustness to estimates including the Creek Chub and other rare species if I were to use a reduced dataset. Lastly, I was interested in preserving the same use-availability ratios across all species and seasons under a single model to facilitate comparison. As a result, I was somewhat confined to using the ratio of the most abundant species in the dataset for all other species. In my case, Smallmouth Bass (~1:5 ratio) is most common. Consequently, I chose to move forward with my microhabitat analysis using a 1:5 use-availability ratio applied to all species in each season.

Appendix A: References

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Appendix A: Tables

Table 1. Distribution of use (N use) and availability (N avail) habitat points contributing to the total number of observations (Model data points) in each dataset used for Creek Chub models. Data were collected in October of 2017 (Spavinaw Creek, Oklahoma), December of 2017 (Spavinaw Creek, Arkansas), and January of 2018 (Spring Creek, Oklahoma). The full dataset consists of all availability points collected. Consequently, used-availability ratios are not proportional between seasons using the full dataset. Reduced datasets (1:5, 1:3, 1:1) were generated by pairing all use observations with a randomly selected subset of availability points to achieve the desired ratio in both seasons.

Dataset (ratio use:avail)	Season	N use	N avail	Final ratio	Model data points
Full	Autumn	85	840	0.10	
	Winter	118	1600	0.07	2643
1:5	Autumn	85	425	0.20	
	Winter	118	590	0.20	1218
1:3	Autumn	85	255	0.33	
	Winter	118	354	0.33	812
1:1	Autumn	85	85	1.00	
	Winter	118	118	1.00	406

Table 2. Distribution of use (N use) and availability (N avail) habitat points contributing to the total number of observations (Model data points) in each dataset used for Smallmouth Bass models. Data were collected in October of 2017 (Spavinaw Creek, Oklahoma), December of 2017 (Spavinaw Creek, Arkansas), and January of 2018 (Spring Creek, Oklahoma). The full dataset consists of all availability points collected. Consequently, used-availably ratios are not proportional between seasons using the full dataset. Reduced datasets (1:5, 1:3, 1:1) were generated by pairing all use observations with a randomly selected subset of availability points to achieve the desired ratio in both seasons.

Dataset (ratio use:avail)	Season	N use	N avail	Final ratio	Model data points
Full	Autumn	159	840	0.19	
	Winter	253	1600	0.16	2852
1:5	Autumn	159	795	0.20	
	Winter	253	1265	0.20	2472
1:3	Autumn	159	477	0.33	
	Winter	253	759	0.33	1648
1:1	Autumn	159	159	1.00	
	Winter	253	253	1.00	824

Table 3. Model estimates for the Creek Chub complete (Full) dataset and varying use-availability ratios (1:5, 1:3, 1:1). The same global model (M1) is used to facilitate comparison across datasets (i.e., no selection process was carried out). M1 contains interaction terms between season (autumn or winter) and environmental covariates, along with main effects for each environmental parameter. “Velocity” is in reference to no velocity and “cover” is in reference to no cover. Interaction terms containing winter are in reference to autumn conditions.

Parameter	<u>Full</u>			<u>1:5</u>			<u>1:3</u>			<u>1:1</u>		
	Estimate	Error	Pr(> z)	Estimate	Error	Pr(> z)	Estimate	Error	Pr(> z)	Estimate	Error	Pr(> z)
Season - autumn	-2.53	0.37	0.00*	-1.79	0.40	0.00*	-1.23	0.35	0.00*	0.24	0.41	0.56
Season - winter	-4.51	0.42	0.00*	-3.28	0.43	0.00*	-2.44	0.41	0.00*	-0.77	0.47	0.10*
Depth	4.65	1.04	0.00*	3.97	0.94	0.00*	3.42	0.90	0.00*	2.75	0.74	0.00*
Depth ²	-4.17	0.93	0.00*	-4.08	0.93	0.00*	-3.45	0.91	0.00*	-4.25	1.05	0.00*
Velocity	-0.36	0.28	0.19	-0.04	0.31	0.91	-0.18	0.32	0.59	0.64	0.49	0.19
Temperature	0.47	0.11	0.00*	0.55	0.13	0.00*	0.40	0.14	0.00*	0.70	0.22	0.00*
Substrate	0.84	0.19	0.00*	0.81	0.21	0.00*	0.92	0.23	0.00*	1.24	0.36	0.00*
Cover	1.01	0.30	0.00*	1.01	0.35	0.00*	0.98	0.38	0.01*	0.95	0.61	0.12
Winter x depth	0.22	1.36	0.87	0.75	1.29	0.56	0.19	1.18	0.87	-0.20	0.99	0.84
Winter x depth ²	0.38	1.17	0.75	0.23	1.18	0.84	0.63	1.12	0.57	2.05	1.21	0.09*
Winter x velocity	1.28	0.41	0.00*	1.08	0.46	0.02*	1.11	0.48	0.02*	0.41	0.66	0.54
Winter x temp	-0.56	0.19	0.00*	-0.60	0.22	0.01*	-0.42	0.23	0.07*	-0.90	0.32	0.01*
Winter x substrate	-1.70	0.22	0.00*	-1.73	0.25	0.00*	-1.69	0.28	0.00*	-2.25	0.43	0.00*
Winter x cover	0.65	0.38	0.09*	0.41	0.45	0.36	0.34	0.48	0.47	-0.30	0.71	0.67

*indicates significance (cutoff: $\alpha \leq 0.10$).

Table 4. Model estimates for the Smallmouth Bass complete (full) dataset and varying use-availability ratios (1:5, 1:3, 1:1). The same global model (M1) is used to facilitate comparison across datasets (i.e., no selection process was carried out). M1 contains interaction terms between season (autumn or winter) and environmental covariates, along with main effects for each environmental parameter. “Velocity” is in reference to no velocity and “cover” is in reference to no cover. Interaction terms containing winter are in reference to autumn conditions.

Parameter	Full			1:5			1:3			1:1		
	Estimate	Error	Pr(> z)	Estimate	Error	Pr(> z)	Estimate	Error	Pr(> z)	Estimate	Error	Pr(> z)
Season - autumn	-2.36	0.55	0.00*	-2.31	0.56	0.00*	-1.54	0.56	0.01*	0.10	0.60	0.86
Season - winter	-2.83	0.40	0.00*	-2.57	0.41	0.00*	-2.00	0.41	0.00*	-0.89	0.43	0.04*
Depth	3.53	0.71	0.00*	3.48	0.70	0.00*	2.76	0.60	0.00*	1.09	0.44	0.01*
Depth ²	-4.22	0.68	0.00*	-4.17	0.68	0.00*	-3.88	0.65	0.00*	-3.07	0.60	0.00*
Velocity	1.04	0.27	0.00*	1.04	0.28	0.00*	1.12	0.30	0.00*	0.78	0.37	0.03*
Temperature	0.29	0.08	0.00*	0.29	0.09	0.00*	0.31	0.10	0.00*	0.33	0.13	0.01*
Substrate	1.13	0.15	0.00*	1.14	0.16	0.00*	1.17	0.18	0.00*	0.72	0.24	0.00*
Cover	1.80	0.25	0.00*	1.79	0.25	0.00*	1.83	0.28	0.00*	1.92	0.38	0.00*
Winter x depth	-1.31	0.84	0.12	-1.33	0.85	0.12	-1.11	0.73	0.13	-0.42	0.51	0.41
Winter x depth ²	1.65	0.80	0.04*	1.64	0.80	0.04*	1.94	0.75	0.01*	1.87	0.67	0.01*
Winter x velocity	-0.68	0.33	0.04*	-0.67	0.34	0.05*	-0.82	0.37	0.02*	-0.30	0.46	0.52
Winter x temp	-0.54	0.14	0.00*	-0.58	0.14	0.00*	-0.58	0.16	0.00*	-0.42	0.21	0.04*
Winter x substrate	-1.13	0.18	0.00*	-1.09	0.19	0.00*	-1.12	0.21	0.00*	-0.90	0.29	0.00*
Winter x cover	0.17	0.31	0.59	0.13	0.32	0.67	-0.05	0.35	0.88	0.15	0.48	0.75

*indicates significance (cutoff: $\alpha \leq 0.10$).

Table 5. Relative importance of cover to Creek Chub during autumn and winter. Odds of use are relative to the reference condition (i.e., likelihood of using cover versus no cover) for each season. Shift represents likelihood of using cover in winter, relative to using cover in autumn (i.e., values greater than one indicate relative higher use of cover in winter).

Ratio	Autumn	Winter	Shift
Full	2.9	4.9	1.7
1:5	2.9	4.2	1.4
1:3	2.1	3.4	1.6
1:1	1.3	2.1	1.6

Table 6. Relative importance of categorical cover variable to Smallmouth Bass during autumn and winter. Odds of use are relative to the reference condition (i.e., likelihood of using cover versus no cover) for each season. Shift represents likelihood of using cover in winter, relative to using cover in autumn (i.e., winter/autumn, values greater than one indicate relative higher use of cover in winter).

Ratio	Autumn	Winter	Shift
Full	2.6	4.8	1.8
1:5	2.2	3.1	1.4
1:3	2.1	2.5	1.2
1:1	1.2	1.3	1.1

Appendix A: Figures

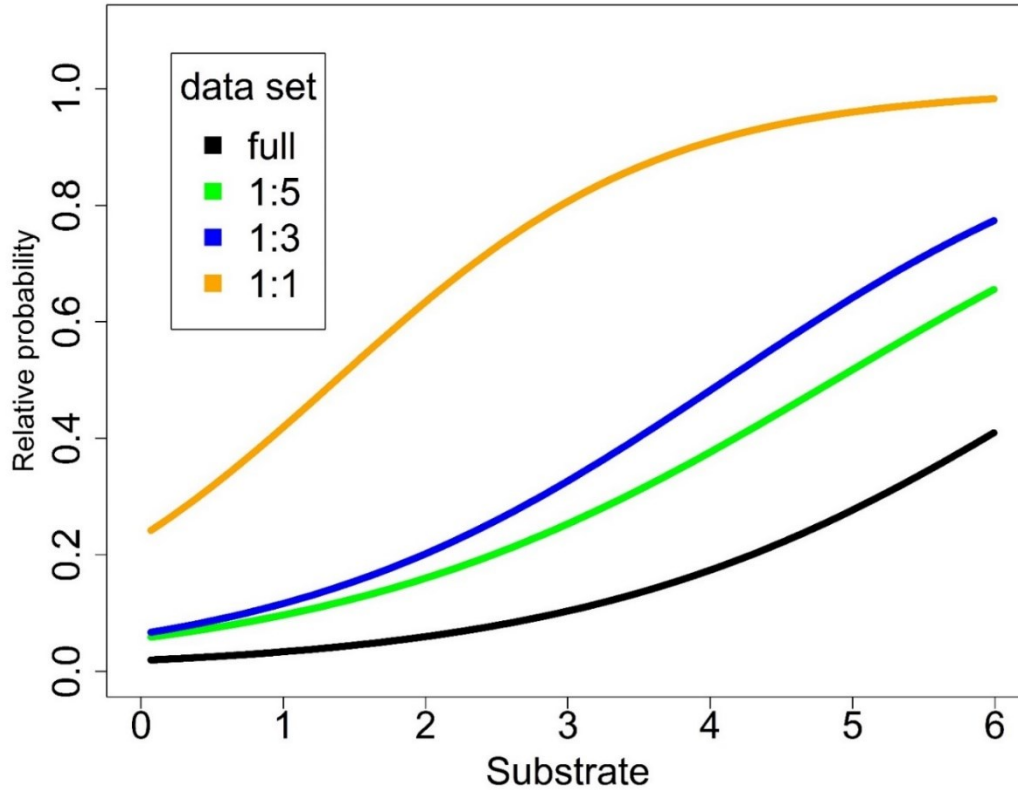


Figure 1. Relative probability of selection of substrate for Creek Chub in autumn using the same model (M1) across the four datasets of varying use-availability ratios (full, 1:5, 1:3, and 1:1 use-available). For simplicity, I show predicted probabilities without confidence intervals. Substrate class (1 – 6) corresponds to modified Wentworth scale (McMahon et al. 1996) consisting of 1) silt ($< 0.06\text{mm}$), 2) sand ($\geq 0.06 - 2\text{mm}$), 3) gravel ($> 2 - 16\text{mm}$), 4) pebble ($> 16 - 64\text{mm}$), 5) cobble ($> 64 - 256\text{mm}$), and 6) boulder ($> 256\text{mm}$).

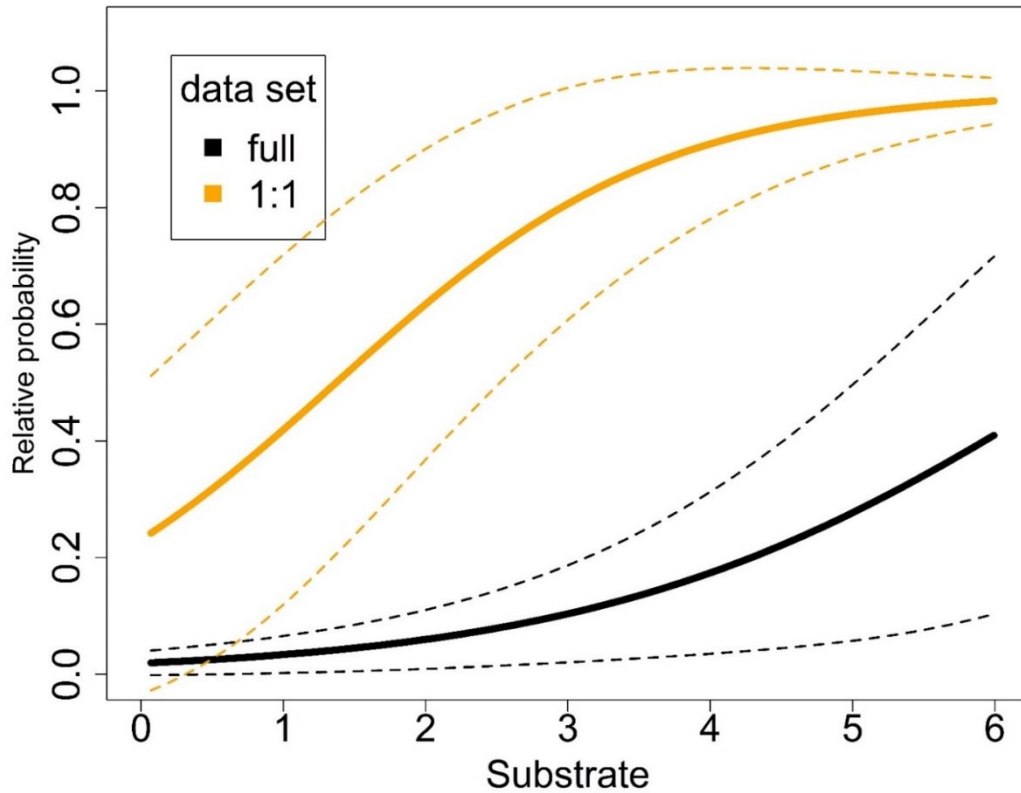


Figure 2. Relative probability of selection of substrate by Creek Chub in autumn from full dataset and most restrictive (1:1 use-available ratio) with associated 95% confidence intervals plotted as dashed lines around each predicted probability. Substrate class (1 – 6) corresponds to modified Wentworth scale (McMahon et al. 1996) consisting of 1) silt (< 0.06mm), 2) sand ($\geq 0.06 - 2\text{mm}$), 3) gravel (> 2 - 16mm), 4) pebble (> 16 - 64mm), 5) cobble (> 64 - 256mm), and 6) boulder (> 256mm).

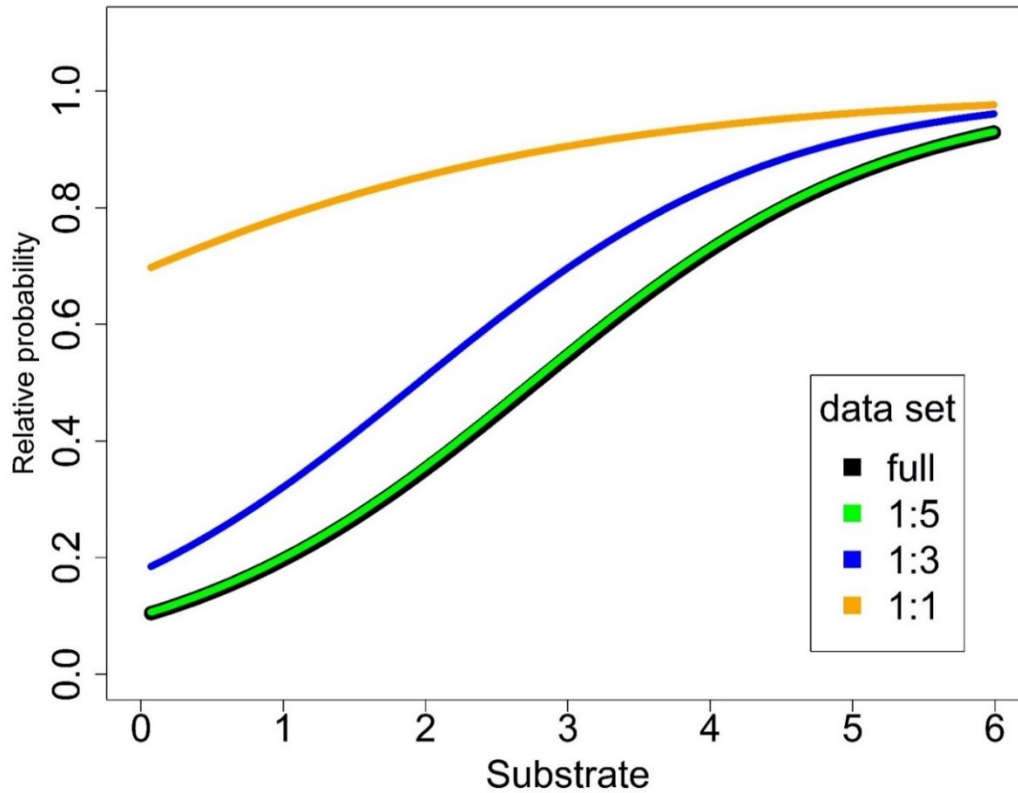


Figure 3. Relative probability of selection of substrate for Smallmouth Bass in autumn using the same model (M1) across the four datasets of varying use-availability ratios (full, 1:5, 1:3, and 1:1 use-available). For simplicity, I show predicted probabilities without confidence intervals.

Substrate class (1 – 6) corresponds to modified Wentworth scale (McMahon et al. 1996) consisting of 1) silt (< 0.06mm), 2) sand ($\geq 0.06 - 2$ mm), 3) gravel (> 2 - 16mm), 4) pebble (> 16 - 64mm), 5) cobble (> 64 - 256mm), and 6) boulder (> 256mm).

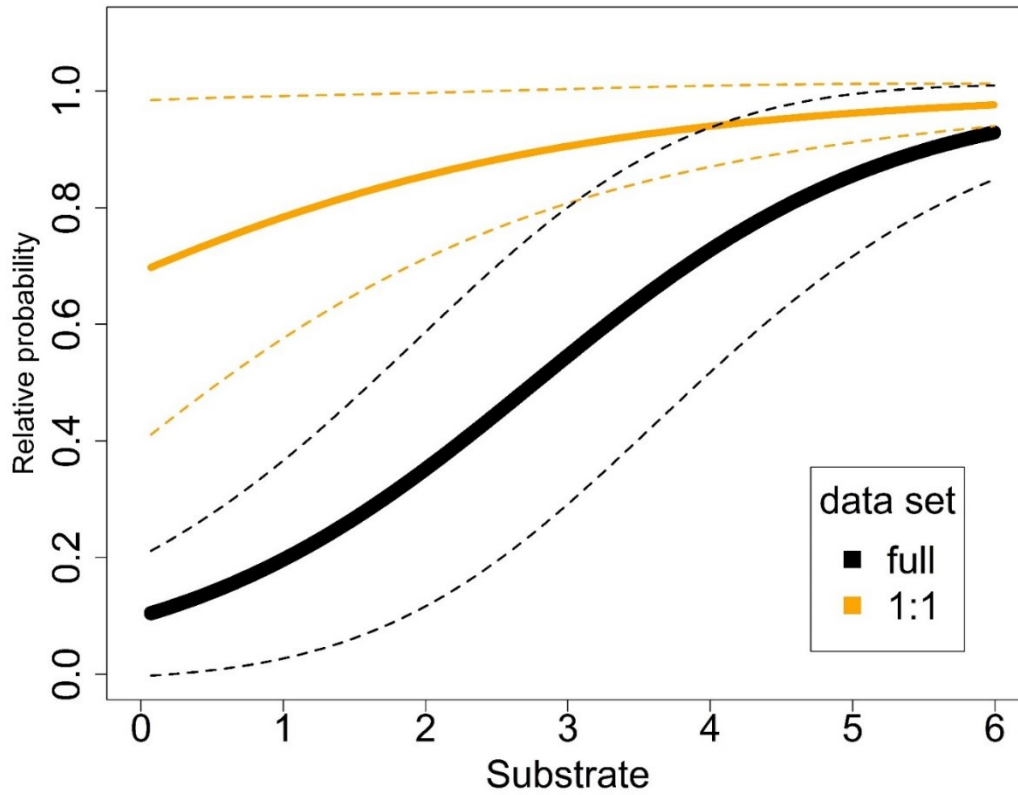


Figure 4. Relative probability of selection of substrate by Smallmouth Bass in autumn from full dataset and most restrictive (1:1 use-available ratio) with associated 95% confidence intervals plotted as dashed lines around each predicted probability. Substrate class (1 – 6) consisting of 1) silt (< 0.06mm), 2) sand ($\geq 0.06 - 2\text{mm}$), 3) gravel (> 2 - 16mm), 4) pebble (> 16 - 64mm), 5) cobble (> 64 - 256mm), and 6) boulder (> 256mm).

APPENDIX B

Table 1. Habitat availability by survey. Day is scaled from 0 – 182 where day 0 is December 21 and day 182 is June 21/22 and is used to represent season. Depth (0.05 m), velocity (0.1 m/s), substrate (class 0 – 6) and deviation temperature (0.05 °C) were continuous variables used in the model. Cover percent was calculated using the percent of total patches that contained cover. Median temperature was not used for analysis but is included as an indicator of ambient water temperature during each survey.

Table 1

Variable	Maris 1	Moss 1	Moss 2
Date (start – end)	10/20/2017 – 10/24/2017	1/9/2018 – 1/11/2018	5/19/2018 – 5/21/2018
Day (start – end)	66 – 70	18 – 21	148 – 151
Depth (mean ± SD)	0.5 ± 0.45 m	0.65 ± 0.60 m	1.05 ± 0.90 m
Depth (min – max)	0.05 – 1.70 m	0.05 – 2.70 m	0.05 – 4.00 m
Velocity (mean ± SD)	0.0 ± 0.1 m/s	0.0 ± 0.0 m/s	0.1 ± 0.2 m/s
Velocity (min – max)	0.0 – 0.3 m/s	0.0 – 0.2 m/s	0.0 – 0.8 m/s
Substrate (mean ± SD)	3 ± 1	4 ± 1	4 ± 1
Substrate (min – max)	1 – 4	1 – 6	2 – 6
Median temp. (mean ± SD)	19.5 ± 0.5 °C	10.5 ± 0.5 °C	18.5 ± 1.0 °C
Median temp. (min – max)	18.5 – 20.0 °C	10.0 – 11.5 °C	17.0 – 19.5 °C
Deviation temp. (mean ± SD)	0.0 ± 0.5 °C	0.0 ± 0.5 °C	0.0 ± 0.5 °C
Deviation temp. (min – max)	-1.0 – 1.5 °C	-1.0 – 1.0 °C	-3.0 – 2.0 °C
Cover percent	40%	20%	29%

Table 1 (cont.)

Variable	Lavern 1	Cisco 2	Lavern 2
Date (start – end)	6/12/2018 – 6/14/2018	9/9/2018 – 9/11/2018	9/19/2018 – 9/20/2018
Day (start – end)	173 – 175	100 – 102	91 – 92
Depth (mean ± SD)	0.40 ± 0.35	0.50 ± 0.50	0.35 ± 3.00
Depth (min – max)	0.05 – 1.60	0.05 – 2.05	0.05 – 1.65
Velocity (mean ± SD)	0.3 ± 0.3	0.1 ± 0.2	0.3 ± 0.3
Velocity (min – max)	0 – 1.3	0 – 1.1	0 – 1.5
Substrate (mean ± SD)	4 ± 2	4 ± 1	4 ± 1
Substrate (min – max)	0 – 6	0 – 6	0 – 6
Median temp. (mean ± SD)	21.5 ± 1.0 °C	21.0 ± 0.5 °C	24.5 ± 0.5 °C
Median temp. (min – max)	20.5 – 23.0 °C	19.5 – 25.0 °C	24.0 – 25.0 °C
Deviation temp. (mean ± SD)	0.0 ± 0.5 °C	0.0 ± 0.5 °C	0.0 ± 0.5 °C
Deviation temp. (min – max)	-2.0 – 1.0 °C	-2.0 – 3.5 °C	-1.5 – 4.5 °C
Cover percent	18%	32%	17%

Table 1 (cont.)

Variable	Moss 3	Moss 4	Moss 5
Date (start – end)	9/28/2018 – 9/30/2018	2/15/2019 – 2/17/2019	6/20/2019 – 6/22/2019
Day (start – end)	81 – 83	56 – 58	181 – 182
Depth (mean ± SD)	0.95 ± 0.80	0.9 ± 0.85	0.85 ± 0.9
Depth (min – max)	0.10 – 4.00	0.05 – 4.50	0.05 – 5.10
Velocity (mean ± SD)	0.0 ± 1.0	0.2 ± 0.3	0.2 ± 0.2
Velocity (min – max)	0.0 – 0.4	0.0 – 1.1	0.0 – 0.9
Substrate (mean ± SD)	4 ± 1	4 ± 1	4 ± 1
Substrate (min – max)	0 – 6	2 – 6	0 – 6
Median temp. (mean ± SD)	22.5 ± 0.5 °C	8.0 ± 1.0 °C	21.5 ± 1.0 °C
Median temp. (min – max)	22.0 – 23.0 °C	6.0 – 9.0 °C	20.5 – 22.5 °C
Deviation temp. (mean ± SD)	0.0 ± 0.5 °C	0.0 ± 0.0 °C	0.0 ± 0.5 °C
Deviation temp. (min – max)	-1.5 – 3.0 °C	-1.5 – 0.5 °C	-3.0 – 4.0 °C
Cover percent	32%	28%	47%

Table 1 (cont.)

Variable	Cisco 1*	Maris 2*	Maris 3*
Date (start - end)	12/16/2017 – 12/19/2017	2/8/2019 – 2/11/2019	6/14/2019 – 6/15/2019
Day (start – end)	2 – 5	49 – 52	175 – 176
Depth (mean ± SD)	0.70 ± 0.55 m	0.35 ± 0.20 m	0.60 ± 0.30 m
Depth (min – max)	0.05 – 1.90 m	0.05 – 1.30 m	0.10 – 1.30 m
Velocity (mean ± SD)	0 ± 0.1 m/s	0.3 ± 0.30 m/s	0.5 ± 0.3 m/s
Velocity (min – max)	0.0 – 0.3 m/s	0.0 – 1.1 m/s	0.0 – 1.2 m/s
Substrate (mean ± SD)	4 ± 1	4 ± 1	4 ± 1
Substrate (min – max)	2 – 6	2 – 5	0 – 6
Median temp. (mean ± SD)	12.5 ± 0.5 °C	9.0 ± 1.0 °C	19.0 ± 1.0 °C
Median temp. (min – max)	10.0 – 14.0 °C	8.0 – 10.5 °C	17.5 – 20.5 °C
Deviation temp. (mean ± SD)	0.0 ± 0.5 °C	0.0 ± 0.5 °C	0 ± 1 °C
Deviation temp. (min – max)	-1.0 – 0.5 °C	-2.5 – 0.5 °C	-1.5 – 7.0 °C
Cover percent	37%	23%	13%

*Rainbow Trout present

Table 2. Final model estimates for microhabitat model. Count is the number estimates (N = 224).

For parameter estimates, alpha estimates (count 1 – 6) reference to species specific intercepts for [1] Creek Chub, [2] Redhorse, [3] Northern Hogsucker, [4] Redspot Chub, [5] Age-1+ Smallmouth Bass, and [6] Juvenile Smallmouth Bass. In the model, each beta (1 – 27) represents a main effect or interaction as defined by “variable”. For each beta, there are six estimates, corresponding to species-specific deflections from the group mean (BetaXmu). The estimate mean and SD were used to calculate 95% High Density Intervals (2.5% - 97.5%) where estimates that had intervals that did not come within 0.01 or overlap zero were considered significant. Rhat is a measure of convergence for each parameter where values less than or equal to 1.1 indicate successful convergence.

Count	Parameter	Variable	Mean	SD	2.50%	97.50%	Rhat
1	alpha[1]	Creek Chub	-1.925	0.304	-2.531	-1.365	0.998
2	alpha[2]	Redhorse	-4.23	0.328	-4.859	-3.614	1
3	alpha[3]	Northern Hogsucker	-1.806	0.305	-2.36	-1.253	1.009
4	alpha[4]	Redspot Chub	-1.302	0.263	-1.81	-0.749	1.001
5	alpha[5]	Age-1+ Smallmouth Bass	-3.253	0.299	-3.806	-2.637	1.015
6	alpha[6]	Juvenile Smallmouth Bass	-1.365	0.271	-1.893	-0.821	1.019
7	alphamu	Species group mean	-2.295	0.668	-3.582	-1.057	1.018
8	alphasig	Species group error	1.532	0.662	0.736	3.347	1.023
9	beta1[1]	Time	0.131	0.16	-0.187	0.44	1.003
10	beta1[2]	Time	0.78	0.188	0.423	1.117	1
11	beta1[3]	Time	-0.931	0.246	-1.398	-0.446	1.005
12	beta1[4]	Time	-0.212	0.087	-0.38	-0.035	1.01
13	beta1[5]	Time	0.265	0.154	-0.057	0.589	1.015
14	beta1[6]	Time	0.19	0.109	-0.013	0.416	0.999
15	beta1mu	Time group mean	0.064	0.326	-0.596	0.791	1.007
16	beta1sig	Time group error	0.802	0.411	0.354	1.707	1.057
17	beta2[1]	Depth	1.655	0.169	1.361	1.989	1.007
18	beta2[2]	Depth	5.799	0.333	5.162	6.419	1.01
19	beta2[3]	Depth	3.954	0.281	3.361	4.49	1.026

20	beta2[4]	Depth	2.202	0.11	1.998	2.404	1.002
21	beta2[5]	Depth	4.019	0.244	3.52	4.472	1.014
22	beta2[6]	Depth	1.324	0.087	1.162	1.492	1.006
23	beta2mu	Depth group mean	3.166	1.027	1.184	5.207	1.013
24	beta2sig	Depth group error	2.22	0.871	1.173	4.643	0.998
25	beta3[1]	Depth ²	-2.33	0.224	-2.77	-1.949	1.002
26	beta3[2]	Depth ²	-1.766	0.135	-2.026	-1.521	1.011
27	beta3[3]	Depth ²	-1.639	0.17	-1.966	-1.306	1.027
28	beta3[4]	Depth ²	-1.748	0.095	-1.947	-1.559	1.012
29	beta3[5]	Depth ²	-1.288	0.119	-1.52	-1.06	1.009
30	beta3[6]	Depth ²	-1.366	0.085	-1.524	-1.202	1.002
31	beta3mu	Depth ² group mean	-1.717	0.25	-2.225	-1.273	1
32	beta3sig	Depth ² group error	0.548	0.282	0.214	1.364	1.004
33	beta4[1]	Temperature	0.134	0.173	-0.198	0.476	0.999
34	beta4[2]	Temperature	-0.38	0.127	-0.632	-0.161	0.999
35	beta4[3]	Temperature	-0.278	0.153	-0.591	-0.002	0.997
36	beta4[4]	Temperature	-0.214	0.093	-0.381	-0.04	1.002
37	beta4[5]	Temperature	-0.267	0.132	-0.558	-0.02	1.003
38	beta4[6]	Temperature	-0.242	0.098	-0.456	-0.046	0.997
39	beta4mu	Temperature group mean	-0.208	0.141	-0.521	0.09	1.006
40	beta4sig	Temperature group error	0.287	0.195	0.036	0.775	1.013
41	beta5[1]	Velocity	-0.159	0.077	-0.306	-0.014	1.005
42	beta5[2]	Velocity	0.199	0.075	0.057	0.34	0.997
43	beta5[3]	Velocity	0.711	0.137	0.464	0.986	1.009
44	beta5[4]	Velocity	0.03	0.046	-0.058	0.118	1.001
45	beta5[5]	Velocity	0.151	0.079	-0.003	0.305	0.998
46	beta5[6]	Velocity	-0.54	0.061	-0.655	-0.423	0.998
47	beta5mu	Velocity group mean	0.061	0.322	-0.495	0.683	1.032
48	beta5sig	Velocity group error	0.595	0.31	0.255	1.277	1.029
49	beta6[1]	Substrate	-0.359	0.059	-0.467	-0.244	1.011
50	beta6[2]	Substrate	-0.212	0.053	-0.324	-0.112	1.003
51	beta6[3]	Substrate	0.314	0.09	0.148	0.519	1.004
52	beta6[4]	Substrate	0.107	0.041	0.026	0.188	0.998
53	beta6[5]	Substrate	0.203	0.061	0.098	0.336	1.006

54	beta6[6]	Substrate	-0.026	0.04	-0.104	0.048	0.998
55	beta6mu	Substrate group mean	0.007	0.178	-0.299	0.392	1.003
56	beta6sig	Substrate group error	0.357	0.204	0.162	0.898	1.022
57	beta7[1]	Trout	-0.3	0.378	-1.013	0.452	0.999
58	beta7[2]	Trout	0.023	0.56	-1.046	1.376	1.008
59	beta7[3]	Trout	-0.506	0.412	-1.382	0.167	1.022
60	beta7[4]	Trout	-0.076	0.242	-0.559	0.372	1.004
61	beta7[5]	Trout	-0.84	0.561	-2.038	0.084	1.006
62	beta7[6]	Trout	0.122	0.386	-0.522	0.931	0.999
63	beta7mu	Trout group mean	-0.248	0.398	-1.112	0.581	1.003
64	beta7sig	Trout group error	0.672	0.519	0.043	1.891	1.015
65	beta8[1]	Cover	1.812	0.142	1.559	2.112	1.001
66	beta8[2]	Cover	0.163	0.094	-0.029	0.338	1.002
67	beta8[3]	Cover	-0.7	0.152	-1.009	-0.416	1.004
68	beta8[4]	Cover	0.168	0.074	0.02	0.298	0.999
69	beta8[5]	Cover	0.749	0.116	0.527	0.973	1.002
70	beta8[6]	Cover	0.64	0.084	0.482	0.805	1.006
71	beta8mu	Cover group mean	0.482	0.54	-0.54	1.614	1.012
72	beta8sig	Cover group error	1.123	0.557	0.545	2.697	1.01
73	beta9[1]	Trout * time	0.347	0.256	-0.076	0.934	1.007
74	beta9[2]	Trout * time	0.393	0.324	-0.193	1.104	1.003
75	beta9[3]	Trout * time	0.175	0.272	-0.408	0.595	1.018
76	beta9[4]	Trout * time	0.19	0.171	-0.164	0.492	1.007
77	beta9[5]	Trout * time	0.449	0.276	-0.024	1.036	1.002
78	beta9[6]	Trout * time	0.475	0.25	0.033	0.992	1.013
79	beta9mu	Trout * time group mean	0.341	0.238	-0.139	0.811	1.015
80	beta9sig	Trout * time group error	0.334	0.27	0.029	1.181	1.004
81	beta10[1]	Trout * depth	2.448	0.801	1.073	4.128	1.007
82	beta10[2]	Trout * depth	3.09	1.558	0.82	6.961	1.007
83	beta10[3]	Trout * depth	2.278	0.976	0.585	4.581	1.034
84	beta10[4]	Trout * depth	0.423	0.326	-0.157	1.059	0.999
85	beta10[5]	Trout * depth	-0.606	0.717	-1.869	0.93	1.008
86	beta10[6]	Trout * depth	1.756	0.644	0.66	3.115	1.002
87	beta10mu	Trout * depth group mean	1.567	1.045	-0.148	3.871	1.019

88	beta10sig	Trout * depth group error	2.039	1.186	0.634	5.077	1.009
89	beta11[1]	Trout * depth ²	-2.482	1.107	-4.939	-0.647	1.002
90	beta11[2]	Trout * depth ²	-1.133	1.518	-4.2	1.628	1.007
91	beta11[3]	Trout * depth ²	-2.387	1.129	-4.876	-0.431	1.011
92	beta11[4]	Trout * depth ²	-0.068	0.356	-0.732	0.638	1.005
93	beta11[5]	Trout * depth ²	2.194	0.539	1.141	3.268	1.006
94	beta11[6]	Trout * depth ²	-3.448	1.256	-6.401	-1.336	0.998
95	beta11mu	Trout * depth ² group mean	-1.246	1.372	-4.194	1.166	1.014
96	beta11sig	Trout * depth ² group error	2.927	1.253	1.286	6.059	1.007
97	beta12[1]	Trout * temperature	0.234	0.519	-1.038	1.123	1.025
98	beta12[2]	Trout * temperature	0.168	0.713	-1.594	1.428	1.008
99	beta12[3]	Trout * temperature	0.524	0.563	-0.69	1.608	1.005
100	beta12[4]	Trout * temperature	0.721	0.223	0.294	1.239	1.001
101	beta12[5]	Trout * temperature	0.932	0.32	0.383	1.661	1.001
102	beta12[6]	Trout * temperature	-0.02	0.294	-0.562	0.59	0.999
103	beta12mu	Trout * temperature group mean	0.424	0.399	-0.452	1.17	1.008
104	beta12sig	Trout * temperature group error	0.718	0.424	0.144	1.853	1.003
105	beta13[1]	Trout * velocity	-1.536	0.372	-2.285	-0.887	1.005
106	beta13[2]	Trout * velocity	0.147	0.386	-0.586	0.912	1.004
107	beta13[3]	Trout * velocity	-1.009	0.372	-1.723	-0.345	1.014
108	beta13[4]	Trout * velocity	-0.241	0.121	-0.464	0.001	0.997
109	beta13[5]	Trout * velocity	-0.528	0.252	-1.016	-0.044	0.995
110	beta13[6]	Trout * velocity	-0.059	0.231	-0.533	0.363	1
111	beta13mu	Trout * velocity group mean	-0.553	0.432	-1.426	0.332	1.003
112	beta13sig	Trout * velocity group error	0.955	0.578	0.381	2.296	1.001
113	beta14[1]	Trout * substrate	0.027	0.148	-0.261	0.339	1.018
114	beta14[2]	Trout * substrate	-0.002	0.183	-0.419	0.368	1.018
115	beta14[3]	Trout * substrate	0.034	0.212	-0.335	0.539	1.01
116	beta14[4]	Trout * substrate	-0.02	0.108	-0.242	0.177	1.001
117	beta14[5]	Trout * substrate	-0.021	0.137	-0.315	0.209	1.006
118	beta14[6]	Trout * substrate	0.07	0.156	-0.188	0.459	1.007
119	beta14mu	Trout * substrate group mean	0.016	0.142	-0.242	0.353	1.02
120	beta14sig	Trout * substrate group error	0.15	0.146	0.005	0.505	1.025
121	beta15[1]	Trout * cover	1.084	0.392	0.323	1.863	1.001

122	beta15[2]	Trout * cover	0.138	0.607	-1.03	1.237	1.002
123	beta15[3]	Trout * cover	0.155	0.577	-0.995	1.157	1.001
124	beta15[4]	Trout * cover	1.006	0.211	0.611	1.423	1.001
125	beta15[5]	Trout * cover	1.161	0.353	0.553	1.866	1.007
126	beta15[6]	Trout * cover	1.501	0.35	0.873	2.26	0.995
127	beta15mu	Trout * cover group mean	0.888	0.51	-0.035	1.881	1.032
128	beta15sig	Trout * cover group error	0.912	0.628	0.112	2.402	1.02
129	beta16[1]	Trout * cover * time	0.31	0.247	-0.209	0.715	1.009
130	beta16[2]	Trout * cover * time	0.319	0.362	-0.561	0.828	1.013
131	beta16[3]	Trout * cover * time	0.586	0.291	0.105	1.244	1.008
132	beta16[4]	Trout * cover * time	0.54	0.139	0.272	0.823	1.008
133	beta16[5]	Trout * cover * time	0.561	0.216	0.162	1.024	1.002
134	beta16[6]	Trout * cover * time	0.5	0.191	0.12	0.925	1.002
135	beta16mu	Trout * cover * time group mean	0.48	0.202	0.087	0.901	1.005
136	beta16sig	Trout * cover * time group error	0.292	0.27	0.01	0.983	1.021
137	beta17[1]	Depth * time	0.313	0.202	-0.079	0.721	1
138	beta17[2]	Depth * time	-1.269	0.28	-1.815	-0.738	1.024
139	beta17[3]	Depth * time	1.49	0.444	0.534	2.378	1.007
140	beta17[4]	Depth * time	0.248	0.114	0.017	0.473	1.016
141	beta17[5]	Depth * time	0.215	0.245	-0.266	0.721	1.007
142	beta17[6]	Depth * time	0.75	0.129	0.503	0.989	1.005
143	beta17mu	Depth * time group mean	0.293	0.585	-0.763	1.308	1.006
144	beta17sig	Depth * time group error	1.265	0.669	0.569	2.666	1.023
145	beta18[1]	Depth ² * time	-1.069	0.237	-1.561	-0.568	1
146	beta18[2]	Depth ² * time	0.375	0.118	0.137	0.599	1.027
147	beta18[3]	Depth ² * time	-0.551	0.247	-1.04	-0.053	1.008
148	beta18[4]	Depth ² * time	0.091	0.098	-0.114	0.288	1.012
149	beta18[5]	Depth ² * time	-0.335	0.119	-0.591	-0.103	1.003
150	beta18[6]	Depth ² * time	-0.249	0.113	-0.465	-0.02	0.996
151	beta18mu	Depth ² * time group mean	-0.311	0.367	-0.986	0.399	1.043
152	beta18sig	Depth ² * time group error	0.721	0.432	0.304	1.608	1.03
153	beta19[1]	Temperature * time	-0.154	0.194	-0.546	0.252	1.006
154	beta19[2]	Temperature * time	0.075	0.144	-0.19	0.352	1.001
155	beta19[3]	Temperature * time	-0.075	0.238	-0.509	0.417	0.997

156	beta19[4]	Temperature * time	-0.374	0.103	-0.571	-0.164	1.009
157	beta19[5]	Temperature * time	0.203	0.164	-0.114	0.548	1
158	beta19[6]	Temperature * time	-0.215	0.122	-0.458	0.008	1.002
159	beta19mu	Temperature * time group mean	-0.096	0.177	-0.474	0.252	1.003
160	beta19sig	Temperature * time group error	0.337	0.181	0.117	0.777	1.023
161	beta20[1]	Velocity * time	-0.133	0.099	-0.33	0.053	1.004
162	beta20[2]	Velocity * time	0.141	0.07	0.008	0.267	0.998
163	beta20[3]	Velocity * time	-0.786	0.162	-1.109	-0.473	1.006
164	beta20[4]	Velocity * time	0.048	0.047	-0.045	0.132	1.002
165	beta20[5]	Velocity * time	-0.082	0.076	-0.228	0.059	1.003
166	beta20[6]	Velocity * time	0.129	0.072	-0.017	0.268	1.008
167	beta20mu	Velocity * time group mean	-0.132	0.214	-0.579	0.266	1.005
168	beta20sig	Velocity * time group error	0.488	0.267	0.196	1.228	1.011
169	beta21[1]	Substrate * time	0.119	0.068	-0.027	0.252	1.001
170	beta21[2]	Substrate * time	-0.125	0.047	-0.217	-0.036	0.998
171	beta21[3]	Substrate * time	-0.235	0.105	-0.436	-0.043	1.006
172	beta21[4]	Substrate * time	-0.057	0.037	-0.127	0.013	0.999
173	beta21[5]	Substrate * time	-0.168	0.055	-0.277	-0.062	0.999
174	beta21[6]	Substrate * time	-0.225	0.047	-0.313	-0.131	0.998
175	beta21mu	Substrate * time group mean	-0.116	0.101	-0.295	0.08	1.011
176	beta21sig	Substrate * time group error	0.196	0.116	0.074	0.499	1.039
177	beta22[1]	Cover * time	0.142	0.166	-0.151	0.476	1.005
178	beta22[2]	Cover * time	0.041	0.099	-0.147	0.234	1
179	beta22[3]	Cover * time	-0.625	0.251	-1.121	-0.197	1.002
180	beta22[4]	Cover * time	-0.191	0.083	-0.358	-0.037	0.999
181	beta22[5]	Cover * time	-0.18	0.112	-0.391	0.043	1.013
182	beta22[6]	Cover * time	-0.4	0.108	-0.6	-0.182	1.003
183	beta22mu	Cover * time group mean	-0.189	0.206	-0.642	0.197	0.999
184	beta22sig	Cover * time group error	0.44	0.258	0.134	1.166	1.006
185	beta23[1]	Trout * depth * time	-0.212	0.326	-0.909	0.485	1.004
186	beta23[2]	Trout * depth * time	-0.162	0.435	-0.957	0.746	1.018
187	beta23[3]	Trout * depth * time	-0.233	0.466	-1.15	0.572	1.027
188	beta23[4]	Trout * depth * time	-0.212	0.216	-0.67	0.181	0.999
189	beta23[5]	Trout * depth * time	-0.286	0.351	-1.186	0.284	1.011

190	beta23[6]	Trout * depth * time	-0.133	0.346	-0.722	0.589	1.001
191	beta23mu	Trout * depth * time group mean	-0.195	0.308	-0.803	0.46	1.006
192	beta23sig	Trout * depth * time group error	0.315	0.324	0.015	1.27	1.038
193	beta24[1]	Trout * depth ² * time	1.933	0.662	0.637	3.226	1.005
194	beta24[2]	Trout * depth ² * time	0.141	0.623	-1.151	1.332	1.001
195	beta24[3]	Trout * depth ² * time	0.443	0.607	-0.674	1.598	1.001
196	beta24[4]	Trout * depth ² * time	0.532	0.219	0.141	0.981	1.003
197	beta24[5]	Trout * depth ² * time	0.844	0.323	0.252	1.484	0.998
198	beta24[6]	Trout * depth ² * time	-1.217	0.725	-2.916	0	0.998
199	beta24mu	Trout * depth ² * time group mean	0.445	0.808	-1.139	1.957	1.001
200	beta24sig	Trout * depth ² * time group error	1.564	1.133	0.51	4.537	1.015
201	beta25[1]	Trout * temperature * time	-0.151	0.369	-0.86	0.508	1.009
202	beta25[2]	Trout * temperature * time	-0.296	0.551	-1.405	0.74	1.004
203	beta25[3]	Trout * temperature * time	-0.299	0.457	-1.241	0.602	1.004
204	beta25[4]	Trout * temperature * time	0.444	0.179	0.086	0.818	1.011
205	beta25[5]	Trout * temperature * time	-0.443	0.269	-1.001	0.046	1.009
206	beta25[6]	Trout * temperature * time	0.523	0.213	0.1	0.958	1.023
207	beta25mu	Trout * temp. * time group mean	-0.081	0.44	-0.856	0.582	1.044
208	beta25sig	Trout * temp. * time group mean	0.75	0.492	0.213	1.72	1.026
209	beta26[1]	Trout * velocity	0.631	0.251	0.084	1.104	0.998
210	beta26[2]	Trout * velocity	-1.232	0.272	-1.778	-0.714	1
211	beta26[3]	Trout * velocity	0.62	0.305	-0.006	1.2	0.999
212	beta26[4]	Trout * velocity	-0.399	0.092	-0.591	-0.226	1
213	beta26[5]	Trout * velocity	-0.47	0.193	-0.874	-0.072	1.003
214	beta26[6]	Trout * velocity	-0.551	0.163	-0.885	-0.251	1.005
215	beta26mu	Trout * velocity group mean	-0.261	0.486	-1.275	0.689	1.007
216	beta26sig	Trout * velocity group error	1.047	0.576	0.44	2.624	1.004
217	beta27[1]	Trout * substrate	0.391	0.183	0.128	0.83	1
218	beta27[2]	Trout * substrate	0.232	0.138	-0.054	0.517	1.011
219	beta27[3]	Trout * substrate	0.355	0.189	0.083	0.79	0.997
220	beta27[4]	Trout * substrate	0.148	0.092	-0.033	0.306	1
221	beta27[5]	Trout * substrate	0.209	0.109	-0.008	0.428	1.005
222	beta27[6]	Trout * substrate	0.277	0.1	0.107	0.509	1.003
223	beta27mu	Trout * substrate group mean	0.271	0.135	0.044	0.574	1.007

APPENDIX C

Table 1. Pairwise Pearson correlation matrix five continuous environmental predictor variables used to build directional movement models. Asterisks represents correlation above a 0.28 threshold and these variables were not included in the same model following the guidelines of Graham (2003).

	Temp _{Max}	Average discharge	Discharge change	Discharge change _{t+1}	TL
Temp _{Max}	1.00				
Average discharge	0.25	1.00			
Discharge change	-0.15	0.19	1.00		
Discharge change _{t+1}	0.06	-0.42*	-0.33*	1.00	
TL	0.28	0.12	-0.10	0.003	1.00

*Excluded from the same model due to multicollinearity.

Table 2. Installation dates and suspected outage periods of fixed arrays on Spavinaw Creek. Loss of power was common during winter when cold temperatures and lack of sunlight prevented prolonged periods of battery charge. These outage periods were recorded in the reader file. However, outage due to broken antennas could only be inferred using a combination of flow data, periods of no recorded detections, and encountering broken antennas upon field visits (i.e., the exact date that the outage began was not known during this period).

Interval	Upstream array	Downstream array
Installed	12/21/2018	2/6/2019
1	1/1/2019 – 1/9/2019	2/9/2019 – 2/16/2019
2	1/13/2019 – 2/2/2019	3/5/2019 – 3/29/2019
3	2/9/2019 – 2/15/2019	3/31/2019 – 4/7/2019
4	4/14/2019 – 4/19/2019	4/29/2019 – 5/15/2019
5	4/29/2019 – 5/14/2019	5/19/2019 – 6/19/2019
6	5/19/2019 – 6/7/2019	NA
7	6/7/2019 – 6/15/2019	NA
8	6/19/2019 – 6/29/2019	NA

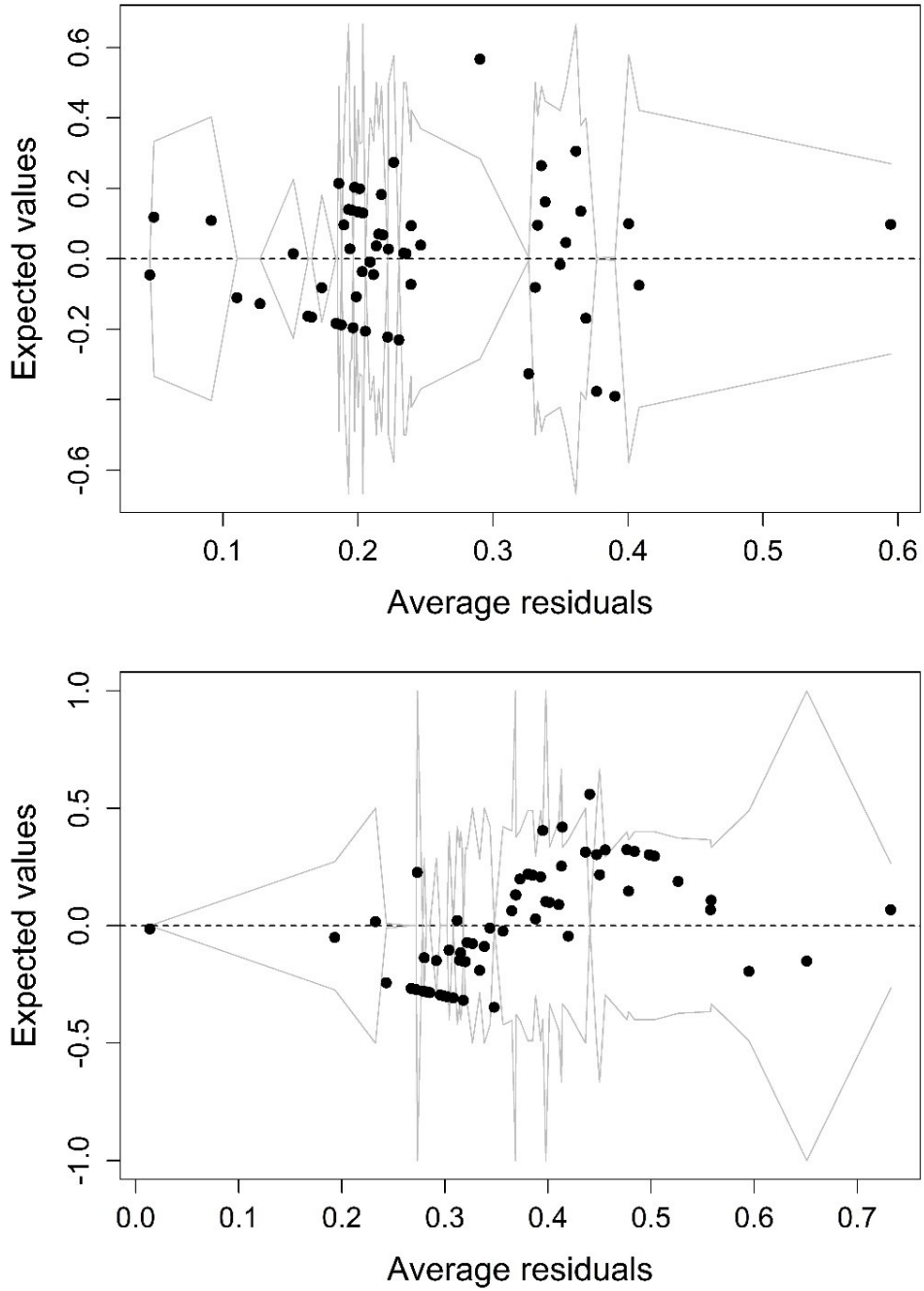


Figure 1. Binned residual plots for the downstream (top) and upstream (bottom) directional movement models. The gray lines indicate approximate 95% confidence intervals which 95% of the residuals (black dots) should fall within if model fit was appropriate.

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