EVALUATING THE RELATIONS BETWEEN FISH POPULATION DYNAMICS, STREAMFLOW, AND GEOMORPHIC CHARACTERISTICS AT MULTIPLE SPATIAL SCALES

by

RACHEL ALLISON KATZ

(Under the Direction of Mary C. Freeman)

ABSTRACT

Streamflow, geomorphology, and network structure play vital roles in the evolution, distribution, and abundances of aquatic species. In the southeastern U.S., where aquatic diversity is high and many species are imperiled, understanding how populations respond to environmental variability across spatial and temporal scales is essential for effective conservation of stream ecosystems and biodiversity. However, linking components of the streamflow regime, considered a master variable driving many biotic and ecosystem processes, to population processes has remained challenging because of methodological and conceptual constraints. This collection of studies uses a range of methods and scales for understanding population responses to streamflow and geomorphic characteristics to help inform management and conservation of stream fishes in the Piedmont province of the southeastern U.S. Specifically; I focus on linking demographic processes (i.e., abundance, survival, recruitment, dispersal, gene flow) to streamflow, geomorphology, and network characteristics. Results of a five-year study show resilient to flow reductions in fluvial-dependent darter species (*Etheostoma inscriptum*) population in a middle order Piedmont river, with high recruitment and local survival during severe and prolonged drought. Additionally, field observations and model results for five species in a suite of Piedmont streams indicate that fish population responses to low- and high-flow events vary with stream size and proximity to larger stream segments. This suggests that stream network characteristics influence the ability for populations to remain stable in response to variable streamflows. Lastly, a population geneticsanalysis of a small-stream cyprinid indicates that populations in close proximity to a river mainstem are well interconnected with substantial gene flow, and likely provide colonizers to smaller stream tributaries that are more vulnerable to local extirpations. Additionally, geomorphic features, as well as dams, likely influence the stepping-stone model of dispersal for this cyprinid. Collective results from this dissertation show that fish populations in larger tributaries are more resilient to changes in streamflow compared to populations in smaller tributaries, and that stream size, geomorphic context, and network position are important factors to include when predicting the biological effects of flow alterations across a watershed to inform management decisions.

INDEX WORDS: abundance, dispersal, flow management,gene flow, geomorphology, population dynamics, stream fishes, streamflow, survival

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DEDICATION

This dissertation is dedicated to my mother and father, who always encouraged me to go, to explore the world around me, and to learn as much as possible long the way.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Freshwater fishes are vital to stream ecosystems and can contribute substantially to ecosystem processes, such as production and nutrient cycling (Lotrich 1973, McIntyer et al. 2008).Approximately 28% of the known native fish species in the southeastern U.S. are extinct, endangered, threatened, or vulnerable, and more species are added to these lists each year (Warren et al. 2000). Dams and road crossings have extensively fragmented and degraded stream habitats, whereas impervious land cover, increased water use, and climate change have drastically altered hydrologic regimes, and are major causes of decline in freshwater taxa (Jelks et al. 2008, Strayer and Dudgeon 2010). Among these direct causes of species loss, streamflow alterations have been identified as the leading threat to freshwater biota (Richter et al. 1997,Naiman and Turner 2000, Strayer and Dudgeon 2010). Natural flow regimes vary spatially and temporally,profoundlyinfluencingphysical and ecological dynamics across local, reach, and network scales (Poff et al. 1997, Bunn and Arthington 2002, Poole 2002) and the evolution and adaptions of species (Lytle and Poff 2004, Mims and Olden 2012).

Changes in the natural flow regimes of freshwater rivers are widespread (Nilsson et al. 2005) and are expected to intensify with climate change and increasing human-water demands (Palmer et al. 2008). A hierarchy of factors influences stream fish populations, from local habitat and resource availability (Schlosser 1991, Schlosser and Angermeier 1995) to stream network structure and connectivity (Labbe and Fausch 2000, Campbell Grant et al. 2007). As humans modify local and regional environments that influence stream habitats and aquatic populations, effective conservation must include hierarchical management strategies and research at biologically relevant temporal and spatial scales (Lowe et al. 2006, Linke et al. 2011).

Streamflow patterns and disturbance regimes (Resh et al. 1988, Townsend 1989,Poff et al. 1997) interact with stream geomorphology andnetwork structure (Frissell et al. 1986, Poole 2002, Wiens 2002) to create a discontinuous distribution of suitable habitats for aquatic species. This hierarchically structured habitat mosaic influences species at scales ranging from individual behaviors, to population demography, and species persistence. For example, flow dynamics at the catchment scale can structure dendritic network topology and channel geomorphology (Benda et al. 2004, Poole 2010), affecting metapopulation dynamics and catchment-wide species persistence (Fagan 2002, Lowe 2002, Hitt and Angermeier 2011, Campbell Grant 2011). At the reach scale, channel geomorphology can strongly influence flow effects on habitat and fish densities (Peterson et al. 2009, McCargo and Peterson 2010), as well as individual fish movements among suitable habitat patches (Schlosser 1991, Roberts and Angermeier 2007). At the local habitat scale, flow reductions during the spawning period can decrease habitat quality and spawning success, resulting in lowered recruitment (Labbe and Fausch 2000, Falke et al. 2010). Although differing streamflow characteristics (e.g., monthly flow variability and magnitude of low and high flow events) have been found to influence fish recruitment (Freeman et al. 2001, Craven et al. 2010) and fish assemblage structure (Poff and Allan 1995, Grossman et al. 1998), quantitative relationships between flow and biological responses remain poorly understood (Poff and Zimmerman 2010). The wide range in streamflow-fish ecology responses may be partly the result of streamflow having interactive effects with local habitat, geomorphology, network dynamics across a range of spatial and temporal scales (Elosegi et al. 2010). Classifying stream segments according to relevant ecological processescan thus be useful for projecting the outcomes of various management actions (Melles et al. 2012, Freeman et al. 2013).

Although studies focusing on relatively short-term population and assemblage response (i.e., < 30 years) can yield important insights into fish assemblage dynamics in hydraulically altered stream systems (Gido and Propst 2012, Kiernan et al. 2012), quantifying the evolutionary outcomes of temporal and spatial variation in demographic processes can provide insights into how species persist over longer time scales (Hughes et al. 2009). Assessing genetic diversity, population structure and dispersal patterns of aquatic species can be useful for understanding how environmental alterations affect species over ecological and evolutionary time-scales (Dunham and Rieman 1999, Moran 2002). Ignoring population structure can impair the effective management of species by underestimating population vulnerability to extinction and lead to unintentional declines in biodiversity (Cooper and Mangel 1999). Population genetics have increasingly been used to assess the spatial structure of populations, to evaluate potential barriers to dispersal, and to identify possible source populations (Neville et al. 2006,Peery et al. 2008, Hughes et al. 2009, Lowe andAllendorf 2010). Although population genetics studies on non-migratory small-bodied fishes are common (Skalski et al. 2008,Boizard et al. 2009,Dehais et al. 2010), few focus on understanding population connectivity and dispersal in relation to geomorphic features at a fine-watershed scale, where management decisions concerning fragmentation and biodiversity monitoring often occur (EPD 2011).

This dissertation evaluates the effects of streamflow, geomorphology, and network characteristics on population processes of stream fishes at fine and broad spatial and temporal scales (i.e., from monthly changes in abundances within a single shoal habitat to genetic differentiation among populations within a watershed). This research uses a combination of field studies and molecular genetics to improve our understanding of how streamflow and geomorphic features influence fishpopulation dynamics at scales relevant to local and watershed management decisions.

In Chapter Two, I evaluate the relative influence of streamflow characteristics on local population abundances and apparent survival of a fluvial-dependent fish species (*Etheostoma inscriptum*) hypothesized to be especially vulnerable to extreme reductions in streamflow. I report results of a 5-year field study in a Piedmont river used for municipal water withdrawal during extreme drought in the Upper Altamaha River basin, GA. Although minimum flow standards (i.e., 7Q10; the lowest 7-day average flow that occurs, on average, once every 10 years) typically constrain water withdrawals, the Georgia EPD has permitted a low-flow exemption to meet human water demands during drought. A relevant management question for this river during low flows is: do extreme reductions in flow from drought or water withdrawal negatively influence stream fish populations? By estimating abundance, apparent survival and growth of a fluvial-specialist species, I evaluate the consequences of extreme low summer and fall flows on population processes. Linking demographic processes, such as apparent survival, to flow characteristics is useful for predicting long-term population responses to future streamflow alterations caused by increased water withdrawals, land use changes, and climate change.

In Chapter Three, I expand my evaluation of the effects of streamflow on fish populations by estimating abundance dynamics (change in seasonal abundances) of five species: two cyprinids, two centrarchids, and a percid. Understanding responses of stream fishes to flow regime characteristics is essential for developing predictive tools to model future projections. However, changes in flow regimes may have differential effects on aquatic populations depending on the underlying geology, reach geomorphology, stream size, network position, and local habitat conditions. Evaluating whether streamflow has predictably different effects in streams that vary in local habitat, reach geomorphology, and network position will be useful for designing monitoring programs across watersheds aimed at detecting short or long-term changes in fish assemblages.

In Chapter Four, I use published and newly developed nuclear markers (microsatellites) to estimate genetic diversity and population differentiation of a native small-stream cyprinid species (*Notropis lutipinnis*) hypothesized to have limited dispersal in larger streams. Connectivity can be critical for maintaining local populations through time, especially as the watershed landscapes change due to increased development and water resource developments. For organisms that primarily occur in smaller tributaries, fragmentation and habitat degradation can be especially isolating and result in local extinctions. I evaluate the influence of distance, natural geomorphic barriers, and low-head dams on the population structure and dispersal across a watershed. Specifically, this study seeks to understand how genetic structure varies across the watershed and how fish recolonize streams following local extinction events caused by flow reductions. Because decisions about watershed connectivity (culvert or dam removal), and local hydrology (water extractions) are often made at the watershed scale, this study aims to understand where local populations may be vulnerable to decline in response to environmental changes in habitat or stream connectivity.

Conclusions from this collection of work are used to inform gaps, uncertainties, and constraints that may limit our ability to manage fish populations for ecological goals, such as maintaining species diversity and promoting ecological resiliency under future climate change and increasing pressures for water resource development.

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CHAPTER 2

RESISILENCE TO LOW-FLOWS BY A FLUVIAL-DEPENDENT FISHSPECIES BASED ON A 5-YR STUDY OF ABUNDANCE AND SURVIALDYNAMICS[1]

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Abstract

Droughts are naturally occurring phenomena that influence multiple aspects of aquatic ecosystems, but human water demands and climate change have the potential to increase the frequency and severity of low-flow events. We estimated survival and abundance dynamics of a locally abundant riverine fish, the turquoise darter (*Etheostoma inscriptum*), over a 5-yr period encompassing historic low-flows in a mid-order, southeastern U.S. river. Data collected for age-0 (young-of-year; YOY) and age 1+ darters using capture-mark-recapture during the summer and fall of 2008–2012 provided weak evidence of an effect of low-flows on 30-d apparent survival, despite 25% to 80% reductions in river discharge compared to the long-term monthly averages. YOY darter survival during the drought increased with the occurrence of high flows, whereas age 1+ darters were more likely to disperse (or perish) from the study site in response to high flows or discharge pulses during low-flows. Adult abundance generally corresponded to YOY abundances in the proceeding year, and YOY recruitment estimates were highest for the three most severe drought years (although YOY growth appeared lower during severe drought). Results suggest that severe droughts can substantially influence recruitment and potentially influence the distribution of a fluvial-dependent benthic consumer. To our knowledge, this is one of the longest studies of fish survival dynamics during drought, and supports the hypothesis that populations in larger streams may exhibit biological resilience to low-flow extremeswithin stream networks.

Introduction

Streamflow alterations are considered a pervasive threat to freshwater ecosystems and aquatic biodiversity (Richter et al. 1997,Naiman and Turner 2000, Strayer and Dudgeon 2010). Changes in the natural flow regimes of freshwater rivers are widespread (Nilsson et al. 2005) and are expected to intensify with climate change and increasing human-water demands (Palmer et al. 2008). Stream ecologists widely recognize that the magnitude, timing, frequency, duration, and rate of change of flows shapestructural aspects of river ecosystems, such as habitat quality and quantity, physiochemical conditions, and resources for stream biota (Poff et al. 1997, Bunn and Arthington 2002). Developing predictive relationships between streamflow and ecological responses is essential for informingstreamflow management strategies aiming to conserve aquatic biodiversity and ecosystem functions (Anderson et al. 2006, Petts 2009, Peterson et al. 2011, Shenton et al. 2012, Freeman et al. 2013). However, quantifying relationships between population responses (i.e., abundance, survival, and recruitment)and streamflow dynamics (i.e., magnitude, duration, frequency) remainschallenging because multiple attributes of streamflow can influence the structure and function of stream communities at a hierarchy of temporal and spatial scales (Bunn and Arthington 2002, Poff et al. 2010).

Previous studies have broadly documented the influence of various flow regime components on stream fish assemblages and populations. Short-term high flowscan reduce the density or abundance of YOY fishes across a variety of species (Freeman et al. 1988, Grossman et al. 1998, Peterson and Jennings 2007, Craven et al. 2010) through increased mortality, dispersal, or both, and result in lower adult population abundances in subsequent years. In contrast, higher flow years (prolonged high flows) and higher flows during spring spawning can positively influence native fish abundances (Marchetti and Moyle 2001, Kiernan et al. 2012). Understanding how short and long-term flows influence species-level responses can explain variation in assemblage structure over time (Kiernan and Moyle 2012). To predict population and community responses to changes in flow, stream ecologists have suggested developing process-oriented relationships between streamflow and population dynamics (i.e., colonization, extinction, survival, and recruitment; Anderson et al. 2006, Poff and Zimmerman 2010, Poff et al. 2010, Shenton et al. 2012). The vast majority of studies linking flow and survival have been limited to salmonids (Riley et al. 2009, Poff and Zimmerman 2010, Grantham et al. 2012) with few flow-demographic studies focusing on smaller-bodied non-migratory species (Labbe and Fausch 2000; Hodges and Magoulick 2011). Quantifying flow effects on local survival of fishes can provide key insights into ecological dynamics of river ecosystems because these consumers directly influence stream productivity, aquatic food webs, and nutrient cycling (Lotich 1973, Power 1990, McIntyre et al. 2008, Cross et al. 2011).

In the southeastern U.S., a global center of temperate freshwater fish diversity (Ross 2013), at least 1 in 4 native fish species are extinct, endangered, threatened, or vulnerable, largely as a consequence of alteration to streamflow and habitat (Warren et al. 2000, Jelks et al. 2008). Species in the subfamily Etheostomatinae ("darters"; Percidae) are exceptionally diverse and exhibit high rates of imperilment (Jelks et al. 2008). The great majority of these small-bodied, non-migratory fishes require flowing water habitat, a condition termed "fluvial dependence" (or "fluvial specialization"; Travnichek et al. 1995) and are predictably concentrated in shoal habitats (analogous to "riffles" in smaller streams). In fact, many species of darters possess morphological adaptations to swift-benthic habitats, including a depressed dorsal profile and expanded pectoral fins (Gatz 1981). Studies have shown that fluvial-dependent fish species, such as darters, are more responsive to changes in flow compared to generalist species capable of persisting in both lentic and lotic habitats (Travnichek et al. 1995, Freeman and Marcinek 2006), yet responses of darter populations to changes in flow are not well documented (Labbe and Fausch 2000, Roberts and Angermeier 2007).

Periods of reduced streamflow, including seasonal low flows and droughts, are naturally occurring events known to influence several aspects of stream fish population dynamics (Labbe and Fausch 2000, Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003, Marsh-Marsh-Matthews and Matthews 2010). The short-term (< 2 years) ecological effects of reduced streamflow are well documented in streams that exhibit periods of flow intermittence. Responses include increased movement into nearby refugia, such as persistent pools (Labbe and Fausch 2000, Scheurer et al. 2003, Roberts and Angermeier 2007, Davey et al. 2006, Hodges and Magoulick 2011), increased mortality (Hodges and Magoulick 2011, Albanese et al. 2004, Marsh-Matthews and Matthews 2010, Grantham et al. 2012), and increased local extinction (Scheurer et al. 2003,McCargo and Peterson 2010). Populations in intermittent streams are highly dynamic and species persistence has often been attributed to the evolution of life history strategies and tolerances to extreme and flashy stream hydrology (Matthews and Marsh-Matthews 2003, Lytle and Poff 2004). Native fishes in perennial streams may be less well-adapted to recover from extremely low flow events that are rare and less predictable (Rolls et al. 2012).

In recent years, exceptional low flows in the summer and fall have been recorded in many southeastern U.S.perennial streams, prompting questions regarding the trajectory of fish assemblages and populations, as well as the adequacy of minimum flow standards to protect aquatic organisms. Management decisions, such as whether to invest in reservoirs that impound and fragment streams,but can augment low flows during periods of high water demand, can be informed by understanding the ability of aquatic populations to recover from extreme low-flow periods. The primary objective of this study is to understand how a population of a locally abundant, flow-dependent darter species responds to recurring drought in a perennial Piedmont stream during the summer and fall, when lower flows often coincide with higher water withdrawals for municipal uses. We hypothesize that fish population responses to low flowswill depend on the relative strength of environmental and biotic factors, and on species-specific strategies to cope with flow reductions (Davey et al. 2006). During extreme low flows, areas of swift-velocity over coarse bed sediment ("shoals" in larger streams and "riffles" in smaller streams) can contract significantly, initially increasing fish densities. Fluvial-dependent fishes may lack the ability to stay and survive in these environments due to increased competition and predation (Magoulick and Kobza 2000), terrestrial predation by birds (Dekar and Magoulick 2013), orphysiological stress caused by physiochemical changes, such as elevated temperature. Reduced flows can also stimulate dispersal (Albanese et al. 2004) and result in fish moving into nearby refugial habitats (Magoulick and Kobza 2003, Roberts and Angermeier 2006), where survival maydepend on the refugial habitat quality (Hodges and Magoulick 2011). In contrast, fishes may show resilience to seemingly harsh or stressful conditions if they are able to locate local, refugial habitats or exploit a variety of prey to reduce resource limitations (Marsh-Matthews and Matthews 2010).

We investigate the ability of a fish population to persist during extreme low flows caused by drought and water withdrawals by estimating young-of-year and adult abundance and local survival of a fluvial dependent darter species during the summer and fall across 5-years (2008–2012). We hypothesized that (1) YOYfall abundances would behigher in years with lower and more stable flows, (2) survival of YOY and adults would be lowerduring periods of extreme low streamflow and in response to high flow events, and (3) total population abundance woulddecline during severe low flow periods due to reductions in local survival. We also evaluated evidence for density-dependent survival and flow-mediated growth in the YOY size class. Variation in abundance, local survival, and growth were used to assess alternative mechanisms of how afluvial-dependent fish population may respond to extreme drought in aperennial river.

Methods

Study site, species, and streamflow conditions

We studied the influence ofstreamflow on the abundance and apparent survival of the turquoise darter, *Etheostoma inscriptum* (Jordan and Brayton) within a 1500 m^2shoal in the Middle Oconee River near Athens, GA (Fig. 2.1). The Middle Oconee River is a sixth order tributary that drains approximately 1000 km^2 in the Piedmont physiographic province in the Altamaha River basin. The study shoal contains swiftflow over cobble and small boulders with interspersed patches of sand and gravel. The shoal is separated from the nearest adjacent shoal upstream by a 500 m long sandy pool and downstream by at least 1 km of lower-gradient run and pool habitat.

The turquoise darter is found primarily in shoals of larger order streamsacross Piedmont drainages of NC, SC, and GA (Rhode et al. 2009). This species characteristically occupies high velocity habitats,even during low flow periods (Henry and Grossman 2007), and forages on macroinvertebrates including midge, black fly, mayfly and caddisfly larvae (Baker 2002; *personal observation*s). Spawning occurs in the spring and early summer (March–June; Richards 1966), with peak spawning in April (Irwin and Foltz 2012). Individuals mature at age one and live up to four years based on length-frequency distributions (Irwin and Foltz 2012). Although movement patterns are unstudied, other *Etheostoma*species exhibit relatively restricted movements (Roberts and Angermeier 2007).

Stream discharge during this study was recorded at aUSGS gage (No. 02217500) located 2.3 km downstream from the study shoal (no major tributaries entered the river between the study site and the gage) and provided a 71-yr record for historical context. We defined "severe" and "less severe" drought years as having average monthly summer and fall discharge less than 25% and between 25% and 50% of the 71-yr long-term average (8.58 m^{-3} $s^{-1}$for July through November). Near-normal flow years were defined as years with summer and fall discharge between 50 and 100% of the long-term average. Accordingly, severe drought occurred in 2007 (the year prior to the start of this study), 2008 and 2011 (1.76 and 1.96 m^{-3} s^{-1}, respectively). In 2009, summer discharge (July–August; 1.81 m^{-3} s^{-1})was also severely below the long-term average, but a large flood increased discharge above the long-term average in mid-September. In 2010, discharge (6.47 m^{-3} s^{-1}) was 75% of the long-term average and classified as "near-normal". The final year, 2012, was considered a less severe drought (2.89 m^{-3} s^{-1}). Consecutive years with less than 50% of long-term average summer and fall discharge occurred previously in 2000–2001, 1986–1988, and 1954–1955; however, 2007 through mid-September of 2009 marked the longest period of continuous severe drought in the 71-yr record.

Fish sampling

We estimated demographic parameters using a capture-mark-recapture (CMR) approach and a robust sampling design (Pollock 1982). We sampled darters on three consecutive days (secondary periods), approximately monthly (primary periods), beginning in late July or early August and continuing through November of each year, 2008–2012 (except when high flows precluded sampling after September in 2009). Sampling in late summer through fall allowed us to assess flow effects on darters during the lowest-flow portion of the year, and after YOY were large enough to capture and tag.

On each sampling day, we collected turquoise darters for one-hour haphazardly throughout the shoal (1500 m^2) using a seine (2.4-m x 2-m with 3.2-mm mesh) and backpack electrofisher (Smith Root model 12-B POW^{TM}). We minimized use of the electrofisher to avoid injuring fish and held fish in insulated and aerated containers for less than 3 hrs after initial capture. We measured the standard length (SL) of each individual to the nearest millimeter (mm) and tagged fish with fluorescent elastomer tags (VIE, Northwest Marine Technology^{TM}). In previous studies, these tags were observed to minimally influence survival and fishes retained tags over several months (Roberts and Angermeier 2004, Weston and Johnson 2008). We only tagged fish greater than 35 mm SL in order to minimize stress and mortality of age-0 individuals. Sixteen body positions and six tag colors were used in combination to make unique (July 2008 only) and batch (all other sampling days) marks that represented the day of capture. YOY (age 0, ≤40 to 45mm SL, depending on the month and year) were marked with different colors than adults to maintain size-class identification through the fall, when YOY grew to comparable sizes as small adults (age 1+). Individuals were retained in aerated coolersto ensure recovery after handling and tagging and then released randomly throughout the study shoal. The population was assumed closed to gains and losses during the 3-d sampling period, but open to mortality, emigration and immigration between primary periods. Water temperature and turbidity (2100P HACH Turbidmeter^{TM}) were recorded on each sampling day.

Data Analysis

<u>*Streamflow statistics*</u>

To evaluate the influence of streamflow components on abundance and survival of YOY and adults, we calculated five flow statistics using 15-minute discharge data recorded at the nearest USGS gage (No. 02217500). We were primarily interested in how acute low and high flow events, average flow condition, duration of low flows, and variability of low flows influenced the ability of darters to survive and stay within the shoal during exceptional drought.

We characterized low flow events as the lowest discharge recorded between sampling periods, reflecting extreme acute low flows caused by drought coupled with upstream water withdrawals. High flow events were characterized by the maximum discharge recorded between sampling periods, reflecting peak run-off following high rainfall. Average flow condition was represented by median flow and the duration of low-flows was characterized by percent of time discharge fell below 7Q10 (the lowest 7-day average flow that occurs on average once every 10 years; 1.3 $m^3 s^{-1}$ near the study site).We represented low-flow variability with the coefficient of variation of flows less than 2.8 $m^3 s^{-1}$ (a low flow that occurred in all years, but that generally excluded large rainfall events), reflecting small rainfall or withdrawal events during low flows when benthic habitat is vulnerable to desiccation and re-wetting.

Based on previous studies, low and stable flows can influence fall abundances of YOY by affecting spring spawning activity andsuccess, survival of eggs and larvae during the rearing period, and survival of juveniles during the growing period (Craven et al. 2010, Grantham et al. 2012). Thus, we hypothesized that YOY abundances in the fall would be higher in years with lower and more stable flows during one or more periods critical for early life stages. We developed period-specific metrics that included average flow condition represented by median discharge, high flow events represented maximum discharge recorded, and flow variability represented by the standard deviation in discharge during four periods: March–June (spawning), April (peak spawning), June–August (egg/larvae stage), and July/August–October/November (juvenile rearing stage).

Tag Retention

Tag loss can lead to substantial underestimation of survival by decreasing the recognition of recaptured fish. We estimated tag retention within and among years by double-taggingYOY and adults during the first primary period in 2009 and 2010. We used a Cormack-Jolly-Seber multistate model (CJSMM; Brownie et al. 1993) with two observable states (a two-tagged state and a single-tagged state that indicated observed tag-loss). We assumed tag loss did not occur during secondary sampling periods and collapsed 3 day capture histories into a single capture occasion. We scaled tag retention between primary periods to 30 d intervals and calculated the cumulative probability that a fish with one tag would remain tagged across the summer and fall season and between years. A Markov chain Monte Carlo (MCMC) Bayesian modeling approach with data augmentation (Kery and Schaub 2012) was used with diffuse priors on probabilities of capture, survival, and transition from a double-tag to single-tag state. We ran each cohort (2009 and 2010) model with 5,000 iterations, a 1,000 burn-in, a thinning rate of 3, and 3 chains using R and JAGS (Plummer et al. 2003). Convergence was assessed using Brooks, Gelman, and Rubin's measure of convergence (R-hat; Brook and Gelman, 1998), visual inspection of chains, and posterior distribution plots.

Demographic parameters and streamflow effects on survival

We estimated capture probability and abundance during each sampling period and apparent survival between primary sampling periods for YOY and adults. We used year-specific models (N = 5) for estimating survival because tag-loss increased substantially after 1-year (see Tag Retention results). We used a dynamic occupancy formulation of a Jolly-Seber*ad hoc* robust design model (Jolly 1965, Seber 1965, Kery and Schaub 2012), which assumes that all emigration is permanent (i.e., no temporary immigration). Capture probability can be influenced by a combination of environmental conditions (e.g., streamflow, temperature, and unmeasured factors such as crew experience) on each sampling day.Thus,we estimated capture probabilities for each size class on each secondary sampling period (N = 54). We assumed individuals within each size class had equal catchability (i.e., no behavioral response to tagging and no substantial individual heterogeneity in capture). YOY and adult abundances were estimated for each primary period (N = 18). Population stability within the summer and fall seasons (N = 2 in 2009; N = 4 in all other years) and between years was calculated using the coefficient of variation of abundances following Freeman et al. (1988) and Grossman et al. (1990).

Survivalrepresented apparent rather than actual survival because mortality and undetected emigration could not be distinguished (Burnham et al. 1987). We scaled apparent survival to 30 d intervals to facilitate comparisons among unequal sampling periods and calculated annual survival rates based on the average 30 d survival rates across the summer and fall of each year. Expressing survival as median residence time (months) provided a measure of the shoal's capacityto retain fish in units that could be compared to expected life span and was calculated usingan instantaneous rate of mortality based on average survival for each year.We also compared the percent of recaptures between years for each cohort to annual survival rates to evaluate variation in cohort-strength across years.

To evaluate the influence of streamflow on apparent survival, we developed six models: five that each containeda flow metric as a single predictor and a time-varying model that included interval-specific survival rates. We did not evaluate flow metrics in combination to avoid multicolinearity (|r| >0.70 for median discharge, percent time less than 7Q10 discharge and minimum discharge). We developed separate models for YOY and adults that included diffuse priors on the probability of capture for each sampling day and survival between sampling periods or the effect of flow on survival. Models were fit using aMCMC Bayesian modeling approach with data augmentation (following Kery and Schaub 2012) and posterior distributions of abundance estimates were plotted to ensure sufficient number of augmented individuals. To facilitate model fitting, flow predictors were normalized (mean = 0 and standard deviation = 1), and we fit time-varying parameters as fixed effects. Models were run for 50,000 iterations, with a 10,000 burn-in, a thinning rate of 10, and 3 chains usingR and JAGS (Plummer et al. 2003). Convergence was assessed using R-hat (Brook and Gelman, 1998), visual inspection of chains, and posterior distribution plots. We used a logit-link function to fit alternative models and calculated odds ratios (Hosmer and Lemeshow 2000) to facilitate interpretation of estimated flow effects on survival. The importance of each flow-effect was evaluated by examining 95% credible intervals and by calculating the percent variation explained by each flow predictor with an analysis of deviance (Skalski et al. 1993). We plotted the predicted 30 d survival rates under the range of observed flow conditions, which incorporated the uncertainty of each estimated effect. To assess model fit, we performed a posterior predictive checkusing a simpler model with collapsed secondary period capture histories and time-varying survival rates for YOY and adults.We assumed adequate model fit when Bayesian p-values neared 0.50 (0.25 to 0.75; Brooks et al. 2000, Kery and Schaub 2012).

Density-dependent population growth due to intraspecific competition has been observed in other stream fish studies (i.e., Grossman et al. 2006). We evaluated evidence for density-dependent survival of both YOY and adults using correlations (Pearson) between YOY survival and YOY, adult, and total abundances, and between adult survival and adult and total abundances. We interpreted negative correlations as evidence of intraspecific competition within or among size classes. We also used correlations (Pearson) to explore relationships between spawning, peak spawning, rearing and growing period flows andYOY fall abundances.

Young-of-year growth

Streamflow-mediated resource availability and density-dependent competition can influence YOY growth and year-class strength (Schlosser 1998, Falke et al. 2010). To evaluate the evidence for streamflow- and density-dependent growth across the summer and fall seasons, we developed nine alternative models that included combinations of Julian day, representing continuous growth over the summer and fall, median discharge between the initial and final sampling period of each year, and maximum YOY abundance estimated from the best-supported CMR model in each sampling year. Streamflow and density-dependent growth were represented by interactions between Julian day and median discharge, and Julian day and maximum YOY abundance, respectively. The response variable included lengths of all unmarked and marked YOY captured in each primary period (N = 3707). To facilitate model fitting, we standardized all continuous variables (mean = 0 and standard deviation = 1). Each candidate growth model was fit using linear regression (lm) and R statistical software package (version 3.1.0; R Development Core Team 2014).

We evaluated the relative support of each candidate growth model using Akaike's Information Criterion (AIC; Akaike 1973) with a small-sample bias adjustment (AICc, Hurvich and Tsai 1989), with lower AICc values indicating better predicting models (Burnham and Anderson 2002). We calculated Akaike weights (*w*), which ranged from zero to one, with the best approximating model having the highest weight (Burnham and Anderson 2002). Models with Akaike weights within 10% of the best approximating model, which is similar to Royall's 1/8rule for evaluating strength of evidence (Royall 1997), were considered plausible models. We constructed a global model with all predictors and assessed model fit by examining the residuals by Julian date and year(Bryk and Raudenbush 2002).

Results

Streamflow conditions

Severely reduced rainfall across the southeastern U.S. resulted in extremely low discharge in the Middle Oconee River during the summer and fall seasons across the 5-year study period. Average annual streamflow during the calendar year was 65%, 42%, and 64% below the 71-yr long-term mean (14.1 $m^3 s^{-1}$) in 2008, 2011, and 2012, respectively. In 2009, discharge was also reduced through the summer, but high rainfall in late September increased flow to > 3 times the long-term September average (19.5 $m^3 s^{-1}$ compared to 6.7 $m^3 s^{-1}$) and precluded sampling for the remainder of the year (Fig. 2.2). Although flows remained high across the fall, winter, and spring, summer and fall flows in 2010fell below long-term monthly averages (Fig. 2.2). Monthly discharge during the study period (July to November) was reduced by 24% to 85% compared to long-term monthly averages in all monthsexcept August of 2010, resulting in atypical contraction of areas with swift flow and exposure of bed sediments in shoals (Plate 2.1).

Despite prevailing low discharge during the study period, occasional high flow events (>30 $m^3 s^{-1}$) occurred between primary sampling periods in2008, 2010 and 2012 (Table 2.1). Conversely, flows fell below the 7Q10flow on 35% of days between primary sampling periods, although never in 2010 (Table 2.1). Periodic water diversions upstream of the study site exacerbated low streamflow events during severe drought years. For example, discharge recorded at the downstream gage fell below 0.3 $m^3 s^{-1}$ in 2008 (Fig. 2.2; Table 2.1), most likely in response to a pulsed water withdrawal event. The coefficient of variation during low-flows ranged from 0.10 to 0.57 (Table 2.1), primarily driven by rainfall events but also by water withdrawals.

Streamflow metrics used to test associations between fall YOY abundance and flow showed substantial interannual variation.Spawning period discharge (March–June) was generally higher (median >10.0 $m^3 s^{-1}$ and maximum >80.0 $m^3 s^{-1}$) and more variable (SD >11) in 2009, 2010, and 2011 compared to 2008 and 2012. However, rearing period (June–August) flows were similar among all years (maximum 10.5–39.1 $m^3 s^{-1}$and SD 1.5–3.4), with the exception of 2010, which had higher and slightly more variable discharge. High flows (maximum) and flow variability (SD) were correlated across spawning, rearing, and growing seasons ($|r| > 0.50$). Flows during the later summer and fall (i.e., initial to final sampling period each year) were considerably less variable than flows earlier in the year during the spring and early summer.

On sample days, water temperatures ranged from 10.5to 28.0 ^{o}C, with an average summer (July–mid September) temperature of 25.1^{o}C and average fall (late September–November) temperature of 17.0 ^{o}C. Water temperatures exceeded 27 ^{o}C in the early summer of all years except 2009, when sampling was delayed until mid-August. Stream discharge varied from 0.6 to 6.4 $m^3 s^{-1}$ and turbidity ranged from 5.5 to 45.9 NTUon sample days; discharge and turbidity were not significantly correlated ($r = 0.06$).

Fish captures and tag retention

We tagged and released 7,887 individual turquoise darters (2,897 YOY and 4,990 adults) in the study shoal over 5-years. Numbers of individuals captured and tagged varied substantially among years, especially for YOY (Table 2.2). Based on the time-varying model, mean capture probabilities in the study shoal on any sampling day (N = 54) was similar between YOY and adults (mean ± SD:0.14± 0.08 and 0.13 ± 0.02, respectively). Sampling over 3 consecutive days (N = 18 primary periods) increased mean capture probability (0.34 ± 0.13 for YOY and 0.34 ± 0.04 for adults); however, adult capture was generally more consistent among primary periods compared to YOY because few YOYwere captured in the early summer months due to their small size (<35 mm SL; Fig. 2.3).

We double-tagged a total of 657 turquoise darters (467 in 2009 and 190 in 2010) to estimate tag retention using a CJS multistate model. We recaptured 36% of double-tagged fish from 2009 and 59% from 2010 at least once during subsequent sampling periods. Within-year cumulative tag retention (from the initial to final primary periods each year) was relatively high for adults (0.96 ± 0.02 in 2009 and 0.92 ± 0.02 in 2010) and YOY (0.94 ± 0.05 in 2009). Recaptures of YOY were insufficient for estimating tag retention in 2010. Retention of a single tag across winter and spring to the next year was lower (0.83 ± 0.15 for 2009 cohort and 0.43 ± 0.25 for 2010 cohort), potentially resulting in underestimation of annual survival. However, we commonly recaptured fish in subsequent years with tags 1 year old or older. Adult recaptures varied among years, with fewest recaptures in 2010 (8.1% compared to 14.0 to 21.1% in drought years), following high winter and near-normal spring and summer flows (Table 2.2). YOY annual recaptures were generally lower than adults, with a range of 2.8% to 17.4% (Table 2.2). Exceptionally high numbers of YOY tagged in 2011 were recaptured in 2012, suggesting high over-winter and spring survival from 2011 to 2012 compared other years. Two YOY and 14 adults were captured with 3-year old tags (Table 2.2).

Young-of-year abundance, growth, and survival

In most years, YOY abundances increased from the summer through late fall and generally reflected continuous recruitment into the catchable size range (>35 mm SL; Fig. 2.3). In 2010, the year with the highest summer and fall flows, YOY abundances did not follow this pattern and slightly declined in the late fall (Fig. 2.3). YOY were especially abundant (1516 ± 145 and 1916 ± 133) in the late fall of the two years with the lowest monthly average flows during the study period (1.76 and 1.96 $m^3 s^{-1}$, respectively). During the less severe drought year (2012), YOY increased through the fall, but did not reach comparably high abundance to previous drought years (Fig. 2.3). YOYfall abundances (the last primary sampling period; N = 4) were weakly, positively correlatedwith increasing median flow in the spawning, peak spawning, rearing and growing periods (r = 0.33, r = 0.13, and r = 0.30, respectively) and negatively correlated with flow variability and high flow events during the spawning and peak spawning period (r = -0.53 and r = -0.25, respectively). Higher flows (median and maximum discharge) and higher flow variability during the study period (i.e. growing season) were all negatively correlated with fall abundances (r = -0.49, r = -0.15, r = -0.20, respectively). High flow magnitude and flow variability were consistently correlated across all periods (r >0.90),and thus had similar correlations with YOY fall abundances.

The best approximating models for predicting YOY growth from the summer into the late fall included an interaction between Julian day and the median discharge over the summer and fall (Table 2.3). This model contained all of the model weight (Table 2.3), thus inferences were only based on this best-approximating model. Parameter estimates indicated that YOY length (mm SL) increased with increasing median discharge and model predictions indicated that YOY were, on average, 2.5 mm larger in the late fall (95% credible interval:41.9–42.5 mm SL) during the highest flow year (2010 summer and fall median = 6.47 $m^3 s^{-1}$) compared to the most severe drought year (2008 summer and fall median = 1.76 $m^3 s^{-1}$; Fig. 2.4). Growth in 2009 was estimated imprecisely due to low sample size (N = 2).

Based on the time-varying survival model, YOY30 dapparent survival across primary periods were similarly low in the first severe drought year of 2008 (mean ± SD: 0.62± 0.25) and near-normal flow year of 2010 (0.66 ± 0.18), slightly higher in the less-severe drought year of

2012 (0.77 ± 0.08), and highest in the latter severe drought years of 2009 (0.91 – a single estimate) and 2011 (0.81± 0.20). We estimated exceptionally low30 d YOY apparent survivalin both a severe drought year (2008 = 0.36 ± 0.06) and higher flow year (2010 = 0.47 ± 0.17; Fig. 2.5). These low survival rates corresponded to median residence time of less than 2 months and possibly high dispersal out of the shoal. Although YOY abundances were lowest in the near-normal flow year (2010), lower survival estimates were not limited to this period and occurred during severe drought years as well. High 30 d survival estimates of YOY (>0.80) were also estimated during extreme drought years, corresponding to potentially high annual retention (>7%).

Variation in YOYsurvival was best approximated with a time-varying model. Alternative flow-models showed weak evidence that short or long-term low flows (median discharge, minimum discharge, and percent time less than 7Q10 discharge) influenced apparent survival (Table 2.4). Although less supported than the time-varying model, the model that included low-flow variability explained 25% of the variation in survival during the summer and fall. Parameter estimates indicated that survival increased with increasing variability of low flows caused primarily by small and large rainfall events during periods of reduced flow (Table 2.4; Fig. 2.6). For every 1 SD increase in the coefficient of variation of low-flows (i.e., 0.13), YOY were, on average, 2.7 times more likely to stay and survive within the study shoal. Additionally, the model including high flow events explained 3% of the variation in survival. Contrary to expectations, this model showed YOY survival increasing with increasing maximum discharge. YOY were, on average, 100 times more likely to stay and survive within the shoal with every 25 m^3s^{-1} increase in maximum discharge. Models that included median discharge, percent time less than the 7Q10 discharge and minimum discharge did not explain any variation in survival and credible intervals included both positive and negative effects (Table 2.4). However, mean estimates consistently suggested that YOY were plausibly more likely to survive as flows declined (Fig. 2.6). YOY survival was weakly negatively correlated with YOY abundances (r = -0.10, p-value = 0.74) and weakly positively correlated with adult and total abundances (r = 0.38, p-value = 0.19 and r = 0.18, p-value = 0.56, respectively). Goodness-of-fit evaluation showed adequate fit for most YOY models with Bayesian p-values of 0.61, 0.21, 0.00, and 0.49 for 2008 and 2010-2012 cohorts, respectively.

Adult abundance and survival

Among years, higher abundances of adults generally corresponded with higher fall abundances of YOY in the previous year (i.e., recruitment into age 1 fish). Abundances were highest in 2009 (mean ± SD; 1603 ±129) and likely reflected high recruitment of YOY in two previous consecutive severe drought years (2007 and 2008) that resulted in large numbers of age 1 and 2 fish. Abundances were slightly lower in 2008 (1380 ± 130) and 2012 (1319 ± 451), years that followed a single drought year (i.e., 2007 and 2011, respectively) that likely also resulted in high numbers of age 1 fish. We observed fewer adultsin 2011 (887 ± 427), a severe drought year that followed a near-normal flow year with fewer YOY. In contrast, fewer adults in the near-normal flow year of 2010 (781 ± 96) corresponded with lowest annual adult recaptures (8.1%), but only slightly lower recapture of YOY (2.8%) compared to the previous drought year (3.7%; Table 2.2). This suggests that increased adult dispersal out of the study shoal between years may have contributed more to reduced adult abundances in 2010.

Within the summer and fall seasons, abundances were relatively stable during the first two severe drought years (2008 = 0.09 CV and 2009 = 0.08 CV) and near-normal flow year (2010 = 0.12 CV) and relatively unstable during the latter two drought years (2011 = 0.48 CV and 2012 = 0.34 CV; Fig. 2.3). Specifically, adult abundances tripled and doubled during the sampling period in 2011 and 2012, respectively, suggesting substantial immigration into the study shoal from adjacent habitats in latter drought years following the near-normal flow year.

Average local 30 d survival of adult turquoise darters in the study shoal across the summer and fall was similar across all years (2008 = 0.88 ± 0.10, 2009 = 0.87 – a single estimate, 2010 = 0.82 ± 0.12, 2011 = 0.77 ± 0.20, and 2012 = 0.81 ± 0.17). However, survival varied substantially between primary periods in all years (Fig. 2.5), with no strong associations with extremely low streamflow conditions. In severe drought years, 30 d survival estimates were both high (>0.90) and low (<0.80), with sixty-two percent (8 of 13) of estimates below 90% and corresponding to median residence times of less than 7 months. Annual survival, based on average survival rates across the summer and fall, indicated a minimum retention of 21, 20, 9, 5, and 8% of adults annually for each cohort (2008 to 2012, respectively). However, annual recapture rates were higher than annual survival estimates in the latter two drought years, even with assumed tag loss (Table 2.2), indicating that the summer and fall were more stressful for adults compared to the winter and spring.

Similar to YOY, adult survival was best approximated with a time-varying model. Alternative flow models again showed weak evidence that low flows or low-flow variability influenced apparent survival (Table 2.4). Although less supported than the time-varying model, the model that included high flow events explained 12% of the variation in survival, with parameter estimates indicating that adults were more likely to leave the study shoal (i.e., through mortality or dispersal) with increasing high flow magnitude. For example, adults were 0.61 to 0.98 times more likely to leave the shoal with every 25 $m^3 s^{-1}$ increase in maximum discharge (Table 2.4, Fig. 2.6). Models that included median discharge, percent time less than the 7Q10 discharge and low-flow variability did not explain any variation in survival (Table 2.4). However, mean parameter estimates of these models indicated that adult survival was plausibly more likely to increase as flow increased (Table 2.4, Fig. 2.6). Evidence of density-dependence in adults was also weak, with a negative correlation with adult abundance (r = -0.39, p-value = 0.19) and total abundance (r = -0.14, p-value = 0.65).Goodness-of-fit evaluation showed adequate fit for adult models with Bayesian p-values ranging from 0.25 to 0.61.

Discussion

The combination of severe, less severe and near-normal flow years during our five-year study provided us the opportunity to evaluate the influence of several streamflow characteristics on fish population dynamics. To our knowledge, few studies have quantifiedchanges in abundance and apparent survival of a non-migratory fluvial-dependent fish species across the summer and fall during multiple drought years in a perennial stream. Using a CMR approach allowed us to evaluate relationships between short and long-term low and high flows on the survival of an abundant benthic darter species (*Etheostoma inscriptum*). Contrary to expectations, we found little evidence that extreme streamflow reduction during the summer and fall (up to 80% belowlong-term monthly average discharge) negatively influenced fish survival, despite substantial habitat dewatering and contraction of swift-velocity habitats. Survival estimates were occasionally high and low over 30 d periods during severe drought years, suggesting that apparent survival may not be directly related to prevailing discharge levels. Observed survival of marked adults across severe, less-severe, and drought years indicated that individual turquoise darters could persist within the study shoal for at least 3-years despite unprecedented low flows, contributing to unexpected resilience of a fluvial-dependent darter population to extreme reductions in streamflow.

Darter population response to variation in streamflow

Changes in annual and within season abundances combined with results from flow-survival models and annual recapture rates indicated that severe drought did not reduce the ability of turquoise darters to survive or persist within the study shoal. We observed higher YOY darter abundances in severe drought years compared to years with higher flows, generally higher adult abundances in years following high YOY abundances, and occasional high immigration of adults into the study shoal during severe drought years. Several studies have documented a similar pattern of higher numbers of YOY following periods of low stable, flows during the rearing period (Schlosser 1985), particularly in rivers that otherwise experience flow fluctuations from hydropower dams (Bain et al. 1998, Freeman et al. 2001, Craven et al. 2010). Lower YOY abundances in higher flow years may have resulted from decreased spawning activity or successin the spring, increased mortality or drift of the egg and larval stages(Harvey 1987,Mion et al. 1998, Weyers et al. 2003) or decreased survival of the juvenile stage(Grantham et al. 2012). Although larval stages are exceptionally vulnerable to mortality (Harvey 1987, Schlosser 1995,Slack et al. 2004), they are substantially less observable compared to later life stages. Consequently,many studies use association between spawning period flows and juvenile abundances in the fall to infer effects of flows on earlier life stages. For example, Craven et al. (2010) found that YOY fall densities of some fishes were positively related to short-term high flows during the spawning period, possibly as a result of beneficial flushing of fine sediments from interstitial habitats that are important for protecting and oxygenating eggs (Huang and Garcia 2000). Similarly, Kiernan et al. (2012) observedhigher proportional abundances of native fish species compared to non-natives after restoring winter and spring flows to higher more-natural historic levels, which were hypothesized to improve spring spawning and summer rearing habitat conditions for native fishes. In contrast to these studies, we found negative correlations between YOY fall abundances and higher magnitude of spring flow events and higher spring flow variability. However, small sample size (four years) and substantial correlations among spawning, rearing, and growing season flows precluded us from concluding that YOY abundances were strongly influenced by flow characteristics.

Abundance and growth of fishes in their first year of life is critical in determining adult population size and stability in subsequent years. Similar to previous multi-year studies (Schlosser 1998, Freeman et al. 1998, Grossman et al. 2006, Beche et al. 2009), we found that YOY abundance had a strong influence on adult population size in the following year. We also observed lower growth rates of YOY fishes in severe drought years when YOY fall abundances were highest. Size has been observed to be an important factor in determining over-winter survival of YOY fishes (Schlosser 1998), with larger individuals more likely recruiting into adults in the subsequent year. Thus, our observation of higher growth of YOY in years with fewer YOY (and higher flows) may slightly mitigate reductions in adult abundances as a result of low juvenile production by increasing YOY survival over-winter to age 1.

Contrary to our expectations, our results indicated that short and long periods of extremely low flows during summer and fall did not substantially influence survival of YOY or adults compared to periods of higher discharge. YOY appeared more likely to survive and stay within the study shoal during periods that included small or larger rainfall events, measured as low-flow variability and maximum discharge. This result may reflect a beneficial effect of flow pulses during drought on habitat quality or resource availability in shallow water habitats where smaller fish are typically found (Freeman and Stouder 1989, Henry and Grossman 2007). For example, extended periods of low flows can increase algal growth and sedimentation in shallow-water habitats, reducing aquatic macrophyte growth (Suren and Riis 2010) and associated macroinvertebrate densities (Hutchens et al. 2004). Thus, high flow pulses could increase survival of juvenile fish by removing accumulated algal and fine sediments in shallow-water habitats, increasing forage and habitat quality for YOY fishes. Alternatively, higher flow periods may encourage competitors (i.e., larger darters) to disperse (Schlosser 1995, Albanese et al. 2004, this study), resulting in reduced competition between small and larger fish for swift-velocity and high quality habitats (Freeman and Stouder 1989, Grossman et al. 2006). However, we did not observe strong evidence for intraspecific competition among juvenile and adult darters. Finally, high flows occurred only sporadically during the summer and fall periods (3 events >30 $m^3 s^{-1}$), potentially limiting our interpretation of the positive influence of high flows due to small sample size.

In contrast to YOY, we observed occasional large increases in adult abundances in severe drought years following years of low YOY production and, conversely, a positive effect of high flows on adult dispersal (or mortality). In combination, these results indicate that adults likely leave the shoal when flows increase and return with the onset of extreme low flows. Our model result indicating that adults are more likely to leave (i.e., disperse or die) during low-flow periods that include small or large rainfall events is consistent with other findings that show increased fish dispersal during higher flow periods (Petty and Grossman 2004, Albanese et al. 2004, Franssen et al. 2006). Lower adult abundancesin 2010 corresponded with low annual recapture rates of adults, likely as a result of high dispersal in response to a large flood in the fall and winter of 2009 followed by higher spring and summer flows. We expected fewer adults in 2011 due to substantially lower local recruitment in the shoal in 2010; however, adult abundances in 2011 and 2012 increased substantially across summer and fall, indicating that adults immigrated into the shoal from adjacent habitats in response to the onset of reduced flows. Although the source of immigrants during this study was unknown, an additional CMR study conducted in the upstream shoal in 2011–2012 indicated that occasional movement of adults and YOY can occur between shoals (across a distance of > 500 m; unpublished data). Local movement of darters may be low-flow mediated (Roberts and Angermeier 2006), but low recapture rates within the upstream shoal limited our ability to test this hypothesis explicitly. Naturally occurring high flows and flow reductions may promote population connectivity of shoal-dependent species by facilitating colonization of potentially isolated habitats or by providing opportunities for demographic rescue of habitats with low local recruitment (i.e., source-sink dynamics; Pulliam 1998, Hanski 1999).

Flow-demography relationships for flow management

Predicting biological consequences of flow management, especially effects of flow reductions due to water withdrawals for municipal or agricultural uses, requires linking streamflow characteristics with dynamic population responses (Poff et al. 2010, Peterson et al. 2011, Shenton et al. 2012, Freeman et al. 2013). In our 5-year study, we found a positive correlation between severe drought years and higher YOY production, and potential population resilience by a fluvial-dependent fish species to extremely low flow periods. Resilience to low flows has been observed in previous fish studies in larger streams. For example, McCargo and Peterson (2010) found that the effect of low flows on fish densities varied with stream size, with fish densities in larger stream sites being reduced less than those in smaller streams. Resilience to low flows in a fluvial-specialist was also observed in a stream mesocosm experiment by Marsh-Matthews and Matthews (2010). The authors observed similar survivorship of orangethroat daters (*Etheostoma spectabile*) after 40 d of extreme flow reduction treatment when compared to a treatment of continuous flow. Although darters were leaner after the 40 d low-flow treatment, individuals returned to similar body fat index to fishes in the continuous-flow treatment after six months of restored higher flows, indicating potentially rapid recovery from effects of increased competition or low-food availability during extremely low flows. Fishes than can persist and survive in slightly deeper habitats may also be more resilient to the effects of low flows (Schaefer 2001, Hodges and Magoulick 2011). Understanding potential resilience to low flows by aquatic biota, including locally abundant consumers, is important for predicting how droughts and flow reductions may alter energy flow, biomass, and production of aquatic communities. Moreover, management decisions, such as whether to invest in reservoirs that impound and fragment streams but also permit flow augmentation during droughts, will be better informed by an accurate understanding of population and ecosystem resilience and resistance to low-flow periods.

Developing flow-ecology relationships is complicated by the multiple interacting factors that influence the spatial and temporal variation in aquatic communities (Poff et al. 2010, Rolls et al. 2013). We were able to sample fishes in a larger stream shoal over 5-years when flows were unusually low, however our data represent a snapshot of the dynamics of a single species and certainly do not fully capture effects of flows on fish communities in this river system. In fact, even relatively long studies may not be adequate to capture the full range of hydrologic variability experienced by fishes and may result in an incomplete understanding of streamflow effects on fish populations (Webb et al. 2010, Kiernan et al. 2012, Rolls et al. 2012). For example, Strange et al. (1992) analyzed a 10-year data set and concluded that two large flood events caused a significant shift in the fish assemblage from dominance by native species to dominance by alien species. In contrast,a 5-year study by Moyle and Vondracek(1985) in the same stream system concluded thatdespite interannual variability in streamflow, the fish assemblage was relatively persistent and stable largely due to density-dependent mechanisms. A longer-term study (30-yrs) focusing on the influence of streamflow on stream fish assemblage dynamics found both strong and weak effects of drought and suggested that temporal sequence of hydrologic events may influence the relative importance of biotic or abiotic factors (i.e., habitat stability, resource availability, and biotic interactions), resulting in multiple alternative states (Kiernan and Moyle 2012).

Our 5-year study showed notable resilience by a fluvial-dependent fish population to rare and extreme low flow events. The duration, frequency, magnitude, and timing of low and high flow events during a study can influence the magnitude of population responses (Magoulick and Zobza 2003,Rolls et al. 2013). Thus, additional studies of population dynamics in streams differing in geomorphic character (McCargo and Peterson 2010) and a range of hydrologic conditions (Rolls et al. 2013) will be necessary for developing a predictive understanding of biotic responses to future hydrological alterations. However, identifying species, population, and ecosystem characteristics that promote resilience and rapid recovery to hydrologic extremes should help inform river management in response to increasing drought intensity and frequency and increasing water demands (Bond et al. 2008, Poff et al. 2010).

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TABLE 2.1 Summary of streamflow metrics between primary sampling periods based on 15-minutedischarge data recorded at the nearest downstream USGS gage (No. 02217500). Metrics included minimum, median, maximum discharge ($m^3 s^{-1}$), low-flow duration (percent time discharge fell below 7Q10; 1.3 $m^3 s^{-1}$), and low-flow variability (coefficient of variation of flows less than 2.8 $m^3 s^{-1}$).

Sampling interval	No. days	Minimum discharge	Median discharge	Maximum discharge	Low-flow duration	Low-flow variability
07/28/08 – 09/01/08	32	0.45	0.71	39.08	77.66	0.565
09/01/08 – 09/29/08	25	0.76	1.10	2.46	80.58	0.283
09/29/08 – 11/03/08	32	0.20	1.25	12.26	52.00	0.351
08/09/09 – 09/14/09	33	0.96	1.56	7.56	8.07	0.238
07/29/10 – 09/02/10	32	2.66	7.31	54.37	0.00	0.095
09/02/10 – 10/04/10	28	1.84	3.68	10.28	0.00	0.146
10/04/10 – 11/22/10	46	2.35	4.84	14.05	0.00	0.137
07/27/11 – 08/29/11	30	0.74	1.27	2.52	53.92	0.233
08/29/11 – 09/27/11	26	0.48	0.93	12.06	75.16	0.477
09/27/11 – 10/25/11	25	0.76	1.22	6.03	53.68	0.354
07/17/12 – 08/20/12	28	0.65	1.87	18.92	18.35	0.288
08/20/12 – 09/26/12	34	0.93	1.53	4.64	29.96	0.261
09/26/12 – 10/22/12	23	0.99	1.93	84.96	12.95	0.277

TABLE 2.2 Number of individual young-of-year and adult *Etheostoma inscriptum* released within the study shoal (Middle Oconee River, Athens GA) during each sampling year (diagonal) and the number (percentage) recaptured in each subsequent year (2008–2012).

	2008	2009	2010	2011	2012
Young-of-year					
2008	911	34 (3.7)	6 (0.7)	1 (0.1)	0 (0.0)
2009		284	8 (2.8)	2 (0.7)	1 (0.4)
2010			207	16 (7.7)	7 (3.4)
2011				1052	183 (17.4)
2012					443
Adult					
2008	1172	247 (21.1)	42 (3.6)	10 (0.9)	0 (0)
2009		926	75 (8.1)	24 (2.6)	4 (0.4)
2010			736	103 (14.0)	24 (3.3)
2011				888	149 (16.8)
2012					1268

TABLE 2.3 Mean deviance, number of parameters (Np), Akaike's information criterion (AIC_c), ΔAIC_c, model weight (w_i), and adjusted-R^2 for each candidate model predicting the size (mm SL) of YOY in the study shoal during the summer and fall of 2008–2012.

Candidate Model	Mean deviance	Np	AIC_c	ΔAIC_c	w_i	R^2
Julian day + median discharge + Julian day x median discharge	22325.99	5	17196.2	0.0	1.000	0.159
Julian day + median discharge + maximum YOY abundance	22599.85	5	17241.4	45.2	0.000	0.149
Julian day + median discharge	22644.70	4	17244.7	48.5	0.000	0.147
Julian day + maximum YOY abundance + Julian day x maximum YOY abundance	22768.35	5	17269.0	72.7	0.000	0.142
Julian day + maximum YOY abundance	23122.97	4	17322.2	126.0	0.000	0.129
Julian day	23210.61	3	17332.2	135.9	0.000	0.126
Median discharge + maximum YOY abundance	25785.29	4	17726.2	529.9	0.000	0.029
Median discharge	25943.12	3	17744.7	548.5	0.000	0.023
Maximum YOY abundance	26538.99	3	17828.9	632.7	0.000	0.001

TABLE 2.4 Mean deviance, parameter estimates, standard deviation (SD), lower and upper 95% credibility intervals (CI), and percent variation explained by each flow predictor for each candidate flow models predicting survival of YOY and adult turquoise darters in the Middle Oconee River (GA) shoal (1500 m^2) during the summer and fall of 2008–2012. Flow variables are normalized (1 SD = 1 unit) and boldface values indicate a significant effect (i.e., the 95% credibility interval does not overlap with zero).

Candidate model	Mean deviance	Estimate	SD	95% CI Lower	95% CI Upper	Unit	% Variation
Young-of-Year							
Time-varying	23933	-	-	-	-	-	-
Low-flow variability	24394	**0.98**	**0.23**	**0.55**	**1.46**	0.13 CV	25.1
Maximum discharge	24533	**4.61**	**1.17**	**2.43**	**6.93**	25.0 $m^3 s^{-1}$	2.6
Median discharge	24552	-0.38	0.39	-0.99	0.60	1.91 $m^3 s^{-1}$	0.0
Minimum discharge	24594	-0.46	0.42	-1.15	0.61	0.75 $m^3 s^{-1}$	0.0
Low-flow duration (<7Q10)	24606	0.08	0.31	-0.54	0.66	31% time	0.0
Adult							
Time-varying	46920	-	-	-	-	-	-
Maximum discharge	47184	**-0.27**	**0.12**	**-0.49**	**-0.02**	25.0 $m^3 s^{-1}$	12.5
Median discharge	47267	0.16	0.21	-0.14	0.70	1.91 $m^3 s^{-1}$	0.0
Minimum discharge	47267	0.12	0.19	-0.19	0.59	0.75 $m^3 s^{-1}$	0.0
Low-flow duration (<7Q10)	47277	-0.07	0.12	-0.32	0.17	31% time	0.0
Low-flow variability	47406	**-0.40**	**0.13**	**-0.65**	**-0.15**	0.13 CV	0.0

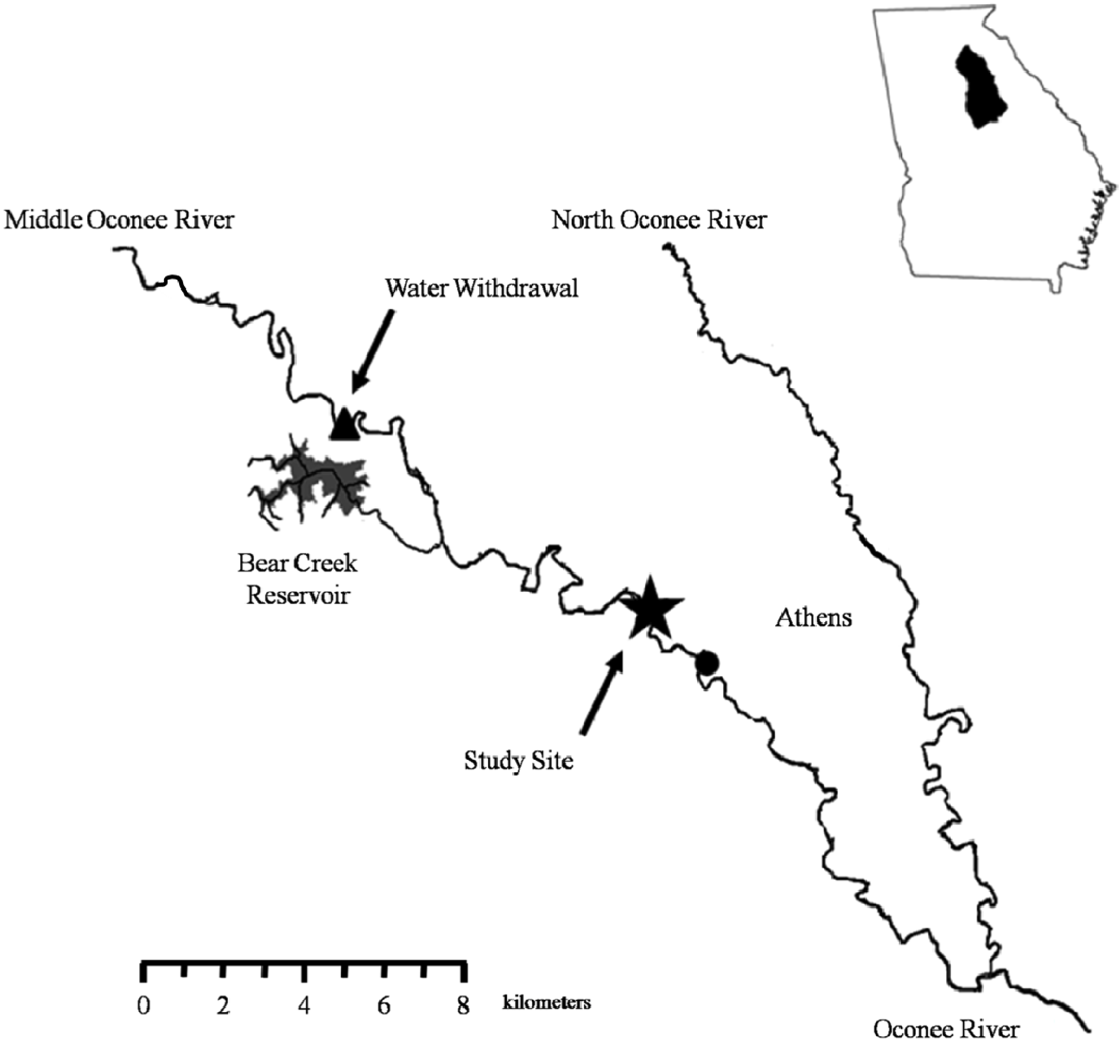

FIGURE 2.1 Study shoal (star) within the upper Oconee watershed (inset) in the Middle Oconee River near Athens, GA. A USGS gage (02217500; circle) is located 2.3 km downstream and a pump-storage water withdrawal facility is located 13 km upstream (triangle) of the study shoal.

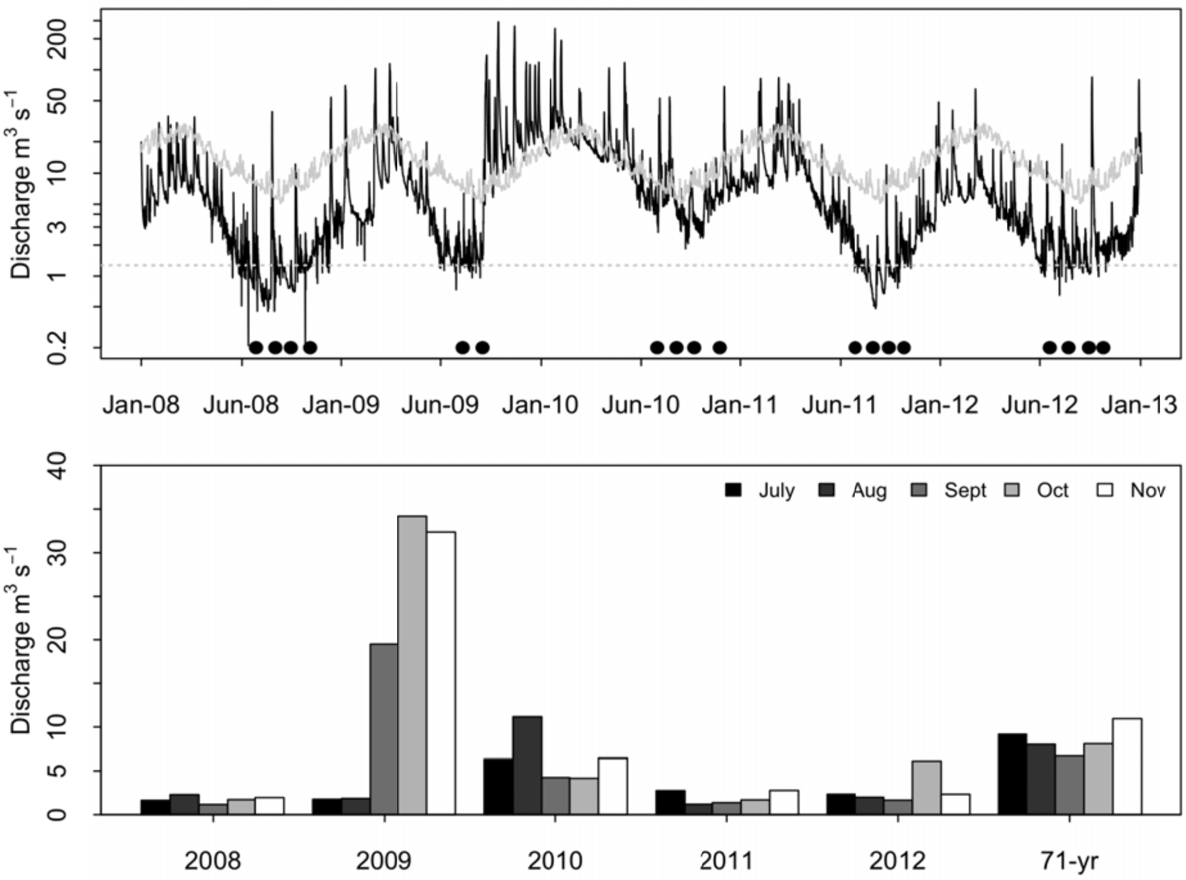

FIGURE 2.2 Discharge (15-minute; m^3 s^{-1}, upper panel) for the Middle Oconee River, Athens GA recorded at a USGS gage (02217500) near the study site from January 2008 to December 2012 (black line) in comparison to the long-term average daily discharge (71-yr record, 1941-2012; grey line) and 7Q10 (1.27m^3 s^{-1}; dotted grey line); and average monthly discharge for July through November of 2008-2012 in comparison to long-term (71-yr record) average for each month (lower panel). Filled circles represent primary sampling periods.

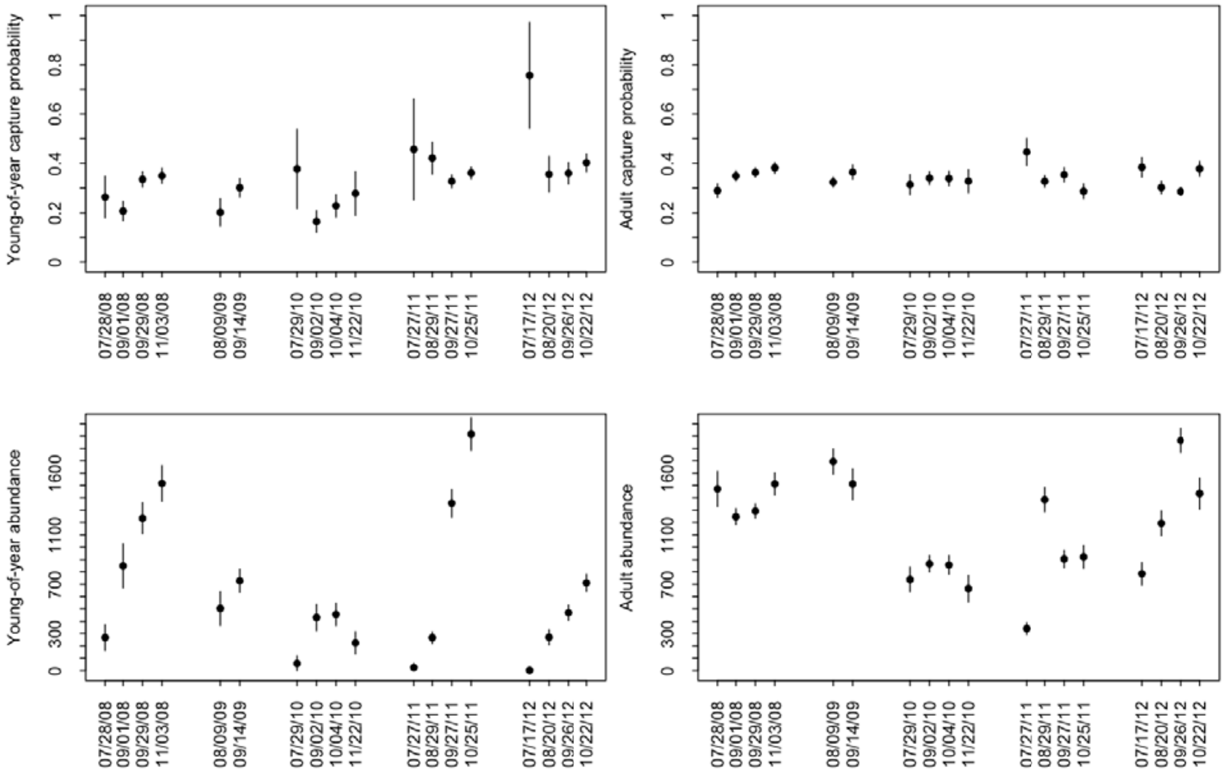

FIGURE 2.3 Mean estimate (SD) of the probability of capture and abundance of young-of-year and adult turquoise darters in the study shoal (1500 m^2) during each primary sampling period (2008 –2012). Capture probabilities represent the probability of capturing a fish at least once over 3-days of consecutive secondary sampling.

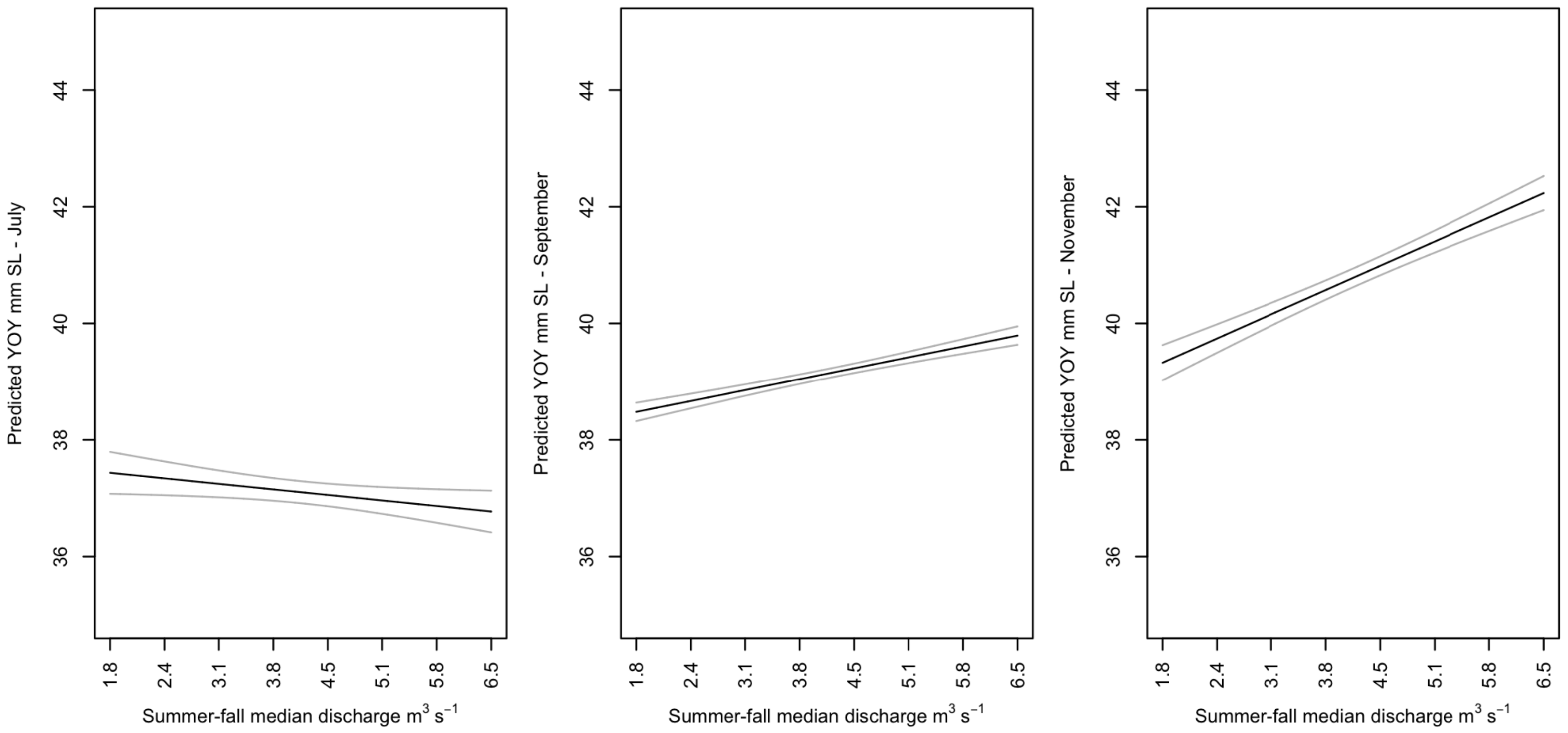

FIGURE 2.4 Predicted size (mm SL; mean = black, 95% credible intervals = grey) of YOY *Etheostoma inscriptum* in the study shoal (Middle Oconee River, Athens GA) in July, September, and November in relation to the summer-fall (July-November) median discharge.

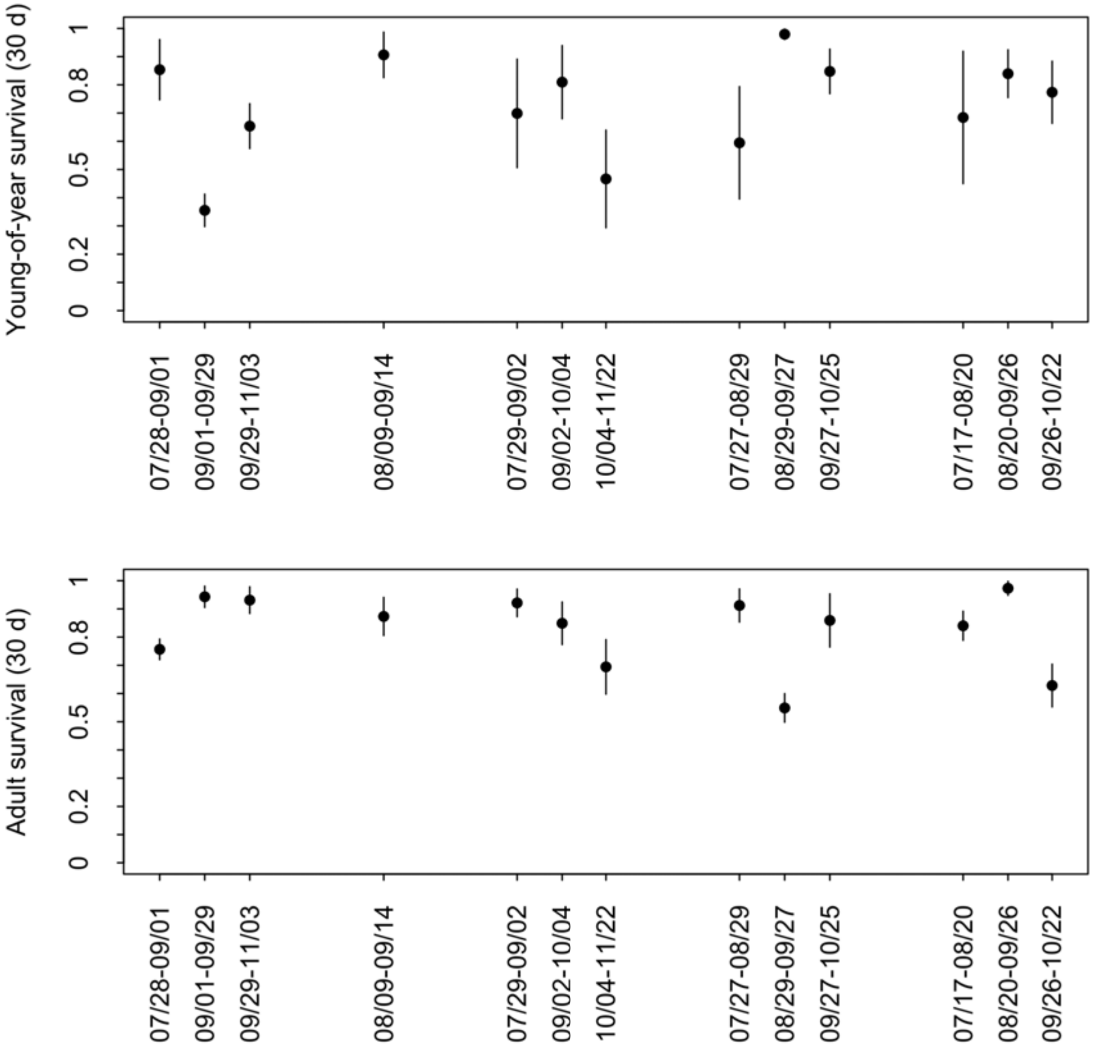

FIGURE 2.5. Mean estimate (SD) of 30 d apparent survival for young-of-year and adult *Etheostoma inscriptum* between sampling periods in the study shoal (Middle Oconee River, Athens GA) during the summer and fall of 2008–2012 based on the time-varying survival model

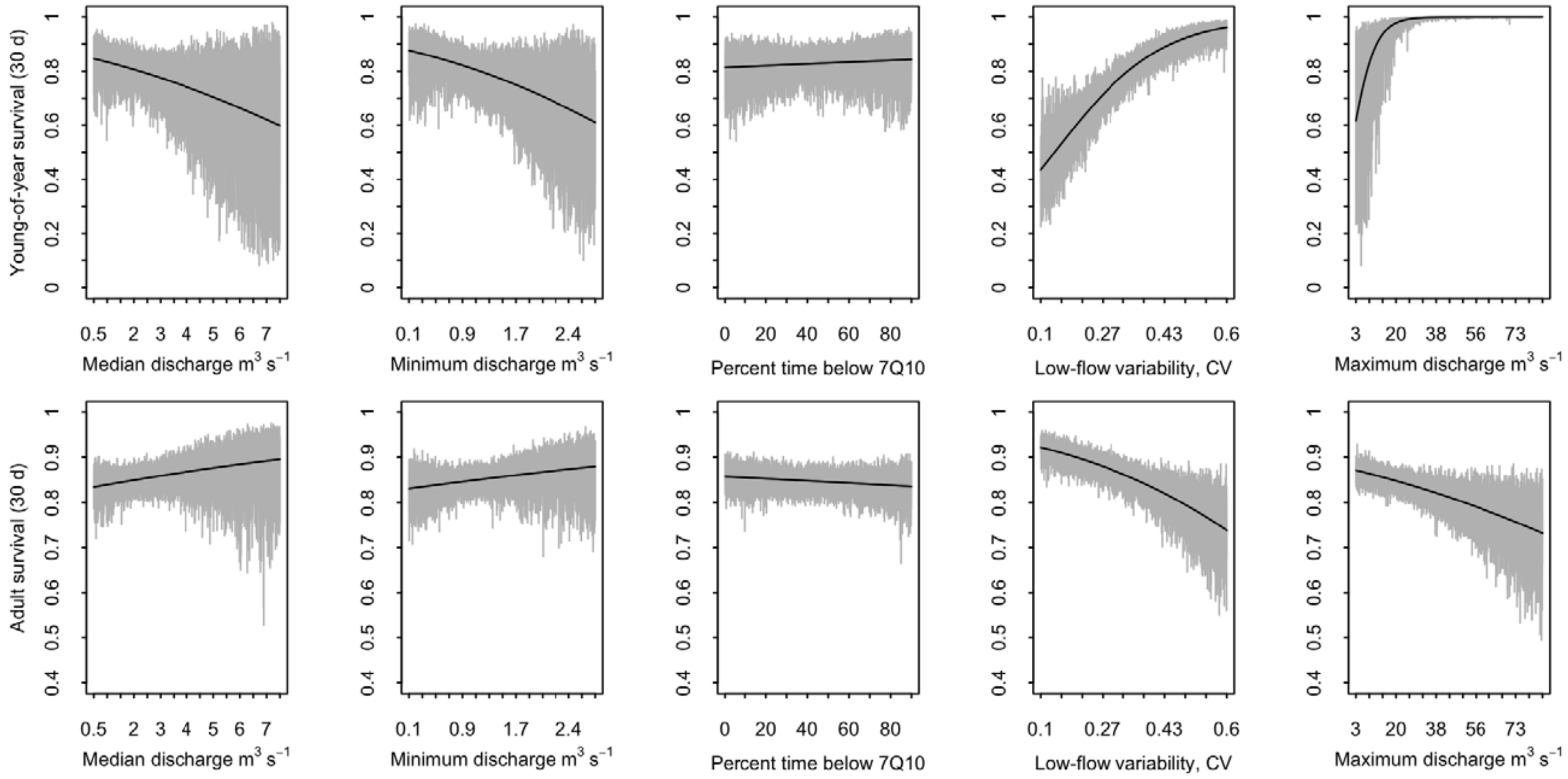

FIGURE 2.6. Predicted mean (black) and variability (grey) in 30 d survival of young-of-year and adult *Etheostoma inscriptum*in the study shoal (Middle Oconee River, Athens GA) based on the mean and 1SD of parameter estimates and the observed range of each flow variable during the study period (2008–2012).

PLATE 2.1 Study shoal (30 m wide x 50 m long) in the Middle Oconee River, near Athens, GA on August 29, 2011 (0.68 m^3s^{-1}; upper) and on November 22, 2010 (5.13 m^3s^{-1}; lower).

CHAPTER 3

STREAMFLOW EFFECTS ON ABUNDANCE DYNAMICS VARY WITH STREAM AND NETWORK CHARACTERISTICS FOR MULTIPLE STREAM FISH SPECIES IN A PIEDMONT WATERSHED[2]

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[2] Katz, R. A., M. C. Freeman, M. M. Hagler, and J. H. LaFontaine. To be submitted to Transactions of American Fisheries Society.

Abstract

Streamflow regimes can have a profound influence on population dynamics of aquatic species; however, linking flow characteristics with changes in fish populations is complicated by imperfect detection of individuals and uncertainty in the mediating effects of local habitat, reach geomorphology or network characteristics. Using a hierarchical modeling approach, we examined the relations between seasonal changes in fish abundance and low and high flow events using sampling data from 12 stream reaches across 4 years (2010–2013) in a Piedmont watershed located in the Upper Flint River basin, GA. We conducted a capture-mark-recapture study at a subset of reaches to estimate capture probabilities of differing stream fishes, and used those capture probabilities to estimate abundances from counts of individuals in habitat units sampled on multiple dates. Simulated daily flows for the stream segment containing each sampled reach were derived from a calibrated precipitation-runoff model and used to estimate levels of low- and high-streamflows during the intervals between samples. We used an information theoretic approach to evaluate the relative support for seasonal 10-d maximum and minimum flows, and of local habitat, channel confinement, stream size, and downstream link magnitude, as predictors of temporal changes in abundance of the five most commonly captured species. Results generally indicated that changes in abundances between sampling periods were positively related to short-term high and low flow events. However, these effects were species-specific and varied with catchment area for two cyprinid species, and with network position for two centrarchids species. High flow events potentially increased dispersal of stream fishes from larger tributaries into smaller tributaries. Additionally, extremely low flow events may have concentrated cyprinids and promoted young-of-year recruitment in reaches draining smaller catchments. These results provide insights into stream characteristics that may influence the

effects of flow events on abundance dynamics of several native stream fishes in Piedmont streams.

Introduction

Stream ecosystems are naturally hierarchical and dynamic, with regional climate, geology, and catchment topology setting the context for streamflow and geomorphic processes that maintain habitat heterogeneity at the reach and local scale (Frisselle1986, Poff and Ward 1990, Fausch et al. 2002, Poole 2002, Thorp et al. 2006, Winemiller et al. 2010). Streamflow variability across spatial and temporal scales is widely recognized to have a profound influence on sustaining reach and local habitat dynamics and ecological processes (Poff et al. 1997, Bunn and Arthington 2002, Poole 2002). Extensive research has linked hydrological and geomorphic processes operating across landscapes and within local habitat to biotic diversity, evolutionary traits, and species occurrence (Poff and Allan 1995, Angermeier and Winston 1998, Mims and Olden 2012). However, there is less understanding of how population dynamics are influenced by streamflow processes at intermediate reach scales (Fausch et al. 2002) –the scale at which many aquatic animals carry out many aspects of their life histories (i.e., 100 – 1000 m and 1-5 years).Evaluating the importance of factors at the reach scale while accounting for local and network characteristics can shed light on how hierarchical processes can regulate fish abundances and species persistence (Labbe and Fausch 2000).

Developing a predictive understanding of how environmental variables influence population dynamics of stream fishes is particularly relevant to aquatic conservation in the southeastern U.S., which is a global center of temperate freshwater fish diversity (Ross 2013). At least 1 in 4 native fish species in the U.S. are extinct, endangered, threatened, or vulnerable, largely as a consequence of alterations to habitat, streamflow, and connectivity (Warren et al.

2000, Jelks et al. 2008). Predicting how species and communities will respond to environmental changes within a particular stream network could help inform conservation strategies, but requires understanding of how variation in local habitat and reach characteristics influence population processes. Local habitat and streamflow-mediated processes are influenced by geomorphic context (Montgomery 1999, Poole 2010). Even in southeastern U.S. streams draining relatively low-relief landscapes, reach geomorphology (i.e., channel shape and slope) can constrain local habitat characteristics (Peterson et al. 2009) and the abundance and diversity of stream fishes (Walters et al. 2003, McCargo and Peterson 2010). Geomorphic context is thus expected to be useful for evaluating the influence of streamflow on fish populations (Poff et al. 2010, Freeman et al. 2013). Streams also vary in their position within the network, which can influence dispersal, local extinction, and long-term population stability (Fagan 2002, Lowe 2002, Campbell-Grant 2011). Quantifying the relative influence local, reach and network characteristics on the trajectory of fish populations within a hierarchical framework may help explain the large variability in correlations between fish counts and streamflow characteristics (Poff and Zimmerman 2010, Craven et al. 2010,Webb et al. 2010) and provide key insights into flow-ecology relationships and ecological dynamics of river ecosystems, such as stream productivity, aquatic food webs, and nutrient cycling (Lotrich 1973, Power 1990, McIntyre et al. 2008, Cross et al. 2011).

Over the last decade, many quantitative advances have allowed for explicit estimation of incomplete detection and accounting for hierarchical structures of ecological data (Royle and Dorazio 2006, Royle and Dorazio 2008). Specifically, hierarchical models have offered flexibility for incorporating observational and process uncertainty, as well as nested and unequal sampling regimes (Cressie et al. 2009), allowing for a flexible framework for analyzing field data from differing studies. The combination of a variety of available data sources (i.e., capture-mark-recapture and count data) has also proven useful for making stronger inferences about factors influencing populations (McCarthy and Masters 2005). Within the Bayesian hierarchical modeling framework, information from one study can be valuable in revealing stronger effects compared to evaluating data from differing studies independently (Ellison et al. 2004) and without a hierarchical structure (Webb et al. 2010).

Our objective was to assess how streamflow characteristics influence abundance dynamics (i.e., the change in population size) of common stream fish species in a southeastern U.S. Piedmont stream system. Specifically, we aimed to evaluate the evidence that streamflow, catchment area, channel shape, network connectivity, and local habitat influence seasonal changes in fish population abundances. We conducted the study across a range of flow conditions (near-, below-, and above-average seasonal streamflows) and were specifically interested in estimating the influence of low and high flow periods on changes in fish abundances in reaches with varying channel shapes. Our sampling design consisted of a mixture of spatial replication of fish counts to estimate abundance dynamicsand capture-mark-recapture at a subset of reachesto estimate capture probabilities. Finding that changes in abundance of species differs predictably in relation to local-level habitat, reach-level channel shape, streamflow or network-level connectivity factors would shed light on the hierarchical structure of influences on stream fish population dynamics, help identifylocations within the watershed where populations may be most vulnerable to population declines, and help inform future monitoring to detect population trends.

Methods

Study area

We evaluated the relative influence of local habitat, reach and network characteristics on fish abundance dynamics in the Potato Creek watershed within the Upper Flint River basin, GA, USA (Fig. 3.1). The Potato Creek watershed (482km^2)contains fish species (from a subset of at least 50 species within the Upper Flint River basin) and geomorphic contexts characteristic of streams draining the Piedmont province of the southeastern U.S. We selected 12 stream reaches having broad differences in reach geomorphology (i.e., channel shape; Table 3.1) and where landowners granted access for sampling over multiple years.

Stream discharge records for a USGS gage (No. 023147500) on the Flint River 19.4 km downstream from the Potato Creek confluence, were used to provide historical context for annual and seasonal variation in streamflow conditions during the study. Average annual discharge (based on the calendar year) was 8%, 54%, and 70% lower than the 77-yr (1937–2013) long-term annual average (60.8 m^3 s^{-1}) in 2010, 2011, and 2012, respectively (Fig. 3.2). In 2013, streamflows increased and average annual discharge was 2% higher than the long-term average (Fig. 3.2). We defined seasons as dry, near-normal, or wet as those with average seasonal discharge >50% below, between 50% below and 50% above, and >50% above the long-term summer (May–August) and fall (September–November) average discharges (43.57 m^3 s^{-1} and 29.38 m^3 s^{-1}, respectively). Accordingly, drought occurred in the fall of all sampling years (2010 through 2013), with average fall discharge 54%, 81%, 85%, and 52% below the long-term fall average, respectively. In contrast, summer discharge was more variable, with near-normal summer flows in 2010 (25% above the long-term summer average), drought in the summer of

2011 and 2012 (60% and 79% below the long-term summer average), and an exceedingly wet summer in 2013 (124% above long-term summer average; Fig. 3.2).

Fish sampling

To estimate fish abundance dynamics, we conducted seasonal surveys in 12 stream reaches from 2010–2013 (Table 3.2). Nine stream reaches were surveyed during the summer and fall of 2011–2013. At these reaches (termed "survey reaches"), we delineated 2 or 3 sample units that comprised replicated riffle-run or riffle-run-pool sequences (average unit length = 50 m, range = 29 to 90 m). The boundaries of each unit occurred near natural breaks in geomorphic features such as hydrologic controls when possible (Peterson et al. 2004).Prior to sampling fishes, we secured 7-mm mesh block nets to the streambed and banks at unit boundaries to prevent fish movement into or out of the sampling reach. Fish were captured by 3 to 5 crew members using a seine (2.4 m x 2 m with 3.2 mm mesh), backpack electrofisher (Smith Root model 12-B POW^{TM}) and dip nets (i.e., the "seine-electrofishing method" of Price and Peterson (2010)). We collected fishes during a single upstream pass and sampled all available habitats in each unit. After sampling, each fish collected was identified to species, measured for standard length (SL) to the nearest millimeter, and released back into the unit where captured. Individuals less than 35 millimeters (mm) SL were counted and released, but not measured. Mortalities during sampling were preserved in 10% formalin and averaged less than 3% of the total number of fish captured.

To estimate capture efficiency, we used capture-recapture sampling at an additional three stream reaches (termed "CMR reaches") during the summer and fall of 2010–2012. We used a closed capture sampling design over two consecutive days. Within each CMR reach, we delineated a single sampling unit (Table 3.3) that generally encompassed 2 to 3 riffle-run sequences. We secured 7-mm mesh block nets to the streambed and banks at unit boundaries to prevent fish movement into or out of the sampling reach, and collected fishes using the same method at survey reaches. After sampling, each fish collected was identified to species, measured to the nearest mm SL, and marked with a day-specific fluorescent elastomer tag (VIE, Northwest Marine Technology^{TM}). In previous studies, these tags were observed to minimally influence survival and fishes retained tags over several months (Roberts and Angermeier 2004, Weston and Johnson 2008). We used MS222 to anesthetize fishes vulnerable to stress during tagging and only tagged fish greater than 35mm SL to minimize mortality of age 0+ individuals. After fish appeared fully recovered from tagging, they were redistributed throughout the block-netted unit and left undisturbed for 24 hr. On the second sampling day, we ensured block nets remained secured, and resampled the sampling unit similar to the first day. We measured and recorded individuals with tags from the previous sampling day, redistributed fish through the unit, and removed block nets. Mortalities found in downstream block nets after sampling each day were removed from the data set. Counts of each species on the first sampling day in CMR reaches were used in conjunction with counts from survey reaches to estimate changes in abundances, accounting for incomplete detection as described below.

Local, reach, and network characteristics

Local stream habitat features known to influence capture probabilities (Bayley and Dowling 1993, Price and Peterson 2010) as well as various aspects of population demography (i.e., recruitment, survival, dispersal) were measured within each sampled unit. Temperature and turbidity (NTU; 2100P HACH Turbidmeter^{TM}) were measured prior to fish sampling on each visit. After fish sampling at survey reaches, water depth and current velocity (to the nearest 0.01 m s^{-1} with a Marsh-McBirney digital flowmeter) were measured at 25, 50, and 75% of channel width, along approximately 10 evenly spaced transects. Mean cross-sectional area was calculated using the average water depth and average wetted width across all transects within each unit. Bed sediments were visually classified as fine (silt or sand) or coarse (gravel or larger) at each transect point, from which we calculated the percent of fine substrate within the unit. The lengths (m) and widths (m) of submerged logs and woody debris jams were measured, and the total wood debris area (m^2) was calculated and divided by unit length to represent wood density.

Reach-level channel confinement can influence water chemistry, habitat complexity, and fish densities (Peterson et al. 2009 and McCargo and Peterson 2010). We defined the degree of channel confinement following McCargo and Peterson (2010), with highly confined channels having well-defined banks (i.e., bankfull-width-to-depth ratios less than 10) and infrequent overbank flows. Less confined channels had lower banks, occasionally braided channels, and evidence of frequent overbank flows into the floodplain. At each site, we measured or estimated bank height and channel width, usually at multiple transects, from which we estimated an average channel width to depth ratio (W:D) to represent the degree of channel confinement. Width to depth ratios near 10 represented relatively confined channels with occasional sloping banks that allowed periodic overbank flows.Stream size, which can influence flow dynamics (Thorp et al. 2006) and reach-scale hydrology (Lamouroux and Cattaneo 2006), was represented by catchment area (km^2) estimated for segments comprising the Potato Creek watershed by Elliot et al. (*in press*). Proximity to larger streams can influence the rate of dispersal of fishes and thus local population stability (Osborne and Wiley 1992) andwas represented by the link magnitude of the nearest downstream segment (dlink; also estimated by Elliot et al., *in press*).

Our main objective was to evaluate evidence that the effects of streamflow on abundances of fishes differed among streams that varied in local, reach, and network characteristics. To estimate streamflow dynamics at our study reaches, we used output from a calibrated, precipitation-runoff model of unimpaired flows developed for the Potato Creek watershed (LaFontaine et al. 2013), updated using precipitation and air temperature data through 2013. The hydrologic model produced simulated daily flows for 221 segments comprising the Potato Creek stream network for each of the study years. We summarized streamflow characteristics for the segments containing sampled reaches, and the time periods between sampling events.

We were specifically interested in evaluating the influence of low- and high-flow events on fish abundance dynamics. We characterized prolonged low flow periods as the 10-d minimum discharge (lowest discharge for 10 consecutive days) and high flow pulses as the 10-day maximum discharge based on simulated time-series of daily discharge between sampling visits. We divided each flow metric by the median daily discharge across the period of record (62 years;1951–2013) for each reach (Fig. 3.3) because stream reaches varied in size and could potentially affect the comparison of the relationship between flow characteristics and changes in abundances. Median discharge was also calculated, but was correlated with high flow periods (Pearson correlation coefficient, $r = 0.73$).

Data analysis

Capture probability

We used recapture data from the CMR reaches to estimate capture efficiency for our sampling method as well as the effects of potentially influential factors to obtain least biased estimates of fish abundance across all study reaches. Specifically, we estimated capture probabilities in relation to species, stream habitat characteristics, and crew experience. To ensure sufficient sample sizes, we restricted our analysis to 11 species with >25% of tagged individuals recaptured at least once (Table 3.4). We pooled data across reaches and sampling dates and used the recapture history on the second consecutive sampling day (0 = not recaptured or 1 = recaptured) for all individuals captured, tagged, and released on the first sampling day as the response variable in a logistic regression model. Variation in capture probabilities among species was examined by using binary coding for species identities, with *Notropis lutipinnis* (Cyprinidae) as the baseline species. To avoid multicollinearity, we evaluated the relationship among habitat covariates using Pearson's correlation coefficient prior to model fitting; strongly correlated variables ($r^2 > 0.49$) were not included in the candidate model that represented habitat (Moore and McCabe 1993). We evaluated ten alternative models that included combinations of species, local habitat conditions and crew experience covariates (Table 3.5). Uncorrelated habitat covariates included wood density, percent fine substrate, the sum of precipitation 7-days prior to sampling, simulated discharge (from the precipitation-runoff model described above), and stream temperature on the sampling day. A binary term representing increased sampling efficiencies after the first two sampling visits (0 = first two visits, 1 = all other visits) was included to allow for increased sampling experience by the crew members. We also included the interaction between species and sampling experience to account for the possibility that capture of some species were more influenced by increased crew experience compared to others.

Capture probabilities were modeled as a linear function of covariates using logistic regression, a logit-link function, and a Markov chain Monte Carlo (MCMC) Bayesian modeling approach with uninformative priors on each covariate effect.To facilitate model fitting, we standardized all continuous variables (mean = 0 and standard deviation = 1). Models were run for 10,000 iterations, with a 5,000 burn-in, a thinning rate of 10, and 3 chains using R and JAGS (Plummer 2003). Convergence was assessed using R-hat (Brooks and Gelman1998), visual inspection of chains, and posterior distribution plots.We evaluated the relative support of each candidate model using Akaike's Information Criterion (AIC; Akaike 1973) with a small-sample bias adjustment (AICc, Hurvich and Tsai 1989), with lower AICc values indicating better predicting models (Burnham and Anderson 2002). We calculated Akaike weights (*w*), which ranged from zero to one, with the best approximating model having the highest weight (Burnham and Anderson 2002). Models with Akaike weights within 10% of the best approximating model, which is similar to Royall's 1/8rule for evaluating strength of evidence (Royall 1997), were considered plausible models. To ensure the best approximating model was not over-fit, we performed posterior predictive checks and assumed adequate model fit when Bayesian p-values neared 0.50 (Brooks et al. 2000).

Abundance dynamics

We evaluated the influence of short-term low and high flows, local habitat, reach geomorphology, and network position on abundance dynamics of multiple species over seasons using species-specific hierarchical state-space models. The model included species-specific counts in units ($i = 1, 2,$ or 3) that were nested within reaches ($j = 1$ to 12), during sequential visits ($t = 1, 2, \dots T$; $T = 4\text{–}6$; Table 3.2). For each species modeled, we assumed that our observed counts, C_{ijt} of fish were binomially distributed given a capture probability p_{ijt} and the true abundance of fish within each unit, denoted as $N.eff_{ijt}$, and that the true abundance was distributed according to a Poisson with a mean that represented the expected abundance:

$$C_{ijt} \sim BIN(p_{ijt}, N.eff_{ijt}),$$

$$N.eff_{ijt} \sim POISSON(N_{ijt}).$$

We incorporated uncertainty in capture probability by drawing coefficients for each covariate present in the best approximating capture model from a normal distribution with a covariate-specific mean and standard deviation. The change in abundance between visits was then modeled as a function of flow and either habitat, reach or network covariates, which represented alternative hypotheses (Table 3.5):

$$N_{ijt+1} = N_{ijt} * \lambda_{ijt}$$

$$\ln(\lambda_{ijt}) = \beta_1 \text{ x flow}_{jt} + \beta_2 \text{ x habitat}_{ij}, \text{reach}_{j}\mathit{or}\text{network}_{\text{j}} +$$

$$\beta_3 \text{ x flow}_{jt} \text{ x reach}_{j}\mathit{or}\text{network}_{j}.$$

We only included species in the analysis that contained sufficient data from capture-mark-recapture analysis to ensure reasonable estimates of capture probability and that were detected at more than 10 reaches to ensure sufficient sample sizes for evaluating reach-level characteristics.

We developed 20 alternative species-specific candidate models to evaluate the relative influence of streamflow on population growth given variations in reach geomorphology, network connectivity, and local habitat characteristics for each species (Table 3.5; Appendix A). We ran candidate models using a Markov chain Monte Carlo (MCMC)Bayesian hierarchical modeling approach and estimated covariate effects on lambda using a log-link function with uninformative priors for each parameter. We included two random effects for sampling date: one for sampling dates of CMR reaches and one for sampled dates at survey reaches. CMR and survey reaches were sampled at differing times of the year (i.e., early compared to late summer and early compared to late fall) and corresponded to differing time intervals. Random effects each had a mean of 0 and random effect-specific standard deviation of 20. The number of iterations, burn-in, and thinning rate were determined by fitting a global model for each species with three parallel chains and testing for convergence using the Gelman–Rubin diagnostic (Gelman and Rubin 1992), visually inspecting chain mixing and posterior distribution plots in R and JAGS

(Plummer 2003). All models were fitted using 200,000 iterations, a 50,000 iteration burn-in, a thinning rate of 5 and three chains, resulting in 90,000 iterations retained.

We evaluated the relative support of each candidate model similarly to capture probability models (AIC_c), with lower AIC_c values indicating better predicting models (Burnham and Anderson 2002). We counted fixed effects and random effects as single parameters. We considered plausible models as those models with model weights within 10% of the best approximating model and assessed the precision of parameter estimates for each model using 95% Bayesian credible intervals (Congdon2001).To assess model fit of the best approximating models, we examined the residuals by sample date and site to detect possible temporal or spatial dependencies(Bryk and Raudenbush 2002).

Results

Forty species were detected across all reaches during the study period. The most commonly observed species were *Lepomis auritus* and *Percina nigrofasciata* (detected at all reaches), *Notropis lutipinnis*and*Lepomis macrochirus* (92% of reaches),and *Nocomis leptocephalus* (83% of reaches).These were the only species that met the criteria for modeling flow effects on abundance dynamics. Specific-specific analyses only included reaches where a species was observed at least once during the study period. Fish counts varied spatially and temporally among these five species, with *N. lutipinnis* having the highest average counts across reaches and sampling periods (mean ± SD: 84 ± 101) and *N. leptocephalus, P. nigrofasciata, L. auritus*, and *L. macrochirus* having lower and similar average counts (20 ± 26, 20 ± 16, 16 ± 18, and 19 ± 27, respectively). Overall, total species counts generally increased in lower flow years (2011 and 2012) compared to higher flow years (2010 and 2013; Fig. 3.4). This increase was partly driven by changes in the counts of smaller, age 0+ fish (i.e., <36 mm SL). In lower flow years (2011 and 2012), the proportion of total captures that were age 0+ was higher for *N. lutipinnis*(39–63%), *N. leptocephalus*(54–55%) and *L. auritus* (22–26%). In the highest flow year (2013) the proportion of total captures that were age 0+ was substantially lower for these species (11%, 13%, and 6%, respectively). In contrast, the proportion of age 0+ captures for *L. macrochirus* was higher during the higher flow year (21%; 2013) compared to lower flow years (2% in both 2011 and 2012). *P. nigrofasciata*age 0+ composed relatively low proportions of total captures across year (5–13%). Two reaches (Unnamed Tributary and Fivemile Creek) were essentially dry during the fall of 2011 (i.e., dry streambeds with periodic small pool habitats) and no fish were collected at either reach during this season.

Capture probabilities estimated from recapture of tagged individuals of 11 species were better predicted by species identity and sampling experience than by any of the tested habitat variables. The best approximating model of capture probability indicated that capture was species-specific and increased after the initial sampling periods for some species (Table 3.6). Precision in capture estimates illustrated considerable uncertainties in capture probabilities. For example, estimates for *N. lutipinnis* on the initial and latter sampling dates (0.372 ± 0.032 and 0.683 ± 0.023, respectively) could result in a wide range of possible capture probabilities (0.216–0.527 and 0.571–0.790, respectively, based on 1M simulations assuming estimates were normally distributed). The best approximating model had a Bayesian p-value of 0.325, indicating adequate model fit. The effects of habitat variables, specifically percent of fine substrate, wood density, precipitation 7 days prior to sampling, simulated discharge and stream temperature were small and imprecise, with mean parameter estimates near 0 with 95% credible intervals including positive and negative values in all candidate models that included local habitat variables (results not shown). We used the mean and standard deviation of species-specific capture probabilities for initial and all subsequent sampling dates (Table 3.7) to estimate corresponding species abundances at CMR reaches and assumed capture at survey reaches were all equal to "subsequent" capture probabilities.

The best approximating models for predicting seasonal changes in abundance (λ) varied among fish species evaluated in this study, but consistently included an interaction between low- or high-flow characteristics and reach or network-scale covariates (Table 3.8). For *N. lutipinnis*, the most frequently captured small-bodied cyprinid across our study reaches, catchment area and both flow covariates were included in the best approximating models. These two models contained essentially all of the total model weight (0.674 and 0.326, respectively; Table 3.8). Parameter estimates from the best approximating model, which was 2.07 times more plausible than the second-best model, indicated that lambda increased with larger high flow pulses in reaches with smaller catchment areas, but slightly decreased in reaches with larger catchment areas (Table 3.9). Conversely, parameter estimates from the second best approximating model indicated that lambda increased as low flows became lower, but this increase was reduced in reaches with smaller catchment areas (Fig. 3.5). Predicted growth rates based on the best approximating model parameter estimates indicated that *N. lutipinnis* populations were likely to increase in reaches with small catchments following seasons containing high flow pulses (Fig. 3.5).

The best and second best approximating models for predicting changes in abundance of *Nocomis leptocephalus*, a larger-bodied cyprinid, included combinations of catchment area and periods of reduced flow (Table 3.8). The top two models contained essentially all of the total model weight (0.887 and 0.113, respectively; Table 3.8). Parameter estimates from the best approximating model, which was 7.84 times more plausible than the second-best model, indicated that lambda increased with decreasing minimum flows, with a slightly larger effect in reaches with larger catchments (Table 3.9; Fig. 3.5). Parameter estimates from second best approximating model were similar to the best approximating model, with lambda increasing with catchment area and in response to lower, low flow periods.

In contrast to the two cyprinids, the best approximating models for predicting changes in abundances of the centrarchid species (*L. auritus* and *L. macrochirus*) included a measure of the proximity of reaches to larger streams, downstream link magnitude (dlink), along with high flow pulses, and the interaction between dlink and flow magnitude. This model contained most of the model weight for *L. auritus* (0.996), although less than half the model weight for *L. macrochirus* (0.458; Table 3.8). Parameter estimates from the best approximating model forboth species indicated that lambda decreased with increasing magnitude of high flow pulses in reaches closer to larger streams (higher dlink), and increased in response to high-flows in reaches farther from large streams (lower dlink; Table 3.9). Parameter estimates from second best approximating model for *L. macrochirus*, which was 2.51 times more plausible than the third best approximating model, indicated a similar trend, with lambda increasing in reaches that were closer to larger streams (high dlink; Table 3.9). Parameter estimates from the best approximating model indicated that *L. auritus* and *L. macrochurus* population abundances likely decline following large high flow events in reaches close to larger stream (Fig. 3.5). In reaches with low link magnitude, population abundances were relatively stable and did not increase in relation to flow covariates (Fig. 3.5).

The only common percid species in these sites, *P. nigrofasciata*, had relatively consistent counts within reaches during the study period compared to other species (Fig. 3.4). Similar to other species, the best approximating model for lambda of this darter species contained high flow pulses. However, in contrast with other species, the best approximating model also contained local habitat covariates (wood density, percent sand, and average maximum water depth). The second best approximating model contained an interaction between channel confinement and high flow pulses (Table 3.8). However, these two models contained only 0.387 of the total model weight (0.209 and 0.178, respectively; Table 3.8), with the best approximating model being only 1.18 times more plausible than the next model. In contrast to other species, the model weights for this species ranged across 11 differing candidate models (Table 3.8), with no clear support for the hypothesis that the effect of flow varies with any single stream characteristic. Based on parameter estimates from the best approximating model, lambda was predicted to increase with increasing percent of fine substrate, decreasing wood density (although this effect was small and imprecise based on 95% credibility intervals overlapping zero), increasing average water depth, and increasing magnitude of high flow events (Table 3.9). Parameter estimates from the second best approximating model indicated that lambda increases with larger high flow events, with a larger positive effect in unconfined reaches (i.e., high W:D ratio; Fig. 3.4). Based on parameter estimates from the best approximating model and average habitat conditions across all units, *P. nigrofasciata* abundances may increase following larger high flow pulses (Fig. 3.5), similar to cyprinids.

Discussion

We used a hierarchical modeling approach to evaluate the relative influence of streamflow, local habitat, reach-level characteristics, and network position on seasonal abundance dynamics of several stream fish species across multiple years (2010–2013). Our study included a wide range of seasonal flows that varied from drought to above-average streamflow conditions. This variation allowed us to assess how different species responded to high and low flow events and how reach-level characteristics influenced the relationship between streamflow and population growth. In general, our results supported the hypothesis that the influence of high flow pulses or prolonged low flows had differing effects on stream fish abundance dynamics depending on catchment area and network position, and that the relative importance of these factors varied among species. This finding suggests that streamflow events likely do not have a consistent effect across the landscape for all populations and species. Thus, to better predict the biotic outcomes of changes in streamflow regimes in response to various management alternatives, the relative size of catchments and their position within the network need to be considered.

In this study, we found that short-term high flow pulses influenced seasonal changes in abundance of several fish species. High flows are important to stream ecosystems (Resh et al. 1988, Wooton, Parker, and Power 1996)and influence many aspects of stream fish populations and assemblages (Bain et al. 1988, Freeman et al. 2001, Kiernan et al. 2012). For example, high flows periods can increase spawning success and movement of fishes, resulting in higher abundances of fishes in the late summer and fall (Craven et al. 2010). Additionally, high flow periods can promote movement of fish upstream (Albanese et al. 2004), which can result in relatively stable population abundances in smaller tributaries. In our study, we found evidence that the magnitude of high flow pulses had a greater effect on changes in abundance of stream fishes in reaches with small stream catchments compared to reaches with larger catchments. For example, our models predicted that cyprinid (*N. lutipinnis*) abundances increased with increasing magnitude of high flow pulses in smaller stream catchments, but slightly declined in larger stream catchments. This was a surprising result given the relatively small range in catchment size (8 to 47 km^2) of the 2nd and 3rd order streams sampled in this study. A study conducted over a broader size range of Coastal Plain streams by McCargo and Peterson (2010) also found a similar effect, with a larger increase in fish densities in smaller streams in response to increasing base flows compared to larger streams. The interaction of higher flows and catchment area may be the result of the mediating influence of catchment area and stream size on local habitat complexity, stability, and channel size (Infante and Allan 2010), as larger catchment areas are generally associated with greater stream widths, depths, and volume (Angermeier and Schlosser 1989, Infante and Allan 2010).

Prolonged low-flow periods appeared predictive of changes in abundance for both cyprinid species (best-supported model for *N. leptocephalus*; second-best supported model for *N. lutipinnis*). The predicted effect was opposite of expected –population abundances increased following periods of lower, low flows, particularly in larger streams. This increase may have resulted from increased immigration of fishes intosome study reaches during the lowest flow periods in response to unsuitable habitat in other parts of the stream network. Numerous studies have documented that fishes commonly emigrate out of intermittent stream reaches and immigrate into refugial habitats, such as deeper pools, during adverse low flow periods (Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003). Most of our stream reaches were selected based on the occurrence of wetted habitat even during the low-flow conditions of 2011, which may have provided refugial habitat during reduced flow periods compared to the surrounding stream habitat. For example, one stream initially selected for capture-mark-recapture sampling dried completely in 2011, and at least three other streams (including two sampled in fall 2011) had dried to disconnected pools in summer 2011. Reach selection was intended to represent available habitat throughout the stream network, but we recognize that some habitats and segments were likely more affected by low-flows based on geomorphology and local habitat conditions (Peterson et al. 2009). Clearly, prolonged low-flows that resulted in local desiccation strongly affected local fish abundances. Our observation of population increases during the fall of low-flow years were at least partly attributed to the addition of age 0+ fish following exceptionally low summer flows.

The proximity of populations to larger streams plays an important role in the dispersal and stability of fish populations (Osborne and Wiley 1992, Fagan 2002, Lowe 2002, Campbell-Grant 2011). In this study, we found changes in population abundances of two species of centrarchids (*L. auritus* and *L. macrochirus*) were strongly related to downstream link magnitude –a measure of relative proximity of the reach to a larger stream segment. Model results indicated that abundances were predicted to increase in reaches that were close to a large stream following periods lacking relatively higher flow pulses. Similar increases were not predicted in reaches farther from larger streams. This could reflect decreased movement during more stable flow periods, as many studies have observed increased fish dispersal during higher flow periods (Petty and Grossman 2004, Albanese et al. 2004).Proximity to larger streams may be particularly important for assessing population stability (Hitt and Angermeier 2008, Nislow et al. 2011). Low emigration rates from sites near the mainstem may suggest that larger streams play an important role in maintaining refugia during adverse flow condition and provide colonizers to into less dense or unoccupied tributary reaches.

Our finding that population abundances may increase following periods of reduced low-flows for two cyprinids, for example, could be interpreted as the result of increased capture probabilities during periods of reduced flows. Flow and associated habitat variables can strongly affect stream fish capture efficiencies (Bayley and Dowling 1990, Price and Peterson 2010). Although evidence from our capture-mark-recapture study does not support an effect of any measured habitat variables on capture probabilities, these data do not extend through samples during the highest flow period of 2013. Accordingly, we also applied published relationships between capture-probability of stream fishes (sampled using a similar “seine-electrofishing” method in block-netted reaches) and two discharge related metrics (average velocity and cross-sectional area) developed for Blue Ridge, Ridge and Valley, and Piedmont streams (Price and Peterson 2010). Price and Peterson (2010) report a decrease in capture efficiency with increasing cross-sectional area (i.e., larger streams) but also an increase in capture efficiency with higher mean velocity. Applying coefficients from the Price and Peterson study to stream cross-sectional area and velocity measurements from our study sites indicates only a slight increase in capture probabilities during our study at higher flows. Nonetheless, variation in capture efficiency has the potential to lead to erroneous inference from field data and warrants further consideration.

Predicting biological consequences of flow alterations requires linking streamflow characteristics with dynamic population responses (Poff et al. 2010, Peterson et al. 2011, Shenton et al. 2012, Freeman et al. 2013). However, developing flow-ecology relationships is complicated by multiple interacting factors occurring at differing spatial scales (Wiens 2002, Lowe et al. 2006, Thorp et al. 2006). In this study, we have assessed evidence that local habitat, channel geomorphology, stream size, and network position mediate the effects of high flow pulses or low flow periods on fish abundance dynamics. We conclude that within Piedmont streams included in this study, stream size and the relative position of reaches in the network influence population responses to low and high flow events. High flows promote connectivity and dispersal among reaches, with strongest effects on small streams. Low flows may increase abundances locally, particularly in large streams that act as refugia during drought and in segments connected to these large stream refugia. Fishes are expected to recover rapidly from drought, once adequate flows resume (Magoulick and Kobza 2003, Davey and Kelly 2007). Thus, short-term severe drought may not have long-lasting effects on fish assemblages (Matthews and Marsh-Matthews 2003). However, barriers or unsuitable habitat that restrict fish movement may dampen the recovery of affected populations. Additionally, a lack of higher flow pulses may similarly reduce population resilience throughout a stream network by impeding fish movement from larger stream refugia into smaller tributaries.

Identifying species, population, and stream network characteristics that promote resilience and rapid recovery following hydrologic extremes should help inform river management in response to increasing flow alterations, drought intensity and frequency, and increasing water demands (Bond et al. 2008, Poff et al. 2010). The frequency and magnitude of lower flows and the intensity of higher flows is expected to increase in many areas under climate change projections (Bates et al. 2008). Our results, in conjunction with previous studies, underscore the importance of incorporating geomorphic and network context to project the consequences of changing hydrologic regimes on stream biota (Thorp et al. 2006, McCargo and Peterson 2010, Perkin and Gido 2012). Understanding the relative role of stream characteristics at differing spatial scales may prove useful for identifying locations within a stream network where fish populations are vulnerable to declines (i.e., smaller streams with limited connectivity to the larger network) and for evaluating likely outcomes of alternative flow and management scenarios.

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TABLE 3.1 Location and reach characteristics of 12 sample reaches within the Potato Creek watershed (Upper Flint River basin, GA) from 2010 through 2013 (CMR = capture-mark-recapture reaches and S = survey reaches).

Stream	Code	Type	Latitude°N	Longitude°W	Catchment area (km^2)	Downstream link (dlink)	Channel W:D ratio
Tenmile Creek	1	CMR	32.976	-84.393	18.00	6	9.65
Threemile Creek	2	CMR	32.995	-84.292	22.00	5	20.01
Turnpike Creek	3	CMR	33.153	-84.261	25.50	8	6.14
Basin Creek	4	S	32.555	-84. 243	8.10	4	3.30
Fivemile Creek	5	S	32.583	-84.184	8.20	66	11.50
Gola Creek	6	S	33.033	-84.170	12.30	7	2.14
Jerry Reeves Creek	7	S	32.520	-84.245	23.80	101	10.68
Rose Creek	8	S	32.584	-84 143	8.26	3	5.00
Willingham Spring Creek	9	S	32.565	-84.223	8.00	9	8.26
Threemile Creek	10	S	33.004	-84.181	16.00	5	3.92
Turnpike Creek	11	S	33.065	-84.146	47.00	12	1.60
Unnamed Tributary	12	S	33.041	-84.130	10.30	31	4.00

TABLE 3.2 Sampling dates (mm/dd/yy) of 12 reaches within the Potato Creek watershed (Upper Flint River basin, GA) from 2010–2013.

Stream	Code	Summer 2010	Fall 2010	Summer 2011	Fall 2011	Summer 2012	Fall 2012	Summer 2013	Fall 2013
Tenmile Creek	1	08/10/10	11/19/10	08/10/11	11/04/11	08/08/12	10/18/12	-	-
Threemile Creek	2	08/10/10	11/06/10	08/11/11	11/04/11	08/09/12	10/19/12	-	-
Turnpike Creek	3	08/12/10	11/06/10	08/11/11	11/02/11	08/07/12	10/17/12	-	-
Basin Creek	4	-	-	-	09/19/11	05/23/12	09/05/12	07/19/13	09/25/13
Fivemile Creek	5	-	-	-	09/15/11	05/23/12	09/04/12	06/26/13	09/24/13
Gola Creek	6	-	-	-	09/16/11	05/21/12	09/06/12	06/25/13	09/24/13
Jerry Reeves Creek	7	-	-	-	09/16/11	05/24/12	09/05/12	-	-
Rose Creek	8	-	-	-	09/15/11	05/21/12	09/06/12	06/25/13	09/23/13
Willingham Spring Creek	9	-	-	-	09/20/11	05/23/12	09/05/12	07/19/13	09/25/13
Threemile Creek	10	-	-	-	09/15/11	05/22/12	09/06/12	07/18/13	-
Turnpike Creek	11	-	-	-	09/20/11	05/22/12	09/07/12	06/26/13	09/24/13
Unnamed Tributary	12	-	-	-	09/15/11	05/22/12	09/04/12	06/26/13	09/23/13

TABLE 3.3 Mean (standard deviation) of local habitat characteristics across sample units of 12 reaches within the Potato Creek watershed (Upper Flint River basin, GA) from 2010–2013. Measurements for sites 1-3 were made on a single date.

Stream	Code	No. units	Unit length (m)		Wet width (m)		Fine substrate (%)		Maximum depth (m)		Wood density (m^2)	
Tenmile Creek	1	1	120.0	(-)	3.96	(-)	0.74	(-)	1.06	(-)	0.09	(-)
Threemile Creek	2	1	155.0	(-)	3.26	(-)	0.56	(-)	0.71	(-)	0.07	(-)
Turnpike Creek	3	1	217.0	(-)	5.42	(-)	0.97	(-)	0.74	(-)	0.02	(-)
Basin Creek	4	3	36.2	(9.7)	2.29	(0.17)	0.40	(0.03)	0.38	(0.16)	0.06	(0.05)
Fivemile Creek	5	2	33.0	(4.5)	3.10	(0.30)	0.68	(0.10)	0.43	(0.17)	0.14	(0.06)
Gola Creek	6	2	66.4	(20.9)	2.88	(0.30)	0.84	(0.07)	0.33	(0.13)	0.06	(0.05)
Jerry Reeves Creek	7	2	40.9	(10.6)	7.06	(0.45)	0.25	(0.23)	0.33	(0.02)	0.02	(0.00)
Rose Creek	8	2	63.5	(14.0)	4.49	(0.61)	0.67	(0.20)	0.43	(0.07)	0.04	(0.04)
Willingham Spring Creek	9	2	73.3	(7.3)	3.81	(0.09)	0.60	(0.11)	0.44	(0.06)	0.06	(0.01)
Threemile Creek	10	3	40.7	(4.0)	4.78	(0.68)	0.36	(0.03)	0.63	(0.12)	0.16	(0.15)
Turnpike Creek	11	2	56.5	(1.1)	6.57	(0.32)	0.99	(0.02)	0.40	(0.13)	0.04	(0.01)
Unnamed Tributary	12	2	37.9	(3.9)	2.94	(0.43)	0.78	(0.11)	0.53	(0.13)	0.03	(0.03)

TABLE 3.4 Species used in the capture-mark-recapture analysis, showing the number individuals tagged and released on the first sampling day (N = 2248) and recaptured on the second sampling day (N = 351 were recaptured on subsequent dates), summed across dates (N = 6) and reaches (N = 3), and the range in standard length (mm SL) of captured individuals.

Species	No. individuals tagged and released on day 1	No. individuals recaptured on day2	Size range (mm SL)
Cyprinella venusta	27	21	48 – 86
Notropis lutipinnis	591	317	32 – 72
Hybopsis sp. cf. H. winchelli	79	30	39 – 64
Ericymba amplamala	82	40	36 – 69
Nocomis leptocephalus	201	51	35 – 178
Semotilus thoreauianus	41	10	35 – 102
Gambusia sp.	21	7	35 – 49
Lepomis auritus	370	96	31 – 137
Lepomis macrochirus	525	110	27 – 123
Micropterus salmoides	12	6	37 – 145
Percina nigrofasciata	299	101	34 – 87

TABLE 3.5 Variables included in candidate models of capture probability and change in abundance (λ) with corresponding interpretation of predicted responses.

Parameter	Interpretation of variable effect on capture or change in abundance
Capture probability	
Species	Capture probability varies among species.
Stream temperature	Capture probability decreases with decreasing stream temperature.
Stream discharge	Capture probability decreases with increasing stream discharge.
Precipitation	Capture probability decreases with increasing 7-day precipitation prior to sampling.
Wood density	Capture probability increases with increasing wood density.
Fine substrate	Capture probability decreases with decreasing finesubstrates.
Turbidity	Capture probability decreases with increasing turbidity.
Experience	Capture probability increases with increased understanding of fish and habitat distributions.
Species group x experience	The effect of experience varies among species.
Change in abundance (λ)	
Wood density	Population growth increases with increasing wood density.
Fine substrate	Population growth decreases with increasing fine substrate for fluvial-dependent species.
Maximum depth	Population growth increases with deeper pool habitat.
Catchment area	Population growth increases with increasing catchment area.
Channel width:depth ratio	Population growth varies with channel confinement.
Downstream link magnitude	Population growth increases with increasing downstream link magnitude.
Prolonged low flows	Population growth decreases with lower, low flows (10-d minimum).
High flow pulses	Population growth decreases with larger high flows (10-d maximum).
Streamflow x catchment area	The effect of low and high flows on population growth varies with stream size.
Streamflow x confinement	The effect of low and high flows on population growth varies with the degree of channel confinement.
Streamflow x dlink	The effect of low and high flows on population growth varies with the proximity to larger streams.

TABLE 3.6 Mean deviance, number of parameters (Np), Akaike's information criterion (AIC_c), ΔAIC_c, and model weight (w_i) for each candidate model predicting capture probability. Models were fit as a logistic regression for second day recapture probabilities (N = 2599). Habitat covariate refers to all uncorrelated habitat covariates.

Candidate model	Mean deviance	Np	AIC_c	ΔAIC_c	w_i
species x experience	3236.3	23	3282.7	0.0	0.987
species + experience	3265.2	13	3291.3	8.6	0.013
species x experience + habitat	3247.0	28	3303.6	20.9	0.000
species + habitat + experience	3273.3	18	3309.6	26.8	0.000
species x habitat + experience	3272.0	24	3320.5	37.7	0.000
species	3318.4	12	3342.5	59.8	0.000
species + habitat	3318.8	17	3353.0	70.3	0.000
species x habitat	3318.8	23	3365.2	82.5	0.000
habitat	3500.6	7	3514.6	231.9	0.000
constant	3506.9	2	3510.9	228.2	0.000

TABLE 3.7 Mean (standard deviation) of capture probabilities predicted from the best approximating capture probability model for initial and subsequent sampling dates.

Species	First two sampling dates	All subsequent sampling dates
Cyprinella venusta	0.445 (0.231)	0.773 (0.081)
Notropis lutipinnis	0.372 (0.032)	0.683(0.023)
Hybopsis sp. cf. H. winchelli	0.341 (0.080)	0.469(0.067)
Ericymba amplamala	0.195(0.076)	0.632 (0.061)
Nocomis leptocephalus	0.292(0.071)	0.290(0.034)
Semotilus thoreauianus	0.179(0.105)	0.358(0.077)
Gambusia sp.	0.277(0.201)	0.345 (0.090)
Micropterus salmoides	0.507(0.166)	0.632(0.138)
Lepomis auritus	0.273(0.054)	0.305 (0.031)
Lepomis macrochirus	0.213(0.029)	0.293(0.025)
Percina nigrofasciata	0.373(0.040)	0.459 (0.036)

TABLE 3.8 Mean deviance, number of parameters (Np), Akaike's information criterion (AIC_c), ΔAIC_c, and model weights (w_i) for plausible candidate models predictingseasonal changes in abundance (λ) for five species within the Potato Creek watershed from 2010–2013.

Candidate model	Mean deviance	Np	AIC_c	ΔAIC_c	w_i
Notropis lutipinnis (Cyprinidae)					
Catchment area x 10-d maximum flow	937.49	6	951.96	0.0000	0.6744
Catchment area x 10-d minimum flow	938.95	6	953.42	1.4565	0.3256
Nocomis leptocephalus (Cyprinidae)					
Catchment area x 10-d minimum flow	579.58	5	591.30	0.0000	0.8869
Catchment area + 10-d minimum flow	586.30	4	595.42	4.1190	0.1131
Lepomis auritus (Centrarchidae)					
Dlink x 10-d maximum flow	579.82	5	591.53	0.0000	0.9752
Lepomis machrochirus (Centrarchidae)					
Dlink x 10-d maximum flow	492.38	5	504.10	0.0000	0.4579
Dlink	497.93	3	504.58	0.4835	0.3595
Dlink + 10-d minimum flow	497.31	4	506.42	2.3249	0.1432
Percina nigrofasciata (Percidae)					
Sand + wood + maximum depth + 10-d maximum flow	598.04	6	612.51	0.0000	0.2090
Channel W:D ratio x 10-d maximum	601.12	5	612.83	0.3237	0.1778
Sand + wood + maximum depth + 10-d minimum flow	598.95	6	613.42	0.9100	0.1326
Sand + wood + maximum depth	602.26	5	613.97	1.4637	0.1006
Channel W:D ratio	608.35	3	615.00	2.4881	0.0603
Catchment area x 10-d maximum flow	603.35	5	615.06	2.5537	0.0583
Catchment area + 10-d maximum flow	606.00	4	615.11	2.6005	0.0570
Channel W:D ratio + 10-d minimum flow	606.49	4	615.60	3.0905	0.0446
10-d maximum flow	609.34	3	615.99	3.4781	0.0367
Channel W:D ratio + 10-d maximum flow	607.23	4	616.34	3.8305	0.0308
Dlink x 10-d maximum flow	605.25	5	616.96	4.4537	0.0225

TABLE 3.9 Parameter estimates, standard deviations, lower and upper 95% credibility intervals (CI) for fixed and temporal random effects (RE) of the best and second best approximating models predicting the change in abundance, ln(λ), for each species. Random effects represent variation in ln(λ) among sampling intervals for CMR and survey reaches.

Parameter	Estimate	SD	Lower 95% CI	Upper 95% CI
Notropis lutipinnis(Cyprinidae)				
Best approximating model (*w* = 0.674)				
Catchment area	0.098	0.017	0.064	0.132
10-d maximum flow	0.519	0.052	0.417	0.620
Catchment area x 10-d maximum flow	-0.280	0.038	-0.354	-0.206
Temporal RE (CMR)	0.982	0.690	0.394	2.707
Temporal RE (survey)	1.391	0.733	0.640	3.252
Second best approximating model (*w* = 0.326)				
Catchment area	0.138	0.012	0.115	0.160
10-d minimum flow	-2.576	0.168	-2.905	-2.248
Catchment area x 10-d minimum flow	-0.168	0.017	-0.202	-0.134
Temporal RE (CMR)	5.248	2.761	2.230	13.031
Temporal RE (survey)	1.717	0.880	0.808	3.970
Nocomis leptocephalus(Cyprinidae)				
Best approximating model (*w* = 0.887)				
Catchment area	0.197	0.028	0.142	0.217
10-d minimum flow	-3.933	0.518	-4.849	-3.539
Catchment area x 10-d minimum flow	-0.155	0.044	-0.241	-0.125
Temporal RE (CMR)	7.458	3.407	3.200	16.629
Temporal RE (survey)	1.717	0.939	0.734	4.062
Second best approximating model (*w* = 0.113)				
Catchment area	0.206	0.029	0.149	0.263
10-d minimum flow	-4.754	0.501	-5.687	-3.812
Temporal RE (CMR)	8.349	3.518	3.735	17.420
Temporal RE (survey)	2.064	1.102	0.915	4.836
Lepomis auritus(Centrarchidae)				
Best approximating model (*w* = 0.975)				
Dlink	0.206	0.052	0.103	0.311
10-d maximum flow	0.094	0.068	-0.039	0.228
Dlink x 10-d maximum flow	-0.232	0.068	-0.364	-0.096
Temporal RE (CMR)	0.229	0.215	0.034	0.713
Temporal RE (survey)	1.159	0.604	0.537	2.677

TABLE 3.9 continued.

Parameter	Estimate	SD	Lower 95% CI	Upper 95% CI
Lepomis macrochirus(Centrarchidae)				
Best approximating model (*w* = 0.458)				
Dlink	0.910	0.119	0.683	1.143
10-d maximum flow	-0.247	0.108	-0.454	-0.032
Dlink x 10-d maximum flow	-0.702	0.195	-1.072	-0.303
Temporal RE (CMR)	1.117	0.784	0.431	3.082
Temporal RE (survey)	0.943	0.534	0.405	2.236
Second best approximating model (*w* = 0.360)				
Dlink	0.647	0.091	0.473	0.831
Temporal RE (CMR)	0.991	0.746	0.380	2.743
Temporal RE (survey)	0.750	0.413	0.320	1.769
Percina nigrofasciata (Percidae)				
Best approximating model (*w* = 0.219)				
Percent sand	0.075	0.027	0.023	0.127
Wood density	-0.023	0.036	-0.094	0.047
Average maximum depth	0.058	0.033	-0.006	0.123
10-d maximum flow	0.153	0.063	0.030	0.281
Temporal RE (CMR)	0.151	0.165	0.004	0.563
Temporal RE (survey)	1.582	0.857	0.716	3.658
Second best approximating model (*w* = 0.178)				
Channel W:D ratio	0.051	0.027	-0.002	0.105
10-d maximum flow	0.122	0.068	-0.020	0.248
Channel W:D ratio x 10-d maximum flow	0.147	0.063	0.024	0.270
Temporal RE (CMR)	0.177	0.172	0.008	0.609
Temporal RE (survey)	1.727	0.935	0.782	4.037

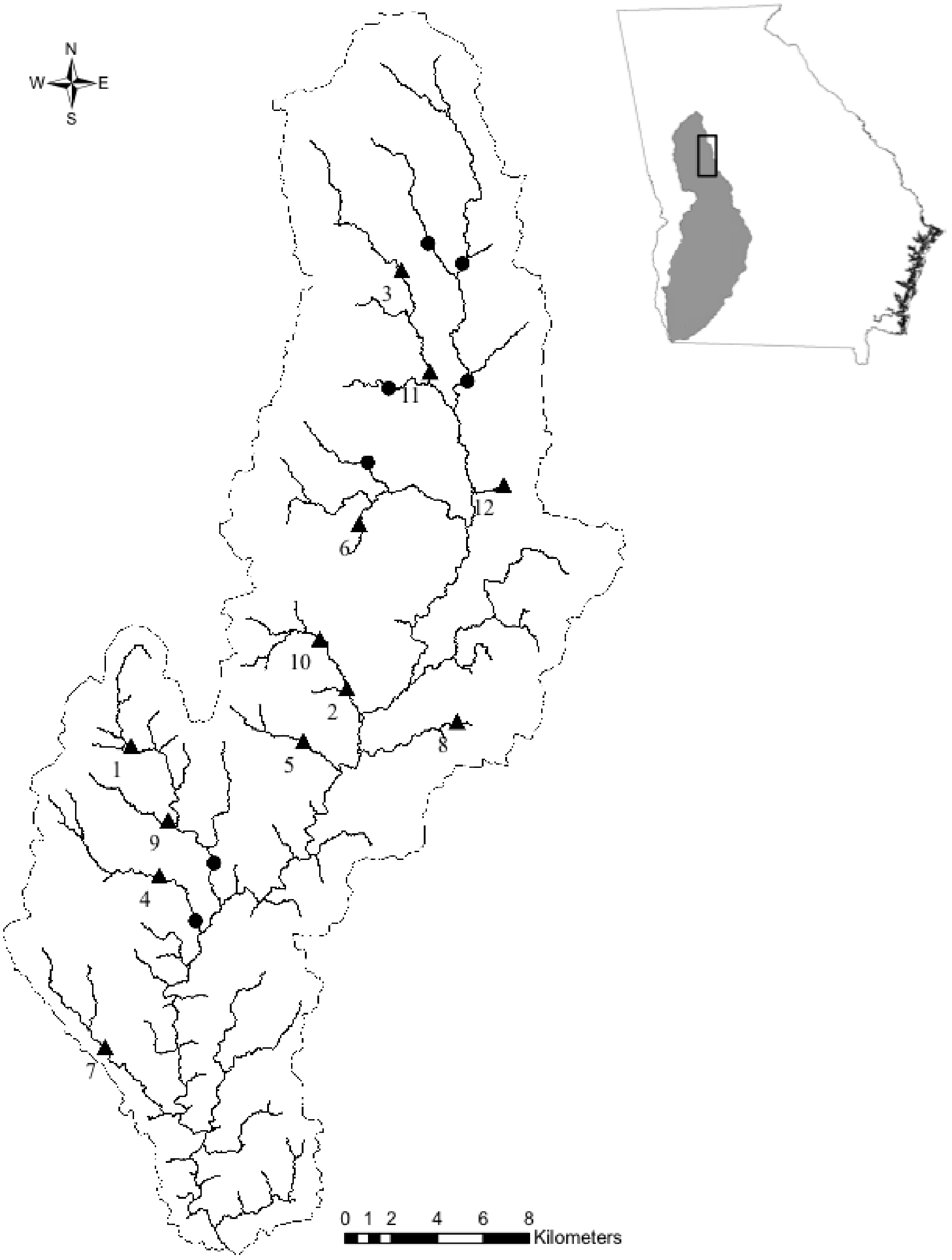

FIGURE 3.1 Locations of 12 study reaches sampled within the Potato Creek watershed located in the Flint River Basin, GA (inset) during the summer and fall of 2010 through 2013. Site numbers correspond to stream reaches listed in Table 3.1 and barriers (low-head dams) are indicated (circles).

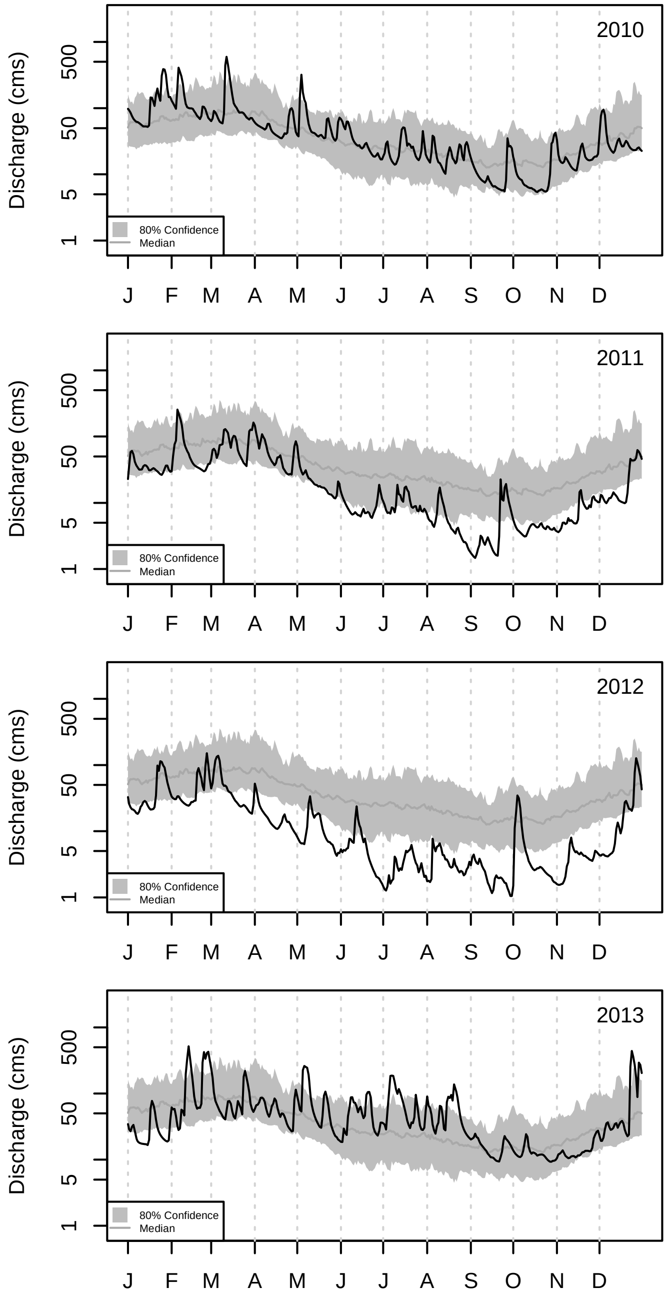

FIGURE 3.2 Daily discharge (m^3 s^{-1}) recorded at the Flint River gage (No. 023147500) located 19.4 km downstream of the Potato Creek confluence during each study year (2010–2013) relative to the observed long-term median (89-yr record; gray line) and 80% confidence intervals of daily discharge (i.e., the 10th to 90th percentile discharges).

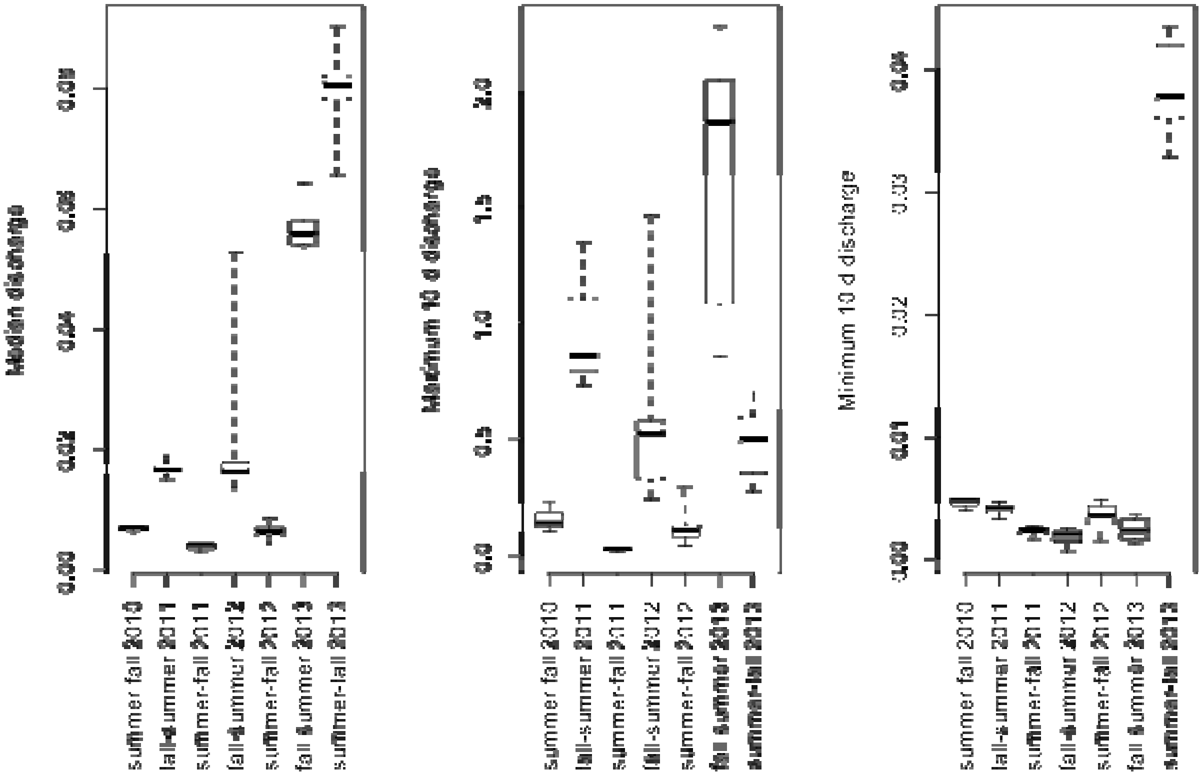

FIGURE 3.3 Median and range in projected median, 10-day maximum, and 10-day minimum discharge (m^3 s^{-1}; proportional to the long-term median for each reach) across sampled reaches for each summer-fall or fall-summer interval between sampling periods. Median and 10-d maximum discharges were correlated (r = 0.73).

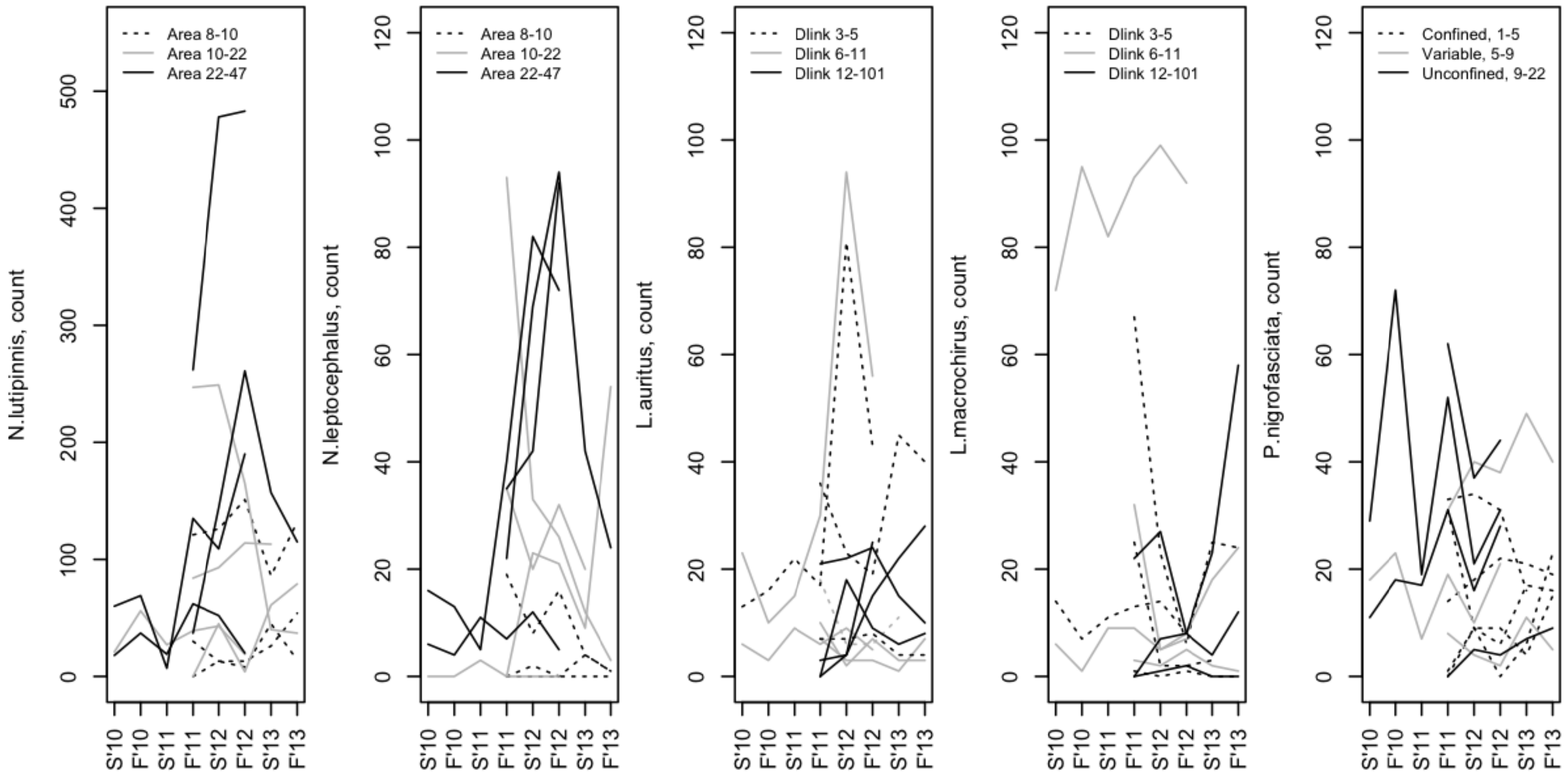

FIGURE 3.4 Species-specific counts (summed across sample units) for each reach during each sampling visit (summer = S and fall = F) of 2010–2013. Counts for reaches are denoted based on the reach-level predictor occurring in the best approximating model for each species (Table 3.9), except *P.nigrofasciata*, for corresponds to chancel W:D ratio. For example, *N. lutipinnis* and *N. lepotcephalus* counts correspond to reaches with small, medium, and large catchment areas (8–10 km^2 = black dotted line, 10–22 km^2 = gray solid line, and 22–47 km^2 = black solid line, respectively).

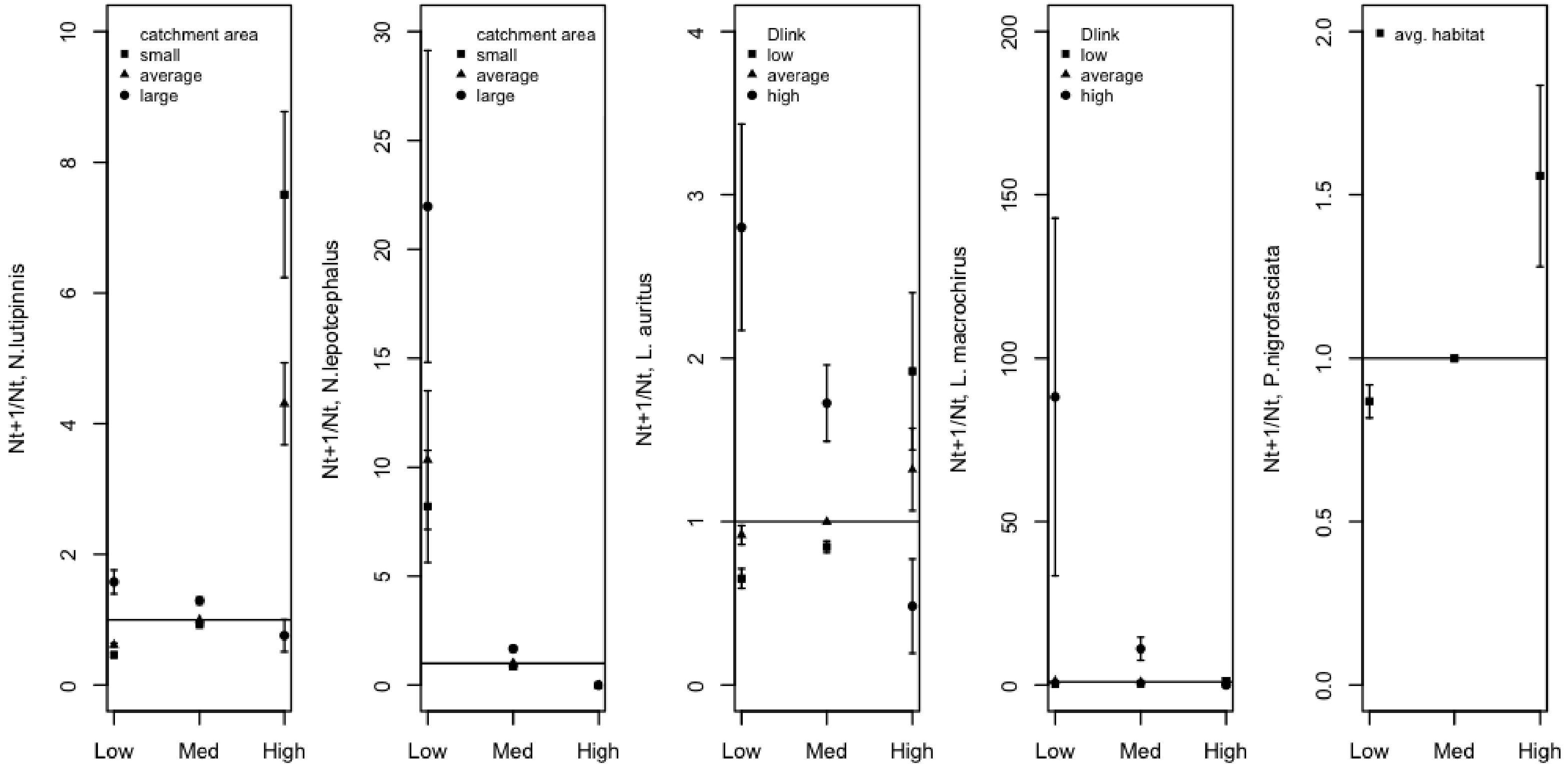

FIGURE 3.5 Predicted mean (SD) change in abundance (N_{t+1} / N_t) between sampling visits, based on predictors occurring in the best-approximating model for five fish species (Table 3.9). Results are shown for the lowest, average, and highest 10-d maximum discharge (0.623, 20.660, and 80.471, respectively) for all species, except for *N. leptocephalus*, which is shown for 10-d minimum discharge (0.023, 0.287, and 1.536, respectively).Results are also shown for the smallest, average, and largest observed catchment area for *N. lutipinnis* and *N. leptocephalus*, dlink for *L. auritus* and *L. macrochirus*, and average habitat conditions for *P. nigrofasciata* across study reaches from 2008–2012.

CHAPTER 4

DISTANCE, MAINSTEM PROXIMITY, AND BARRIERS PREDICT FINE-SCALE POPULATION STRUCTURE AND DISPERSAL OF A NATIVE SMALL-STREAM CYPRINID (*NOTROPIS LUTIPINNIS*)[3]

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[3] Katz, R. A., J. P. Wares, and M. C. Freeman. To be submitted to the Ecology of Freshwater Fish.

Abstract

Understanding the population structure and dispersal patterns of aquatic species is essential for predicting how species persist over ecological and evolutionary time-scales. However many population genetic studies of Cyprinidae, the largest family of freshwater fishes with many species imperiled, typically focus on broad scale patterns in diversity and divergence, which may not be relevant for local management. In this study, we investigated factors influencing stream fish population connectivity and dispersal of the Yellowfin shiner (Cyprinidae: *Notropis lutipinnis*), at a fine-spatial scale across a single watershed. Genetic diversity and genetic differentiation were relatively high among sites (H_E range = 0.638 to 0.838 and F_{ST} mean = 0.044 and max = 0.167), given the maximum geographic distance between sites of 65km. Populationsabove high-gradient bedrock outcrops and dams were most divergent from all other populations. Genetic differentiation was positively related to geographic distance and negatively related to the proximity to the mainstem based on parameter estimates in the best-supported Bayesian generalized linear mixed model. Dispersal estimates (BIMr) indicated that populations with local extinctions were more likely recolonized by geographically close populations, and that migration was asymmetrical downstream of an historic milldam. Results indicate that this small-stream cyprinid generally follows a stepping-stone model of dispersal within tributaries, but that the mainstem is not a barrier to dispersal as previously hypothesized. Given our finding of increased gene flow among populations near the mainstem compared to far or isolated from the mainstem, maintaining connectivity of tributaries to the mainstem may be essential to minimize the impacts of environmental and demographic processes on populations of small-stream species.

Introduction

Knowledge of the factors influencing connectivity of populations within dendritic stream networks is essential for evaluating the long-term persistence of aquatic species (Fagan 2002, Lowe 2002, Dudgeon et al. 2006, Campbell-Grant, Lowe, and Fagan 2007). Assessing population structure and dispersal patterns of aquatic species is key to understanding how environmental changes such as alterations in stream habitat and connectivity may affect species over ecological and evolutionary time-scales (Dunham et al. 1999, Schick and Lindley 2007, Freeman et al. 2013). Ignoring population structure can impair the effective management of species by underestimating population vulnerability to extinction and lead to unintentional declines in biodiversity (Cooper and Mangel 1999).

Stream fishes are disproportionally imperiled aquatic fauna largely due to habitat loss, fragmentation, and streamflow alterations, which have led to the genetic isolation of numerous species (Jelks et al. 2008, Strayer and Dudgeon 2010) and elevated conservation concerns (Warren et al. 2000). Many studies have focused on population connectivity of large-bodied, migratory salmonids (Neville et al.2006, Horreo et al. 2011, Warnock and Rassmussen 2010, Weigel et al. 2013), which may be poor models for non-migratory fishes with differing life history characteristics. Studies of population connectivity of cyprinids are less common, despite Cyprinidae being the largest family of freshwater fishes with many species imperiled (Jelks et al. 2008). Those studies that have occurred of cyprinids focus on broad spatial patterns in large river networks (i.e., drainage area >4000 km^2; Blum et al. 2012, Dehais et al. 2010), with fewer studies occurring at smaller spatial scales (drainage area <500 km^2; but see Waits et al. 2008 and Skalski et al. 2008).Evaluating factors that influence population differentiation, structure, and migration at the watershed level (i.e., hydrologic unit code 8–12) may be especially valuable because management agencies have adapted this scale for local decision-making regarding water allocation, habitat management and aquatic biodiversity, and water quality monitoring (EPD 2011).

Understanding factors that influence the spatial structure and connectivity of fish populations at the watershed scale remains difficult because dispersal is difficult to measure empirically using capture-mark-recapture methods. Using genetic markers, many fish species have been found to follow a stepping-stone model of dispersal (Kimura and Weiss 1964), with migration occurring more frequently between neighboring populations, which gives rise to a positive correlation between genetic differentiation and geographic distance between populations (i.e., isolation by distance, IBD; Wright 1943). Additional studies have found that barriers, such as instream dams, waterfalls, and beaver dams, can restrict dispersal and increase genetic differentiation among populations more than expected by distance alone (Skalski et al. 2008, Horreo et al. 2011, Roberts and Angermeier 2013, Boizard et al. 2009, Meeuwig et al. 2010, Dehais et al. 2010). Less pronounced barriers to movement, such as unsuitable habitats and intermittent stream reaches, can also limit gene flow and result in increased population fragmentation (i.e., isolation by resistance, McRae 2006). Evaluating the relative importance of distance, natural and anthropomorphic barriers, as well as habitat features that may limit the extent of dispersal is critical for predicting how populations persist within a stream network and the potential success of alternative watershed management actions related to fragmentation.

Stream networks are intrinsically dynamic, with the degree of hydrologic connectivity and flow permanence influencing local population stability and movement of stream fishes (Poole 2010). For example, Falke et al. (2012) found that groundwater connectivity played an important role in local extinction, with higher extinction probabilities across a variety of fish species at sites that were not influenced by groundwater inputs during drought. The interaction between groundwater connectivity (i.e., springs and seeps) and fragmentation has not been explicitly incorporated into population connectivity studies of stream fishes. Additionally, many studies have found that dendritic network topology (i.e., the distance to the mainstem) can influence the recovery of populations after disturbance events that cause local extinction or decreased population sizes (Hitt and Angermeier 2008, Campbell-Grant 2011, Huey et al. 2011). For example, Albanese et al. (2004) found that larger downstream or mainstem reaches can be a source of colonizers for locally extinct populations in smaller tributaries. Thus, distance from the mainstem may play an important role in gene flow and the rate of recolonization (i.e., Simberloff and Wilson 1969). Depending on whether the mainstem serves as a migration corridor or barrier to fish dispersal, tributary populations may show high or low levels of genetic connectivity.

In this study, we investigated factors influencing stream fish population connectivity and dispersal in the Yellowfin shiner (Cyprinidae: *Notropis lutipinnis*), a common fluvial-dependent fish species native to southeastern U.S. Piedmont streams. Similar to many imperiled small-bodied fish species, Yellowfin shiners typically occur in smaller order streams, with limited use of larger streams and rivers (Georgia Museum of Natural History and GA Department of Natural Resources field collection records) and relatively restricted movement patterns (Goforth and Foltz 1998). This species reproduces annually, is an obligate nest-associate that requires gravel nests built by Bluehead chubs (*Nocomis leptocephalus)* for spawning (Wallin 1989) and is relatively short-lived (~ 4 years maximum). Yellowfin shiners are restricted to a small region within the southeastern U.S. and have similar life history attributes compared to other species within the subgenus *Hydrophlox* (Cashner et al. 2011). A combination of factors, such as distance, barriers, habitat complexity, and hydrologic connectivity likely affects the gene flow of

N. lutipinnis at the watershed scale. Our objectives in this study were 1) to estimate genetic diversity and differentiation across a watershed, 2) to evaluate the effects of distance, dams, and habitat (i.e., wetlands) in generating observed population differentiation, and 3) to identify potential sources of migrants for populations with recent apparent local extinctions by estimating short-term asymmetrical migration rates following recolonization events.

Methods

Study system and sample collection

The Potato Creek watershed (482 km^2 at USGS gauge 02346500) was located within the Upper Flint River basin in southwest Georgia, USA (Fig. 4.1). Impoundments were identified throughout the watershed using the National Inventory of Dams (NID), National Hydrography Database (NHD) and Google Earth (Google Inc., Mountain View, CA, U.S.A.). We restricted impoundment identification to instream structures that occurred on perennial second order streams or larger. We identified five impoundments throughout the watershed, two large impoundments on the mainstem of Potato Creek in the upper portion of the watershed, two farm pond dams on two differing tributaries to the mainstem, and an historic milldam on a tributary to the mainstem (Fig. 4.1). Natural barriers to dispersal throughout the watershed included high-gradient outcrops (Boizard et al. 2009) and low-gradient wetland habitats. High-gradient outcrops were identified as reaches with stream slopes greater than 3% based on stream-elevation data (Elliot et al. *in press*). Three high-gradient outcrops were present in the lower portion of the watershed: two were restricted to the mainstem and one was located on a tributary (Jerry Reeves Creek). The two mainstem outcrops were located on either side of the Jerry Reeves Creek tributary confluence, potentially isolating this tributary from all other populations. Low-gradient wetlands were represented by the percent of stream length that occurred within a wetland habitat greater than 50 km^2, identified using the National Wetland Inventory (NWI) database, and confirmed using field observations and Google Earth. Identified wetlands were restricted to the upper portion of the basin and occurred in both the mainstem and tributaries (Fig. 4.1). Streams directly influenced by springs could provide refuge for fish populations during periods of low flows by maintaining wetted habitat and cool water temperatures (Labbe and Fausch 2000, Falke et al. 2012), potentially buffering against declines in population size and associated potential for genetic drift. Sites located downstream of a spring source were considered to be directly influenced by spring streamflow. Spring sources were identified based on local topology maps and field observations of temperatures and streamflow regimes during drought. Two tributaries were identified as directly influenced by spring connectivity (Threemile Creek and Spring Creek).

We collected Yellowfin shiners from two sites in 2011 and sixteen sites in 2012 (Table 4.1; Fig. 4.1). At each site, we used a seine (2.4-m x 2-m with 3.2-mm mesh) to collect specimens within a 50–250 m stream reach, where geographic coordinates were recorded. Tissue was preserved in the field in 95% ethanol as caudal fin clips or whole individuals, with the number of samples per site varying based on catchability (Table 4.1). In 2011, we observed two sites (Fivemile Creek and Unnamed Tributary) with extensive streambed drying and apparent local extinctions of all stream fishes. In the following year, flows increased and Yellowfin shiners were collected at each site after recolonization. Despite substantial sampling effort over multiple years, Yellowfin shiners were never detected in a site located above an impoundment on a tributary to the mainstem (Basin Creek).

Laboratory methods

We extracted DNA from fish tissues using standard proteinase-K digestion followed by Purgene isolation buffer and ethanol precipitation. We genotyped samples at five microsatellite loci in 20ul reactions containing 1ul of diluted (20–50ng ul^{-1}) DNA, 4 ul of *GoTaq*® 5x Buffer, 1.5ul $MgCl_2$ solution, 1.5uldinucleotide triphosphates (dNTPs), 0.5ul of both forward and reverse primers, and 0.2 ul of *GoTaq*® DNA Polymerase. We used two sets of primers developed for *Notropis mekistocholas* (*Nme208* and *Nme93*, Gold et al. 2004) and developed three sets of primers for *Notropis lutipinnis* (*Nlu14*, *Nlu23*, *Nlu21*; see Appendix B). Forward primers were labeled using HEX and FAM fluorescent dyes (Applied Biosystems, Inc., Foster City, CA, U.S.A.). PCR multiplex reactions were used for two pairs of loci (Table 4.2) and all reactions were performed with initial denaturation at 95^{o}C for 3 min, followed by 20 cycles of denaturation at 95^{o}C for 30 s, locus-specific annealing at temperatures, extension at 72 ^{o}C for 40 s, and a final extension of 3 min at 72^{o}C. Amplification products were separated using a Genetic Analyzersequencer (3730XL, Applied Biosystems, Inc.) and sized using ROX500 size standard (Applied Biosystems, Inc.) in GeneMarker version 2.4.0 (SoftGenetics, LLC, State College, PA, USA). We screened for the presence of null alleles, large allele dropout, and scoring errors due to stutter using MICROCHECKER version 2.2.3 (van Oosterhout et al. 2004). Genotyping error rate was estimated for approximately 5% of individuals as the ratio between observed number of allelic differences and total number of allelic comparisons (Bonin et al. 2004).

Data Analysis

Microsatellite variation

We tested for significant departures from Hardy–Weinberg equilibrium (10^5 iterations following a burn-in of 10^4) at each site using ARLEQUIN version 3.5 (Excoffier and Lischer

2010). In ARELQUIN, evidence for linkage disequilibrium between loci was tested using a likelihood-ratio test, whose empirical distribution was obtained by a permutation procedure (10^3 permutations; Slatkin and Excoffier 1996). Average allele richness per locus (A) and observed (H_O) and expected (H_E) heterozygosity were estimated for each site. Using an analysis of variance (ANOVA), we tested whether genetic diversity (H_E) was 1) lower in sites above dams and outcrops compared to sites not isolated from the mainstem, 2) lower in upstream sites compared to downstream sites (i.e., within 2.5 km of the mainstem), 3) lower in sites with no spring influence compared to sites with a direct spring influence and 4) higher in tributaries with a high proportion of wetlands compared to tributaries lacking wetlands. We hypothesized that genetic diversity would be higher in streams with direct spring influence, lower in sites isolated from the mainstem by a barrier, and higher in downstream sites closer to the mainstem (Lamphere and Blum 2012, Dehais et al. 2010).

<u>*Population structure*</u>

We estimated population structure among sites using allele-frequency and Bayesian clustering-based approaches. First, we estimated genetic differentiation (F_{ST}), among sampling sites based on allele frequencies using a pairwise distance matrix in ARLEQUIN under the infinite alleles model with 10^3 permutations. Significant pairwise F_{ST} values were evaluated using a Bonferroni adjustment for a value of 0.05. Linearized pairwise genetic distances ($F_{\mathrm{ST}}/(1-F_{\mathrm{ST}})$, Rousset 1997) were regressed against pairwise stream distances (km) to evaluate the strength of isolation by distance (Wright 1943, Slatkin 1985). Geographic stream distances between sites were determined using GIS in ArcMap (version 10.1, ESRI Inc.). R_{ST} was also estimated (assuming the stepwise mutation model; Slatkin 1995).

Second, population structure was assessed using a spatially implicit Bayesian clustering approach (STRUCTURE 2.1;Pritchard, Stephens, and Donnelly 2000), which probabilistically assigns individuals into populations by assuming populations are in Hardy-Weinberg and loci are in complete equilibrium. Simulations allowed for admixture and correlation of allele frequencies among clusters for 10^5 iterations following a burn-in of 10^4 iterations for 10 replicate runs for each potential number of genetic clusters (K = 1 to 18). The best-approximate number of clusters (K) was chosen using the criterion by Evanno et al. (2005) in STRUCTURE HARVESTER (Earl and von Holdt 2012). We summarized results over replicate runs for the best-approximate number of clusters using the Greedy Option (M = 2) with 1000 randomizations in CLUMPP version 1.1.2 (Jakobsson and Rosenberg 2007). Resulting population structure was visualized graphically using DISTRUCT version 1.1 (Rosenberg 2004).

To further assess support for genetic structure among differing tributaries, we used a hierarchical analysis of molecular variance (AMOVA, Weir and Cockerham 1984), which partitions total genetic variance at the site-level (i.e., among sites within groups) and group-level (i.e., among groups), and includes residual variance (i.e., among individuals within sites). We ran AMOVA's in ARLEQUIN with 10^3 permutations. We compared the variance partitioned among and within groups for three alternative hierarchical groupings informed by genetic differentiation (F_{ST}) and STRUCTURE analyses results. The first grouping (HM1) represented the mainstem acting as barrier to dispersal among tributary populations and consisted of eleven groups, one corresponding to each tributary system with sites pooled within each tributary (mainstem sites were excluded). The second grouping (HM2) represented a single large population throughout the watershed that has been fragmented by barriers (dams or outcrops) and consisted of six groups, one corresponding to sites that were not isolated by a barrier from the mainstem (a single population) and one corresponding to each isolated tributary (five tributary populations). The last grouping (HM3) represented those groups supported in STRUCTURE analysis and consisted of three groups: one corresponding to two distinct clusters and one corresponding to two clusters with substantial admixture.

Factors influencing genetic differentiation

We used an information theoretic approach and Bayesian generalized linear mixed models to test alternative hypotheses about the factors most influential in structuring population differentiation. Candidate predictors hypothesized to influence gene flow included stream distance between sites (km), a binary term representing dams as anthropomorphic barriers to dispersal, and two terms representing natural barriers to movement: a binary term corresponding to high-gradient outcrops and a continuous variable corresponding to the proportion of stream flowing through a wetland habitat between two sites. Unfortunately, sites that were separated by a high-gradient outcrop were also most distant from each other (Pearson's correlation coefficient: $r = 0.586$) and hada lower proportion of low-gradient habitat (Pearson's correlation coefficient: $r = -0.676$). To minimize potentially confounding interpretations of high-gradient outcrops, we excluded four sites that wereeither separated from all others by outcrops and or by the historic milldam. These sites were considered most divergent from most other sites according to clustering by STRCTURE and high F_{ST} values. Thus, our analysis focused on predicting fine-scale differences in differentiation throughout the watershed. We used linearizedF_{ST} values between remaining sites ($N = 66$) from ARLEQUIN as the response variable and we included random site effects to account for correlations among pairwise-site comparisons (Browne et al. 2001, Hadfield 2010). We evaluated 14 alternative models and compared relative support for each competing model using the deviance information criterion (DIC, Spegielhalter et al. 2002), with smaller DIC values indicating better supported models. Models with model weights within 10% of the best approximating model, which is similar to Royall's 1/8rule for evaluating strength of evidence (Royall 1997), were considered plausible models.Model fit was assessed using pseudo-R^2, estimated as the squared correlation between the observed and model-predicted values of linearized F_{ST} (Efron 1978). All models were run using the *MCMCglmm* package (Hadfield 2010) in R version 2.11 (R Development Core Team, 2013). F_{ST} was assumed to be Gaussian distributed. Models were run with diffuse priors (mean = 0 and variance = 10^4), 10^4 iterations following a 20^3 burn-in, and every 10 iterations were retained. Convergence was assessed visually using traceplots and replicate runs to ensure similar posterior estimates. We hypothesized that increased stream distance, the presence of a dam, and increased proportion of low-gradient wetland habitat would increase divergence among populations (positively related to linearized F_{ST}).

Dispersal among populations

We estimated recent migration into sites with apparent local extinction events (i.e., two sites were dry in 2011 and sampled after recolonization in 2012: Unnamed Trib and Fivemile Creek) using BIMr (Bayesian inference migration rates, Faubet and Gaggiotti 2008). BIMr estimates asymmetrical migration rates (the proportion of alleles that were derived in the previous generation from other populations) by assuming drift-migration equilibrium at the previous generation. However, natural populations are likely not in drift-migration equilibrium at any recent time-step and *N. lutipinnis* has up to four overlapping generations. Thus, migration estimates were interpreted as a relative index of recent gene flow rather than a precise estimate of migration in the previous generation. According to a simulation study conducted by Faubet et al.(2007), BIMr estimated migration rates are fairly accurate when F_{ST} values between populations are moderate ($\geq$0.05) and when migration rates are low ($\leq$0.10). Potential inaccuracies in individual assignments may occur when F_{ST} values are lower (i.e., $\leq$0.02) and migration rates are higher ($\geq$0.15). To reduce potential bias in estimates of recent migration, we first grouped sites close in geographic distance that also had low and insignificant F_{ST}values. To reduce the number of potential source populations, which minimizes potential errors associated with migration rate estimates (Faubet et al. 2007), we selected a subset of grouped sites to represent source populations based on whether they had relatively highF_{ST} values compared to each recently recolonized population (Fivemile Creek and Unnamed Tributary). This resulted in the identification of three source populations of ecological interest: one population was located in the upper portion of the watershed and near the mainstem (Turnpike Creek US and DS), another population occurred in the lower portion of the watershednear the mainstem (Potato Creek DS and Dean Creek), and a third population was located above the historic milldam (Tenmile Creek US and Spring Creek). We hypothesized that individuals would more likely migrate from nearby populations, as opposed to distant populations or populations above the dam, thus following a stepping-stone model of dispersal. We ran 20 replicate runs of 20^3 iterations with a 50^4 iteration burn-in and retained every 100 iterations. For each replicate, we first ran 50 pilot replicate runs of 5000 iterations each to obtain acceptance rates between 25% and 45%, which adjusts the initial values of parameters used to estimate migration. The replicate run with the lowest Bayesian deviance (D_{assign}) was considered most supported (Faubet et al. 2007, Fauebet and Gaggiotti 2008) and the 95% HDPI’s were used to assess the significance of pair-wise migration rates.

Results

Genetic diversity

A total of 491 individuals were genotyped at five polymorphic microsatellite loci. Allelic richness varied among sites (mean = 9.7, range = 5.6 to 12.8; Table 4.2), with 2 to 21 alleles detected at a single locus. There was some evidence of departures from Hardy-Weinberg equilibrium (19 of 90 tests), with loci *Nlu14* and *Nlu23* deviating at a single site, *Nme208* deviating at three single sites, and *Nlu21* deviating significantly at 14 sites. *Nlu21, Nlu14* and *Nlu23* deviated due to excess homozygotes, which is suggestive of null alleles (alleles not amplified in PCR due to mutation at the priming site) or disproportionate inbreeding at these loci. *Nme208* deviated at a single site due to excess homozygotes and at two sites due to excess heterozygotes. The total number of significant tests was slightly greater than would be expected by chance alone (5% of 90 tests = 4.5). Linkage-disequilibrium was rejected in 12 of 180 tests (6.7%), distributed across 8 sites and 4 loci, which was only slightly more than expected at random (5% of 180 tests = 9). No evidence of large allele dropout was detected, however, stuttering error was detected for loci *Nlu21*.

Population structure

Estimates of F_{ST}, H_E, and river distance ranged from -0.020 to 0.167 (mean 0.044), 0.638 to 0.838 (mean 0.777) and 1.4 to 65.0 km (mean 30.1 km), respectively among paired sites (Table 4.2; Table 4.3). F_{ST} values were generally low (<0.02) between sites within the same tributary system, with the exception of sites within the Tenmile Creek tributary. For example, Tenmile Creek US and Spring Creek were significantly divergent from Tenmile Creek DS (F_{ST} = 0.029 and 0.038, respectively, Table 4.2), which was separated from the two upstream sites by the milldam. Eighty-four percent of pairwise comparisons (129 of 153) were significantly divergent at the 0.05 level. F_{ST} values were consistently greatest for all sites paired with either of two sites within the Jerry Reeves tributary system, which were also, on average, most distant from all other sites (mean distance = 42.2 km, Fig. 4.2). Relationships between genetic differentiation and geographic distance were significant ($r^2 = 0.196$, p-value =9.7E-09), even when the Jerry Reeves tributary sites were removed ($r^2 = 0.135$, p-value = 3.7E-05; Fig. 4.2). Heterozygosity (H_E) was not higher in sites directly influenced by a spring (ANOVA: F = 0.1442, p-value = 0.7091), but was lower in sites separated from the mainstem by a dam or an outcrop compared to sites without a mainstem barrier (F = 23.4, p-value = 0.0002), and lower in sites more than 2.5 km from the mainstem (F = 7.6994, p-value = 0.0135; Fig. 4.3). The effects of distance and barriers on heterozygosity were somewhat confounded because sites farther from to the mainstem also tended to be isolated by a barrier from the mainstem (Pearson's correlation coefficient: r = -0.62, p-value = 0.006). Heterozygosity was only slightly higher in sites upstream from the mainstem wetland (sites 1-10 were hypothesized to be strongly connected to the mainstem) compared to sites downstream from the mainstem wetland (F = 4.1293, p-value = 0.0591; Fig. 4.3).

The hierarchical analysis of genetic variance did not supported the hypothesis that the mainstem acted as a barrier to migration among tributaries or that populations more distant from the mainstem were more divergent than populations closer to the mainstem. Instead, analysis of variance supported three broad population groups. Using the clusters derived from STRUCTURE (HM3; Table 4.4), most of the total molecular variation was attributed to individuals within clusters (92.0%), 6.43% was attributed to differences among clusters and only 1.60% was attributed to differences among sites within clusters (Table 4.4). Variation among groups was lower for HM1 and HM2 hierarchical groupings (3.9 and 4.1%, respectively), suggesting that the mainstem did not act as a barrier to dispersal and that Potato Creek did not consist of a single population with divergence only in sites isolated from the mainstem.

Among the 14 BLGMM candidate models predicting population differentiation, three models contained 99% of the total model weight and were considered plausible models (Table 4.5). The best-supported model was 1.45 times more plausible compared to the next supported model and indicated that F_{ST} was positively related to stream distance and negatively related to being a pair of sites within 2.5 km of the mainstem (Table 4.6). Based on parameter estimates from the best-supported model, genetic differentiation increased by 0.0040 ± 0.0010 (mean ± SD) with every 10 km increase in stream distance and decreased by -0.0109 ± 0.0029 when both sites were within 2.5 km of the mainstem. The effect of the farm pond dam was included in the second best-supported model, which was 2.31 times more plausible than the third best model, but the effect was considered inconclusive (0.0030 ± 0.0067). The third best approximating model additionally included the percent of wetland habitat between sites, but the direction of the effect was inconclusive (0.0007 ± 0.0016).All plausible BGLMM models showed similarly adequate fit, with a pseudo-R^2 values of 0.215 (Pearson's correlation coefficient between observed and predicted values: r = 0.464), 0.234 (r = 0.484), and 0.226 (r = 0.476), respectively (Fig. 4.4). In general, the model predicted that fish from sites close to the mainstem were more similar to each other than those from sites far from the mainstem, and that populations separated by the dam may be more divergent than those with no dam as a barrier (Fig. 4.4).

Four population clusters (K = 4) were supported using the Bayesian clustering approach implemented in STRUCTURE (Fig. 4.5). While some individuals were strongly assigned to one of two populations (Jerry Reeves tributary and Tenmile Creek tributary upstream of a milldam), the majority of individuals were not assigned to a specific cluster (Fig. 4.6). Individuals without clear assignment were slightly more likely to be assigned to the Tenmile Creek tributary population upstream of the milldam compared to Jerry Reeves tributary population. However, equal partitioning of individual ancestries into additional clusters with no geographic trend suggests caution in interpreting more than three genetic clusters.

Dispersal among populations

BIMr model fit, as measured by Bayesian deviance (D_{assign}), for each of 20 replicate runs for each recolonization model were relatively similar (Fivemile Creek model: mean ± SD = 39.5 ± 10.6, Unnamed Tributary model = 73.1 ± 7.8). The replicate with the lowest deviance indicated that mean migration rates between the four populations ranged from no migration up to 26% of alleles being assigned from another population in the Unnamed Tributary model and up to 21% in the Fivemile Creek model (Table 4.7). In both models, there was no migration upstream over the historic milldam from sites located in the lower or upper portion of the basin. In the Unnamed tributary model, migration was symmetrical between the recolonized site and the population closest to the recolonized site (Turnpike Creek US and DS), suggesting higher gene flow between sites in close proximity geographically. In contrast, we estimated no migration into the Fivemile Creek recolonized site from either far or close populations (Table 4.7). Turnpike Creek US and DS population consistently received migrants from all other populations in both models, suggesting that fishes can potentially disperse downstream over dams, as well as upstream through the mainstem of Potato Creek.

Discussion

Using microsatellite genetic markers, we evaluated fine-scale population genetic structure of a small non-migratory species inhabiting tributaries of a watershed influenced by natural and anthropogenic barriers, wetland habitat, andspring sources. Genetic diversity was highest in populations near the mainstem, and lower in sites isolated from the mainstem by either a dam or high-gradient outcrop and in sites greater than 2.5 km from the mainstem. Tributary populations exhibited isolation by distance and tributary populations near the mainstem were less divergent from each other compared to populations far from the mainstem. Dams and high-gradient outcrops substantially fragmented populations and limited upstream dispersal and population connectivity. Estimates of Bayesian migration rates suggested that tributaries with recent apparent local extinctions due to reductions in streamflow were most likely recolonized from sites close rather than distant and that dams may be barriers to upstream gene flow.

Genetic diversity

We observed lower genetic diversity (heterozygosity) and allelic diversity in tributaries isolated by a barrier from the mainstem compared to sites with no barriers and lower in sites farther from the mainstem. Patterns of genetic diversity are not only influenced by dispersal between populations, but also by rates of genetic drift and inbreeding associated with small population sizes, highly variable spawning success, and local extinction and recolonization dynamics (Waples 1990, Lynch et al. 1995). Low diversity may be also indicative of reduced individual fitness (due to inbreeding depression) or low population resiliency (due to loss of favorable alleles and small effective population sizes). Thus, populations isolated by dams or high-gradient outcrops with low genetic diversity may be vulnerable to both demographic and environmental stochastic processes. Even if lower diversity does not directly reflect small population sizes, our results cannot exclude the possibility that dams, high-gradient outcrops, and distance may reduce gene flow and beneficial alleles from migrating from the mainstem into headwater tributary populations. Similarly, Lamphere and Blum (2012) as well as Dehais et al. (2010) observed lower heterozygosity in upstream populations of creek chubs

(*Semotilusatromaculatus*) and the European chub (*Squaliuscephalus*), respectively, compared to downstream populations. Our observation of lower heterozygosity above barriers may be confounded with the fact that these populations are also distant from downstream sites near the mainstem.

Increased genetic diversity downstream may reflect larger population sizes downstream, movement bias of fishes in the downstream direction, or the presence barriers or unsuitable habitat that restricts upstream dispersal. Because the frequency of heterozygotes is assumed to be correlated with population size (Frankham 1996), our observation of lower diversity above barriers may be the result of smaller population sizes in smaller headwater streams (i.e., lower discharge and associated habitat area upstream). However, *N. lutipinnis* is considered a small-stream dwelling fish and reach-scale abundance estimates can be large in smaller order streams (*personal observation*). Evidence that populations are large in larger streams may be limited due to low catchability in larger streams (i.e., five individuals were captured across two sites within the Potato Creek mainstem according to GAMNH collections database and no individuals were captured according to GA DNR collections). Additionally, asymmetrical dispersal may result in downstream populations receiving more new alleles than upstream populations, thus maintaining higher diversity downstream. This may be plausible in our study of *Notropis lutipinnis*, as we also estimated asymmetrical migration from the sites from above the historic milldam into populations downstream of the dam, with no evidence of upstream migration over the dam. This pattern was also observed in a fine-scale study on a fluvial-dependent species by Junker et al. (2012), which found that barriers completely blocked upstream movement, likely contributing to lower genetic diversity near the headwaters. We suggest that limited upstream migration of alleles more likely explains observed of lower diversity above barriers and in sites farther from the mainstem than increased drift and inbreeding in smaller order streams because of small population sizes.

Isolation by distance and population structure

Our significant isolation by distance (IBD) relationship suggests a spatial structuring of *Notropis lutipinnis* populations because of geographic distance. Two populations from the Jerry Reeves tributary, which were most distant from all other sites and isolated from the mainstem by a high-gradient outcrop, largely contributed to the IBD relationship. However, even after removing these sites and two others isolated by an historic milldam, the IBD relationship was still evident, suggesting that tributary populations exhibit a stepping-stone pattern of dispersal. The finding of significant isolation by distance is not a surprising result among studies of small-stream non-migratory fishes (Skalski et al. 2008, Sterling et al. 2012, Lamphere and Blum 2012, Franssen 2012). In this study, we observe an increase in genetic differentiation (F_{ST}) by 0.01 with every 50 km increase in geographic stream distance between sites. Similarly, Roberts et al. (2013) used BLGMM to estimate that genetic differentiation increased by 0.01 for every 100 km increase in distance for a larger-bodied and more mobile fluvial specialist (*Percina rex*). Although not directly comparable, our maximum F_{ST} value of 0.167 over 65 km is higher than estimates for *Cyprinella lutrensis* in a reservoir system (max =0.078 over 300 km; Franssen 2012), but lower than estimates for*Cottusgobio* in an Alpine river system (max = 0.32 over 34km; Junker et al. 2012).

According to our genetic differentiation (F_{ST}) results, the mainstem did not appear to be a barrier to migration among tributaries. Tributary populations near tributary-mainstem confluences were less genetically divergent than populations farther from the mainstem. If our AMOVA results had partitioned most of the genetic variation among tributaries, this would have supported the hypothesis that the mainstem acts as a barrier to migration among tributaries. However, our results did not follow such a pattern. In fact, genetic variation was partitioned among only four groups, two of which were isolated from the mainstem by either a dam or outcrop and two others had mixed ancestry (potentially caused by homozygote excess at one locus). This suggests substantial gene flow among sites not isolated by barriers from the mainstem. This result is contrary to a study by Sterling et al. (2012), which found that populations of Yazoo darters (*Etheostoma raneyi*) experienced low levels of migration across large and channelized mainstem reaches within watersheds, leading to high population differentiation among tributaries.

Influence of barriers

Instream barriers such as water diversion structures, dams, and weirs are known to influence movement and population connectivity of a variety of migratory and non-migratory stream fishes (Wofford et al. 2005, Meeuwig et al. 2010, Roberts and Angermeier 2013, Weigel et al. 2013). In this study, we found that both a historic milldam and more recent farm pond dam increased population divergence. Using Bayesian migration rate estimates, we also found evidence that populations above the milldam may have unidirectional dispersal downstream, which can contribute migrants to relatively distant populations. A study by Weigel et al. (2013) found that the number of water diversion obstructions and the obstruction height-to-depth ratio were better predictors of recent migration rates than distance in steelhead trout. Thus, obstructions, such as culverts and dams, may have cumulative effects on the dispersal of aquatic species, but we were unable to investigate their influence on a non-migratory species in this study. Three additional low-head dams existed within the Potato Creek watershed: two on the mainstem of Potato Creek and another above a mainstem dam on a large tributary (Fig. 4.1).

However, we were unable to collect genetic samples of *Notropis lutipinnis* above these dams because of lack of access and inadequate sampling habitat. We predict that these dams may cumulatively increase population differentiation in the upper portion of the basin and that dam size may be important for downstream migration and connectivity throughout the watershed.

In previous studies, relatively high values of F_{ST} have been reported among sites separated by natural barriers such as high-gradient stream reaches, including cascades and waterfalls (Boizard et al. 2009, Lamphere and Blum 2012). We found some evidence that high-gradient reaches (greater than 3%) may limit dispersal of *Notropis lutipinnis*in the Potato Creek watershed because of the observed high genetic differentiation between sites paired with Jerry Reeves Tributary, which was separated from all other tributaries by at least two high gradient reaches: one on the mainstem and another on the tributary. Additionally, asymmetrical migration rates were low from sites below the mainstem outcrop into populations in the upper portion of the watershed above the outcrops, suggesting that outcrops may impede upstream dispersal in the mainstem.

Management implications

Understanding population structure, connectivity and dispersal is essential for the effective conservation of fish species. Studies in speciose groups of fishes, such as minnows are rare at small-spatial scales (Alo and Turner 2005, Boizard et al. 2009, Franssen 2012). Evaluating factors that contribute to the long-term population persistence remains challenging partly because of the limitations associated with using capture-mark-recapture methods for small-bodied fishes with large population sizes. Using microsatellite genetic markers, we found support for the hypothesis that populations upstream of small milldams and high-gradient outcrops may be vulnerable to local extirpations, with little potential for recolonization following local extirpation. In fact, despite substantial effort sampling fishes in a stream located above a dam and small reservoir (Basin Creek), we captured only a subset of species known from the Potato Creek watershed and no evidence of a population of Yellowfin shiners. In this watershed scale study, we found support for the idea that the mainstem of Potato Creek, which was previously thought of as a barrier to dispersal of small-stream fishes, did not prohibit movement among stream tributary populations. We did find that populations farther from the mainstem were more divergent than those close, suggesting a stepping-stone model of dispersal within tributaries. To effectively evaluate watershed management actions that often occur at this watershed level, we encourage researchers to conduct studies focusing on patterns of asymmetrical migration to identify populations potentially vulnerable and resilient to local extirpation events and to identify tributaries or habitats with large populations that may disproportionally contribute alleles to neighboring populations (i.e., source-sink dynamics). Small populations isolated from the mainstem may lack the ability to adapt to changing environmental conditions and this inflexibility may make them exceptionally vulnerability to these same changes (Frankham and Ralls 1998). Additionally, exploring other landscape factors that potentially limit recolonization potential of stream segments within the stream network (other than firm barriers –i.e., landscape resistance models) may prove informative for understanding fine-scale genetic structure of aquatic biota.

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TABLE 4.1 List of microsatellite primers used in this study. Loci that were multiplexed are noted on annealing temperatures.

Genbank No.	Locus Name	Primers 5’- 3’	Repeat motif	Annealing temp (°C)	No. alleles	Allele size range
AY460199[1]	*Nme208*	TACATCATGGCCCTAACACA GGGCTAAAATTTGGACGAA	$[AC]_{13}$	51[a]	8	180–211
AY460194[1]	*Nme93*	CACCAAACTGTCATTCAAATAAG GACCCTGGGCGTTCTCTG	$[CA]_{13}$	51[a]	9	85–102
NA[2]	*Nlu21*	TGCAGTTGTCATTGTCCACG GGCAGTAAATCCAAAGCCTCC	$[AAGAG]_{20}$ $[TCTCC]_{25}$ $[AAGAG]_{30}$ $[TCTCC]_{25}$ $[AAGAG]_{50}$ $[AAGAG]_{15}$	59	30	198–421
NA[2]	*Nlu14*	AACCGTTCTGTAGTCAATCAGGC ATCGAGCGAGAGAGTGGAGC	$[TCTG]_{64}$ $[ATCT]_{48}$ $[TCTG]_{64}$ $[ATCT]_{96}$	51[b]	35	125–381
NA[2]	*Nlu23*	TGGAAGATGTGGAATTAACACG GGATCCATTAGAAAACAACGGG	$[TCTG]_{28}$ $[ATGG]_{36}$ $[ATCT]_{88}$	51[b]	38	125–361

[1] Gold, J. R., E. Saillant, C. P. Burridge, A. Blanchard, and J. C. Patton. 2004. Population structure and effective size in critically endangered Cape Fear shiners *Notropis mekistocholas*. Southeastern Naturalist 3:89–102.

[2] Primers developed in this study.

TABLE 4.2 Location, sample size (N), distance to the mainstem (km), potential barriers to the mainstem, spring influence (1 = yes, 0 = no), mean allelic richness (A), expected and observed heterozygosity (H_E and H_O, respectively) and inbreeding coefficient (F_{IS}) for eighteen *Notropis lutipinnis* sampled sites. Sites are organized by stream network. Asterisks denote samples collected in 2011 and not in 2012.

Network	Stream	ID	Lat ^{o}N	Long ^{o}W	N	Mainstem distance (km)	Mainstem barrier	Spring influence	A	H_O	H_E	F_{IS}
Turnpike	Turnpike Creek US	1	33.153	-84.261	24	8.45	wetland	0	10.6	0.700	0.794	0.121
	Turnpike Creek DS	2	33.114	-84.249	25	2.85	wetland	0	11.0	0.704	0.800	0.123
Potato	Potato Creek US	3	33.097	-84.237	31	0.00	none	0	12.2	0.768	0.821	0.066
Unnamed	Unnamed Tributary	4	33.071	-84.217	32	2.00	wetland	0	12.0	0.813	0.838	0.031
Gola	Tributary to Gola Creek	5	33.081	-84.287	32	7.73	dam, wetland	0	12.8	0.763	0.797	0.071
	Gola Creek	6	33.057	-84.284	27	7.42	wetland	0	11.0	0.719	0.772	0.044
Threemile	Threemile Creek US	7	33.014	-84.304	31	5.00	wetland	1	10.2	0.794	0.799	0.006
	Threemile Creek MS	8	32.995	-84.292	31	1.93	wetland	1	10.6	0.735	0.800	0.082
	Threemile Creek DS	9	32.986	-84.286	31	0.51	wetland	1	11.0	0.716	0.787	0.091
Rose	Rose Creek	10	32.982	-84.241	32	5.78	wetland	0	9.4	0.756	0.773	0.022
Fivemile	Fivemile Creek	11	32.976	-84.312	18	2.27	none	0	8.0	0.744	0.768	0.032
Tenmile	Tenmile Creek US	12	32.976	-84.393	30	11.02	dam	0	9.4	0.720	0.766	0.061
	Spring Creek	13	32.945	-84.372	32	5.85	dam	1	6.2	0.569	0.727	0.221
	Tenmile Creek DS	14	32.924	-84.357	28	1.29	dam	1	9.6	0.700	0.811	0.139
Jerry Reeves	Womble Creek	15	32.885	-84.432	24	10.10	outcrop	0	5.6	0.558	0.654	0.159
	Jerry Reeves Creek	16	32.862	-84.408	32	5.96	outcrop	0	5.6	0.538	0.638	0.149
Potato	Potato Creek DS*	17	32.793	-84.359	11	0.00	none	0	8.6	0.636	0.812	0.225
Dean	Dean Creek*	18	32.799	-84.339	20	2.50	none	0	10.6	0.760	0.825	0.081

TABLE 4.3 Summary data for spatial population structure of *Notropis lutipinnis* in the Potato Creek watershed. Entries below the diagonal are pairwise F_{ST} values (N = 491), with non-significant differences at Bonferonni correction p-value < 0.05 in bold. Entries above the diagonal are stream distances between paired sites (km). Site ID's correspond to Table 4.2.

Site ID	1	2	3	4	5	6	7	8	9
1	-	5.2	7.8	13.4	20.8	21.3	31.4	28.5	27.2
2	**-0.020**	-	2.6	8.2	15.7	16.1	26.2	23.4	32.3
3	0.013	0.012	-	5.6	13.0	13.5	23.6	20.7	19.4
4	0.011	0.010	**0.005**	-	10.9	11.4	21.5	18.6	17.3
5	0.013	0.012	**0.005**	0.009	-	4.8	25.0	22.2	20.8
6	0.014	0.015	**0.009**	0.029	**0.009**	-	25.4	22.6	21.2
7	0.034	0.032	0.016	0.015	0.031	0.045	-	2.8	4.2
8	0.012	0.011	**0.000**	**0.009**	**0.006**	0.015	**0.006**	-	1.4
9	0.028	0.026	0.018	0.012	0.014	0.030	0.015	**0.007**	-
10	0.020	0.020	0.012	0.019	0.027	0.026	0.028	0.015	0.034
11	0.033	0.032	0.029	**0.010**	0.016	0.036	0.027	0.016	**0.002**
12	**0.003**	**0.004**	0.018	0.015	0.018	0.023	0.036	0.017	0.026
13	0.030	0.030	0.043	0.037	0.041	0.045	0.039	0.031	0.038
14	0.022	0.021	**0.007**	**0.009**	**0.009**	0.022	0.023	**0.005**	0.018
15	0.139	0.136	0.124	0.102	0.103	0.146	0.103	0.096	0.088
16	0.158	0.154	0.143	0.124	0.129	0.167	0.115	0.116	0.113
17	0.045	0.044	0.032	0.029	0.034	0.055	0.032	**0.015**	0.041
18	0.031	0.029	0.016	0.024	0.019	0.030	0.025	**0.009**	0.034

TABLE 4.3 continued.

Site ID	10	11	12	13	14	15	16	17	18
1	31.8	32.3	53.0	48.1	43.6	60.8	64.7	62.6	65.0
2	26.6	27.1	47.8	43.0	38.5	55.7	59.5	57.5	59.9
3	24.0	24.5	45.2	40.3	35.8	53.0	56.9	54.8	57.2
4	24.0	22.4	43.1	38.2	33.7	50.9	54.8	52.7	55.1
5	27.6	25.9	46.7	40.6	36.1	54.5	58.3	56.3	58.7
6	28.0	26.4	47.1	41.0	37.7	54.9	58.7	56.7	59.1
7	11.9	10.2	31.0	26.1	21.6	38.8	42.6	40.6	43.0
8	9.0	7.4	28.1	23.2	18.8	36.0	39.8	37.8	40.1
9	7.7	6.0	26.8	21.9	17.4	34.6	38.4	36.4	38.8
10	-	7.2	30.1	25.3	20.8	38.0	41.8	39.8	42.2
11	0.026	-	25.2	20.3	15.8	33.0	36.8	34.8	37.2
12	0.030	0.037	-	6.1	9.4	29.3	33.2	31.2	33.5
13	0.056	0.049	**0.007**	-	4.5	24.4	28.3	26.3	28.6
14	0.019	**0.012**	0.029	0.038	-	20.0	23.8	21.8	24.2
15	0.138	0.085	0.134	0.132	0.118	-	3.8	13.7	16.1
16	0.153	0.113	0.156	0.154	0.140	**-0.004**	-	17.6	19.9
17	0.055	0.036	0.061	0.070	0.037	0.058	0.072	-	2.4
18	0.031	0.030	0.038	0.052	0.017	0.077	0.088	**0.003**	-

TABLE 4.4 Analysis of molecular variance (AMOVA) between groups of *Notropis lutipinnis* populations in the Potato Creek watershed under three alternative hierarchical models. HM1 represents the mainstem as a barrier to dispersal among tributaries, resulting in 11 distinct tributary populations. HM2 represents five fragmented tributary populations isolated from the mainstem by a dam or outcrop and one unfragmented population throughout the remainder of the watershed. HM3 represents three populations derived from STRUCTURE analysis, resulting in two populations fragmented from the mainstem by a dam and high-gradient outcrop, respectively, and a third population throughout the remainder of the watershed.

Model	Number of groups	Source of variation	Degrees of freedom	Sum of squares	Variance component	% of variation	Fixation index
HM1	11	Among groups	10	96.30	0.079	3.900	0.039
		Among populations within groups	7	20.24	0.016	0.810	0.008
		Within populations	964	1868.54	1.938	95.290	0.047
		Total	981	1985.08	2.034		
HM2	6	Among groups	5	78.50	0.083	4.070	0.041
		Among populations within groups	12	38.05	0.023	1.130	0.012
		Within populations	964	1868.54	1.938	94.790	0.052
		Total	981	1985.08	2.045		
HM3	3	Among groups	2	60.30	0.136	6.430	0.064
		Among populations within groups	15	56.24	0.034	1.600	0.017
		Within populations	964	1868.54	1.938	91.970	0.080
		Total	981	1985.08	2.108		

TABLE 4.5 DIC, ΔDIC, and model weights (w_i) for each candidate model predicting variation of pairwise F_{ST} among 11 *Notropis lutipinnis* sites (66 pairwise comparisons). Model weights within 10% of the best approximating model are interpreted as plausible candidate models.

Candidate model	DIC	ΔDIC	w_i
Geographic distance + within 2 km of the mainstem	-441.088	0.000	0.502
Geographic distance + within 2 km of the mainstem + dam	-440.342	0.746	0.346
Geographic distance + within 2 km of the mainstem + dam + percent wetland	-438.666	2.422	0.150
Within 2 km of the mainstem + percent wetland	-428.415	12.673	0.001
Within 2 km of the mainstem + dam + percent wetland	-428.030	13.058	0.001
Geographic distance + percent wetland	-424.468	16.620	0.000
Geographic distance	-423.419	17.669	0.000
Geographic distance + dam + percent wetland	-421.716	19.372	0.000
Geographic distance + dam	-421.252	19.836	0.000
Within 2 km of the mainstem	-420.185	20.903	0.000
Dam + Within 2 km of the mainstem	-418.711	22.376	0.000
Percent wetland	-418.247	22.841	0.000
Dam + percent wetland	-416.102	24.986	0.000
Dam	-409.228	31.860	0.000

TABLE 4.6 Parameter estimates, standard deviation, lower and upper 95% credibility intervals for plausible BGLMM candidate models for predicting variation of pairwise F_{ST} among 11 *Notropis lutipinnis* sites (66 pairwise comparisons). Stream distance and percent wetland habitat between sites were normalized with mean = 0 and standard deviation = 1 (1SD = approximately 10 km and 21% of stream km in wetland habitat, respectively). The dam predictor represents a single farm pond. Bolded predictors indicate significant effects (95% CI do not overlap zero).

Parameter	Estimate	SD	Lower 95% CI	Upper 95% CI
Best approximating model (*w* = 0.502, R^2 = 0.215)				
Intercept	**0.0204**	**0.0037**	**0.0134**	**0.0283**
Geographic distance	**0.0043**	**0.0010**	**0.0023**	**0.0063**
Within 2 km of the mainstem	**-0.0109**	**0.0029**	**-0.0167**	**-0.0051**
Second best approximating model (*w* = 0.346 R^2 = 0.234)				
Intercept	**0.0200**	**0.0038**	**0.0126**	**0.0275**
Geographic distance	**0.0042**	**0.0011**	**0.0022**	**0.0064**
Within 2 km of the mainstem	**-0.0108**	**0.0030**	**-0.0165**	**-0.0049**
Dam	0.0032	0.0067	-0.0100	0.0168
Third best approximating model (*w* = 0.150 R^2 = 0.226)				
Intercept	**0.0201**	**0.0040**	**0.0123**	**0.0279**
Geographic distance	**0.0040**	**0.0011**	**0.0016**	**0.0061**
Within 2km of the mainstem	**-0.0108**	**0.0032**	**-0.0170**	**-0.0045**
Dam	0.0028	0.0070	-0.0115	0.0170
Percent wetland	0.0007	0.0016	-0.0030	0.0037

TABLE 4.7 Mean (standard deviation) migration rates among sites for each dry-site model (Unnamed Tributary model and Fivemile Creek model). Each model contains four populations: a nearby site close to the mainstem in the upper portion of the watershed (Turnpike Creek US and DS), a distant site close to the mainstem in the lower portion of the watershed (Potato Creek DS and Dean Creek), a site upstream of a historic milldam (Tenmile Creek US and Spring Creek), and a site with recolonization following apparent local extirpation from drought (Fivemile Creek or Unnamed Tributary). Pairwise estimates greater than corresponding estimates are bolded and indicate asymmetrical migration and gene flow.

Unnamed Tributary model

Into/From	Unnamed Tributary	Tenmile Creek US and Spring Creek	Potato Creek DS and Dean Creek	Turnpike Creek US and DS
Unnamed Tributary	0.422 (0.125)	**0.240** (**0.085**)	**0.120** (**0.082**)	0.218 (0.110)
Tenmile Creek US and Spring Creek	0.000 (0.000)	1.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Potato Creek DS and Dean Creek	0.000 (0.000)	0.000 (0.000)	1.000 (0.000)	0.000 (0.000)
Turnpike Creek US and DS	0.218 (0.105)	**0.258** (**0.080**)	**0.056** (**0.045**)	0.468 (0.117)

Fivemile Creek model

Into/From	Fivemile Creek	Tenmile Creek US and Spring Creek	Potato Creek DS and Dean Creek	Turnpike Creek US and DS
Fivemile Creek	1.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Tenmile Creek US and Spring Creek	0.000 (0.000)	1.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Potato Creek DS and Dean Creek	0.000 (0.000)	0.000 (0.000)	1.000 (0.000)	0.000 (0.000)
Turnpike Creek US and DS	**0.064** (**0.073**)	**0.208** (**0.080**)	**0.045** (**0.067**)	0.683 (0.091)

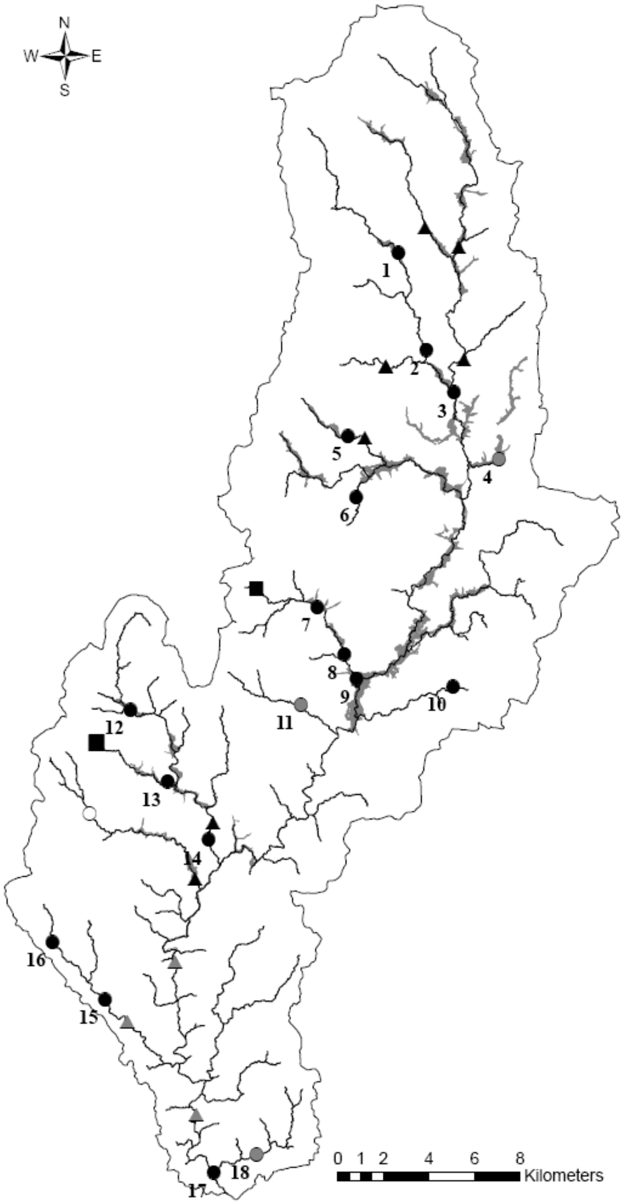

FIGURE 4.1 Locations of site sampled (circles) for *Notropis lutipinnis* within the Potato Creek watershed (482 km^2) of the Upper Flint River basin, GA (add inset). Site numbers follow Table 4.1. Sites with apparent local extinction in 2011 are denoted with gray circles. Open circle denotes where no *N. lutipinnis* were captured despite sampling effort. Locations of dams (black triangles), bedrock outcrops (gray triangles), and wetlands (shaded gray) are indicated. Location of potential spring inputs to downstream sites are indicated by black squares.

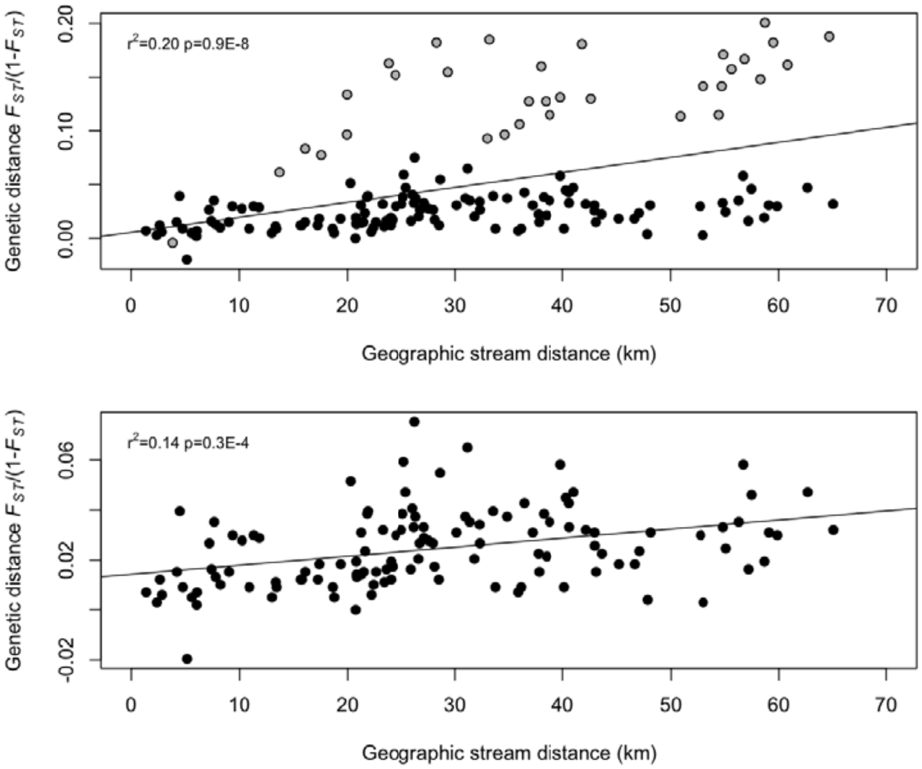

FIGURE 4.2 Relationship between pairwise genetic distance, $F_{\mathrm{ST}}/(1-F_{\mathrm{ST}})$, and geographic stream distance (km) among *Notropis lutipinnis* at 18 sites within the Potato Creek watershed for all sites (paired sites with Jerry Reeves tributary population in gray) and sites excluding those paired with Jerry Reeve tributary population. The solid line represents the predicted linear relationship. Pearson correlation coefficients are shown.

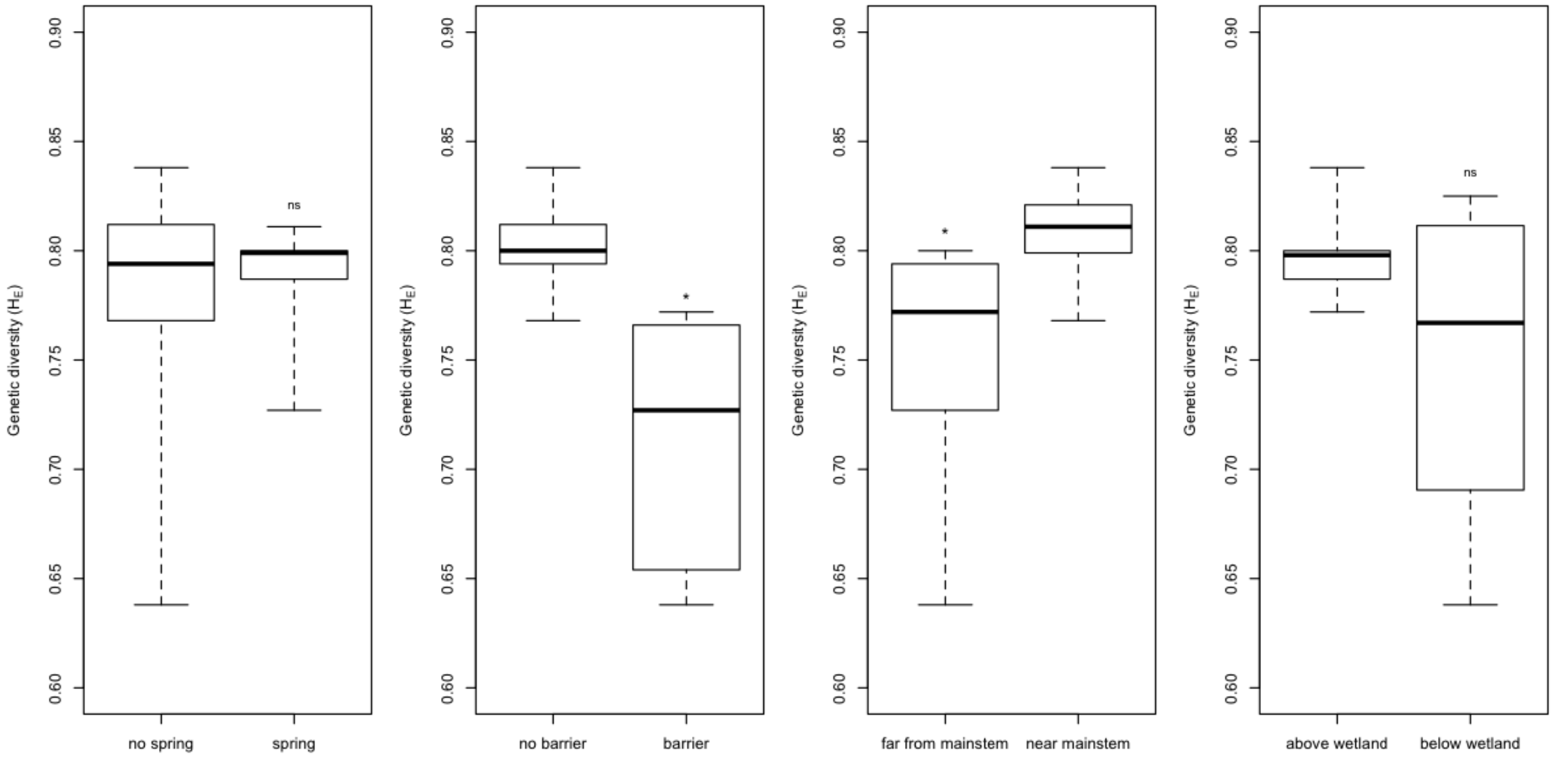

FIGURE 4.3 Comparison of genetic diversity (H_E) between *Notropis lutipinnis* populations influenced by springs and populations with no spring influence (ANOVA: p-value = 0.7091), populations not isolated from the mainstem and populations isolated from the mainstem by a dam or high-gradient outcrop barrier (p-value = 0.0001), populations far from the mainstem(more than 2.5 km) and populations close to the mainstem (within 2.5 km;p-value = 0.0150), and populations above the mainstem wetland compared to populations below the wetland (p-value = 0.0590). Non-significant comparisons are indicated by “ns”, while an asterisk indicates significant differences (p-value < 0.05).

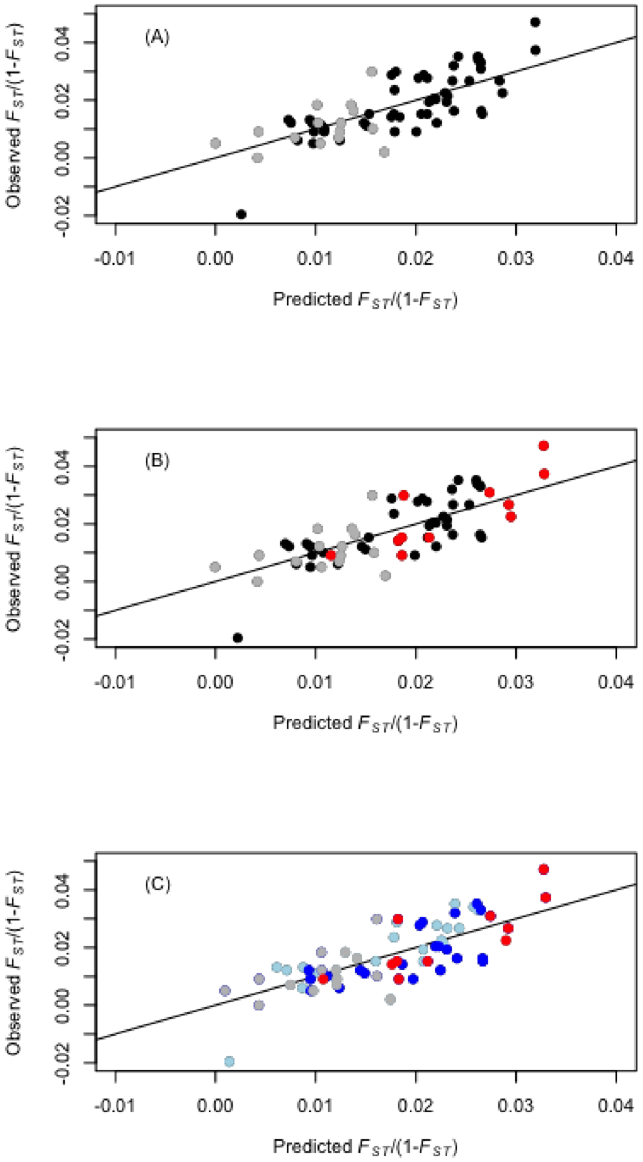

FIGURE 4.4 Relationship between observed and predicted linearized F_{ST} values, (F_{ST}/(1-F_{ST})), for the best (A), second-best (B), and third-best (C) approximating Bayesian generalized linear mixed models.Sites within 2.5 km of the mainstem (gray), isolated by a dam (red), and with less and more than average wetland habitat (mean = 63%; light blue and dark blue, respectively) are shown for each corresponding model.

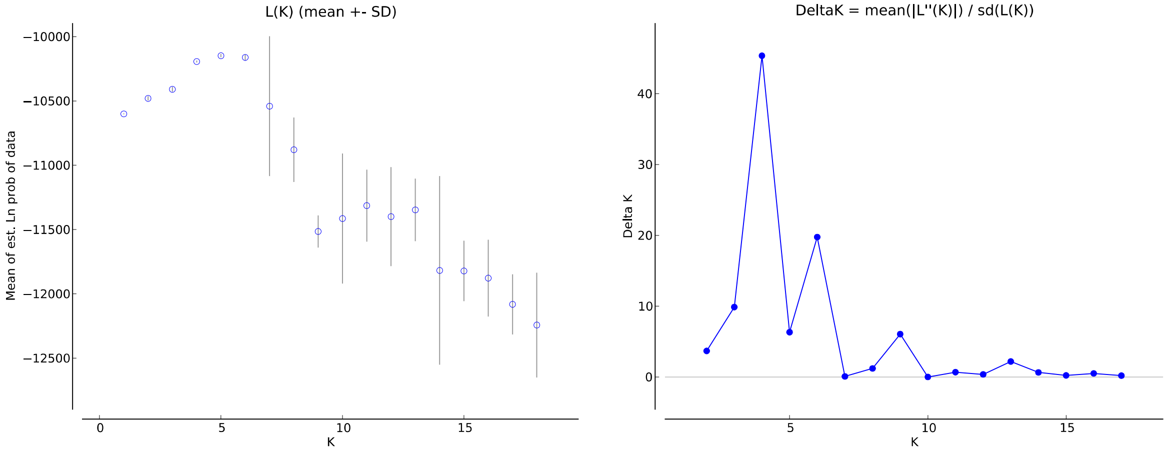

FIGURE 4.5 Mean likelihood values (averages across all 10 replicate runs; left panel) and Delta K values (right panel) for *Notropis lutipinnis* clusters (K = 2 to 18) obtained from STRUCTURE HARVESTER. Low likelihood variance and high delta K indicate support for K = 4.

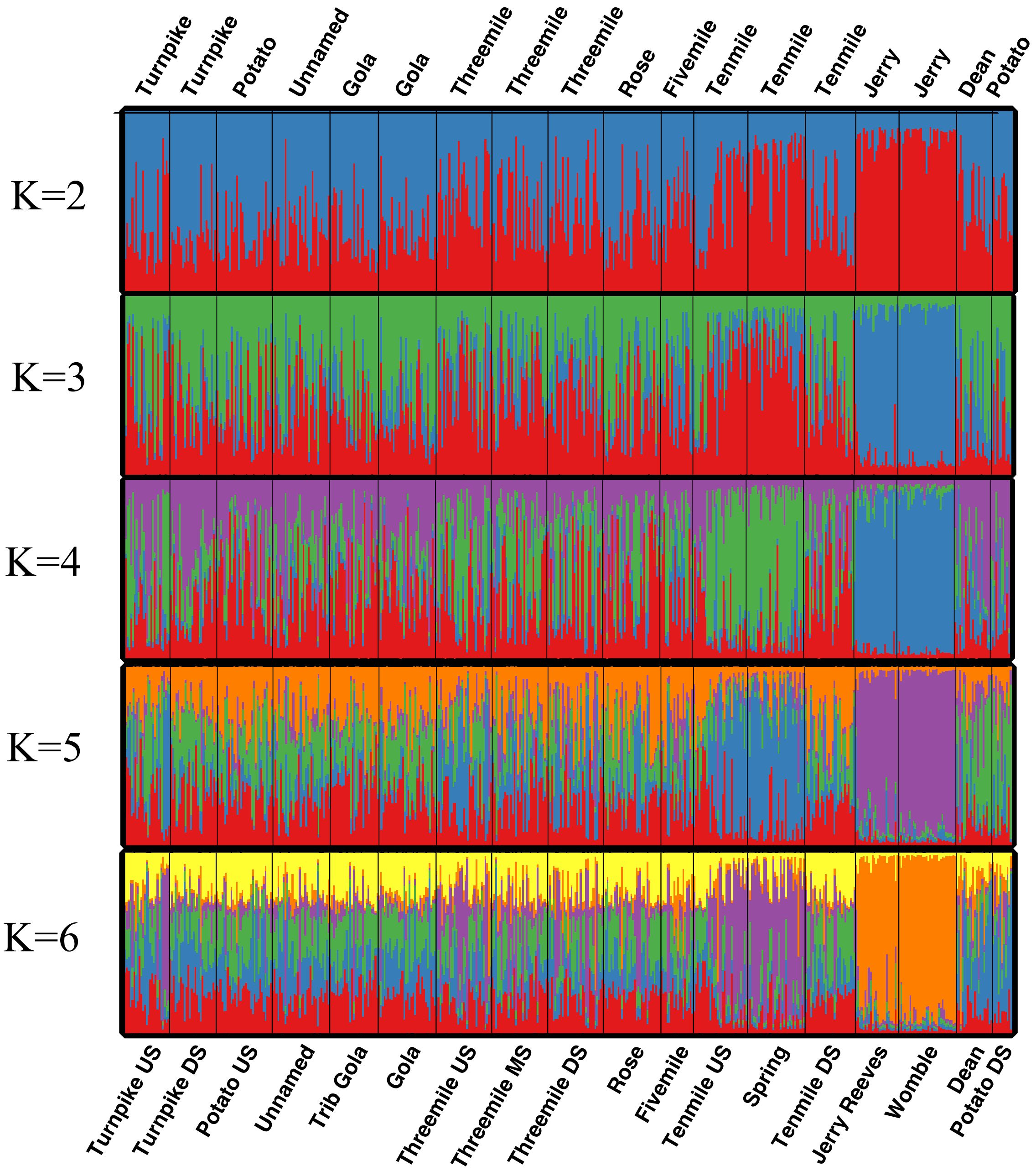

FIGURE 4.6. Results from STRUCTURE models showing K = 2 to 6 (10 replicate runs each) of *Notropis lutipinnis* at 18 sites within the Potato Creek Watershed. Colors indicate the proportion of each individual's ancestry originating from differing clusters. Top labels refer to tributary system and lower labels refer to sites.

CHAPTER 5

CONCLUSION

This dissertation evaluated the effects of streamflow, geomorphology, and network characteristics on population dynamics of stream fishes across a range of scales relevant to stream conservation and flow management. In Chapter 2, I conducted a unique long-term capture-mark-recapture study on a fluvial-dependent darter (turquoise darter, *Etheostoma inscriptum*) population in a middle order Piedmont stream. I sampled across several consecutive severe droughts, which was unprecedented in this river based on the historic-flow record. Middle order streams can typically be difficult to effectively sample because of higher flows, but the drought provided a rare opportunity to measure local survival of a darter species during extreme reductions in streamflow. In this study, I found evidence that the turquoise darter was unexpectedly resilient to extremely low flow conditions, with high recruitment and relatively high apparent survival. Consequently, fish reached high abundances during drought, which did not appear to negatively influence survival. Thus study provided an opportunity to evaluate whether extensive streambed drying caused by drought and water withdrawals substantially reduced populations of shoal-dependent species. To my surprise, the population was generally not negatively affected, but instead recruited young-of-year that survived relatively well during the unprecedented low flow conditions.

Using capture-mark-recapture methods was useful for detecting effects of high flow pulses on apparent survival dynamics in this study. Our effort (3-day consecutive sampling) allowed us to detect increased young-of-year apparent survival and decreased adult apparent survival (likely through dispersal) in response to short-term high flow events. However, if low flows in fact had an effect on local survival, we were unable to detect it with this sampling regime. The effort required to detect a smaller effect if present may be impractical (> 3 consecutive days) using current tagging methods for small-bodied fishes (VIE). If alpha-numeric tags were available for use in this species (permitting individuals to be uniquely tagged and monitored), then continuation of using a CMR approach may prove useful for estimating smaller changes in local dynamics in relation to environmental drivers. Until then, estimates of recruitment may be sufficient to evaluate population trajectories in response to variable streamflow conditions in this middle order river.

In Chapter 3, I quantified fish abundances across many smaller streams in response to low- and high-flow events, to evaluate whether low flows negatively affected populations in smaller streams. I found that several common species responded differently to high and low flow events and that the effects of these flows varied with stream size and proximity to larger stream segments, suggesting that stream and network characteristics influence the ability for populations to remain stable in response to variable streamflows. During the severe drought in 2011, we observed the dewatering and streambed drying of at least three streams, resulting in complete streambed drying or isolation of stagnant pools. However, following rewetting in the following year fish populations returned to these streams, which were all fairly close to the mainstem. From this observation, small stream catchments close to the mainstem may be particularly resistant to low flow conditions. We observed that populations of cyprinids increased following periods of higher high flows and lower low flow periods, potentially because of increased dispersal from larger tributaries or increased recruitment and survival of young-of-year prior to sampling, respectively. Specifically, young-of-year generally increased for three species after low flow periods in smaller streams. Conversely, populations of centrarchids generally responded to high flow events more in streams that were closer to larger stream segments with little impact in smaller streams.

Despite sampling mostly smaller stream tributaries (2nd and 3rd order streams), I found that changes in seasonal abundance of stream fish were not only dependent on streamflow events, but also on stream size, which was unexpected. Factors related to hydrologic connectivity and aquatic-terrestrial linkages may explain why populations in smaller catchments responded differently to flows compared to larger catchments. For example, we observed potential spring influences in some of the smallest catchments, which may have confounded our ability to measure population responses to streamflow in these streams. Smaller catchments may also be more directly influenced by riparian zones and the terrestrial landscape, resulting in greater variation in the input of organic matter and associated basal food resources. Nonetheless, including stream size and network position into projections of species responses to streamflow may help inform flow-management decisions in stream networks.

Addressing the relative robustness of our model results to variations in model assumptions concerning capture probabilities and occupancy may be useful for understanding how capture rates and colonization and extinction dynamics may affect the interpretation of our results. For example, simulating model outcomes assuming precise or imprecise capture rates compared to small and large capture rates would be useful for evaluating if concurrent capture-mark-recapture studies should be conducted with studies of counts in order to obtain least biased results of the effects of flow on abundance dynamics. Lastly, since abundance is a function of many demographic processes (births, deaths, immigration, and immigration) and varies markedly across streams, it may be a better composite metric of population response than occupancy or dynamic occupancy (colonization/extinction) responses alone. A combination of abundance and dynamic occupancy responses (i.e., multistate dynamic occupancy models) may be useful for gaining insights into the resilience of populations to maintain a minimum occupancy or abundance across a watershed. In this study, many species were not captured across all reaches, indicating that colonization and extinction dynamics likely play an important role in the distribution of species.

In Chapter 4, I used population genetics to assess the relative importance of distance, geomorphic barriers and dams on the genetic structure and dispersal of a small-stream cyprinid (*Notropis lutipinnis*). Surprisingly, I found that gene flow was generally not inhibited by the larger river mainstem that was hypothesized to act as a barrier because of previously low capture rates of this species in the mainstem. In fact, I observed that populations in close proximity to the mainstem were well interconnected with substantial gene flow. This cyprinid may be more widespread and have higher dispersal capabilities in larger streams than previously hypothesized. Population genetics analysis showed that migrants into recently extirpated streams likely originated from populations higher in the watershed and sites closer to the extirpated stream, suggesting a stepping stone model of dispersal. However, I did find some evidence of downstream and upstream dispersal throughout the mainstem. Additionally, I found that a population occurring in a high-gradient stream tributary had relatively high divergence (more than expected by distance) from all other populations, indicating that this geomorphic feature may be important to include when predicting population connectivity throughout a watershed. Fine-scale population structure was expected in this species this species with limited dispersal, however our results may have been confounded by the number of polymorphic loci used, mutation model assumptions, potentially hidden alleles, and neutrality assumptions (loci not under selection). Additionally, microsatellite markers used and developed in this study will be used to evaluate whether the Flint population of *N. lutipinnis* is genetically divergent from populations neighboring basins, as previously suggested based on preliminary analysis of other markers (unpublished data). Results may elevate the status and conservation concern of this species within the unique and diverse Flint River basin.

Collectively, this research adds to the growing body of literature aimed at linking streamflow, geomorphology, and network structure with short- and long-term biotic responses and the development of flow-ecology linkages to better inform stream management decisions. Results from this dissertation contribute evidence that fish populations in larger tributaries are more resilient to changes in streamflow compared to populations in smaller tributaries and that larger stream tributaries may be particularly important as refugia and sources of colonizers to smaller tributary populations. To promote ecological resilience, ecologists must understandthe degree to which stream ecosystems can be altered before a large and irreversible shift in population states or assemblage structure occurs. Focusing on the resiliency of larger streams may prove useful for evaluating the impacts of extreme events on fish assemblages throughout a watershed. It may be possible to identify critical factors pushing species into alternative states by studying species' ability to recover to previous states and maintain genetic diversity despite adverse environmental conditions. Ultimately, understanding the interactions between the scales of species responses, scales of ecological processes, and scales of management should be a major goal of stream ecology.

APPENDIX A

CHAPTER 2

Example Bayesian model codefor the time-varying open robust design for a single age-class across one sampling year with four primary periods (n1) and three secondary periods (n2) within each primary period using data augmentation (M = captured individuals + augmented individuals).

```
model{
#####PRIORS – MODIFY TO INCLUDE FLOW-EFFECTS HERE#####
        for (t in 1:n2){time.p[t]          ~dunif(0,1)}
        for (t in 1:n1){gamma[t]           ~dunif(0,1)}
        for (t in 1:(n1-1)){time.phi[t] ~dunif(0,1)}
        for (i in 1:M){
                for (t in 1:(n1-1)){phi[i,t]       <-time.phi[t]}
                for (t in 1:n2){p[i,t]             <-time.p[t]}
        } # M
#####LIKELIHOOD#####
        for (i in 1:M){
                # First occasion, state process
                z[i,1] ~ dbern(gamma[1])
                # First occasion, observation process
                for (j in 1:nss[1]){
```

```
                mu1[i,j] <- z[i,1] * p[i,j]
                y[i,j]   ~ dbern(mu1[i,j])
            } # nss
            # Subsequent occasions
            for (t in 2:n1){
            # State process
            q[i, t-1] <- 1-z[i, t-1]                    # Availability for recruitment
            mu2a[i, t] <- phi[i, t-1] * z[i, t-1]       # Prob surviving to t given alive at t-1
            mu2b[i, t] <- gamma[t] * prod(q[i,1:(t-1)])    # Prob entering pop given available
            mu2[i, t] <- mu2a[i, t] + mu2b[i, t]
            z[i, t] ~ dbern(mu2[i, t])
            # Observation process
            for (j in 1:nss[t]){
                mu3[i,(cnss[t]+j)] <- z[i,t]*p[i,(cnss[t]+j)]
                y[i,(cnss[t]+j)]   ~ dbern(mu3[i,(cnss[t]+j)])
            } # nss
            } # n1
        } # M
##### CALCULATE DERIVED POPULATION PARAMATERS #####
        for (t in 1:n1){
        qgamma[t]     <- 1-gamma[t]
        } # n1
        cprob[1]        <- gamma[1]
```

```
        for (t in 2:n1) {
                cprob[t]            <- gamma[t]*prod(qgamma[1:(t-1)])
        } # n1
        psi<- sum(cprob[])                                  # Inclusion probability
        for (t in 1:n1){
                b[t] <- cprob[t]/psi                        # Entry probability
        } #n1
        for (i in 1:M) {
                recruit[i, 1] <- z[i, 1]
                for (t in 2:n1) {
                        recruit[i, t] <- (1-z[i,t-1])*z[i,t]
                } # n1
        } # M
        for (t in 1:n1) {
                N[t] <- sum(z[1:M,t])                       # Actual population size
                B[t] <- sum(recruit[1:M,t])                 # Number of entries
        } # n1
        for (i in 1:M) {
                Nind[i]   <- sum(z[i, 1:n1])
                Nalive[i] <- 1-equals(Nind[i], 0)
        } # M
        Nsuper<- sum(Nalive[])                              # Superpopulation size
##### CONVERT TO 30-d and 90-d SURVIVAL #####
```

```
        for (t in 1:(n1 -1)){phi.30d[t] <- 1-((1-time.phi[t])^time.between.n1[t])}
        phi.90d          <-phi.30d[1]*phi.30d[2]*phi.30d[3]
##### CONVERT TO CAPTURE AT LEAST 1x DURING 3-d SAMPLING #####
        p.primary[1]   <-       1-(1-time.p[1])*(1-time.p[2])*(1-time.p[3])
        p.primary[2]   <-       1-(1-time.p[4])*(1-time.p[5])*(1-time.p[6])
        p.primary[3]   <-       1-(1-time.p[7])*(1-time.p[8])*(1-time.p[9])
        p.primary[4]   <-       1-(1-time.p[10])*(1-time.p[11])*(1-time.p[12])
} # end model
```

APPENDIX B

CHAPTER 3

List of 20 alternative candidate models predicting the relative influence of streamflow, local habitat, reach geomorphology, and network position on changes in fish abundances.

Candidate model
Null
10-d maximum flow
10-d minimum flow
Sand + wood + maximum depth
Sand + wood + maximum depth + 10-d maximum flow
Sand + wood + maximum depth + 10-d minimum flow
Catchment area
Catchment area + 10-d maximum flow
Catchment area + 10-d minimum flow
Catchment area x 10-d maximum flow
Catchment area x 10-d minimum flow
Confinement
Confinement + 10-d maximum flow
Confinement + 10-d minimum flow
Confinement x 10-d maximum flow
Confinement x 10-d minimum flow
Dlink
Dlink + 10-d maximum flow
Dlink + 10-d minimum flow
Dlink x 10-d maximum flow

APPENDIX C

CHAPTER 4

Methods for developing and testing microsatellites for *N. lutipinnis* generally followed those outlined by Castoe et al. (2012). Tissue samples (whole fish and finclips) of *Notropis lutipinnis* were collected in the field, placed in 95% ethanol, and accessioned to the Georgia Museum of Natural History Tissue Collection (GMNHTC). We removed muscle tissue from the caudal peduncle of a single individual (GMNHTC No. 11921) for the development of new microsatellites.We extracted DNA from fish tissues using standard proteinase-K digestion followed by Purgene isolation buffer and two washes of ethanol precipitation at the final step. A total of 2.7 ug of DNA (20ul of a 140 ng ul^{-1} solution) was used to make an Illumina paired-end (IPE) shotgun library. Illumina sequencing was conducted on a HiSeq platform at Georgia Genomics Facility (University of Georgia). A total of 14.2 M Illumina reads were returned, sequence quality was checked using FastQC , adapters (overrepresented sequences) were clipped (3.7 M), and short sequences were removed (45,100), resulting in 1.4 M potential loci.

To extract potential microsatellite sequences and associated primer pairs, we used programs PALFINDER (Castoe et al. 2013) and Primer3 (version 2.0.0 Rozen and Skaletsky2000). Longer repeats (3-6mers) have high variability in many taxa (Bachtrog et al. 2000). Thus, we identified reads as microsatellites if they contained simple repeats of at least 12 bp in length for 2–4mers (e.g., 6 tandem repeats for dinucleotides), and at least 3 repeats for 5mers or 6mers. We selected an optimal primer size of 20 (min = 18 and max = 30) and optimal annealing temperature of 62^{o}C (min = 56^{o}C and max = 65^{o}C). Then, reads were sorted by the number of tandem repeats and only primer sets with PALS =< 10 reverse and forward primers were included in the candidate set, resulting in 139,532 potential microsatellite sequences. Primer pairs corresponding to microsatellites that included approximately 50% TC context were haphazardly selected (Bachtrog et al. 2000) and had greater than 100 bp but less than 400 bp were selected. The performance of selected potential primer pairs were initiallyevaluated using relatively inexpensive protocols with M13 Universal primers (Scheukle et al. 2000).We used two universal primers labeled with HEX and FAM fluorescent dyes (Applied Biosystems, Inc., Foster City, CA, U.S.A.) and a1:49 dilution. We used a 20ul reaction with 9.58ul of H_20, 4ul of 5x Buffer, 3ul of MgCL, 1.6ul of NTP, 0.08ul forward primer, 0.32ul reverse primer and 0.32ul of M13 universal primer, 0.1ulTaq, and 1ul of diluted (20–50 ng ul^{-1}) of DNA. Amplified products were separated using a Genetic Analyzer sequencer (3730XL, Applied Biosystems, Inc.) and sized using ROX500 size standard (Applied Biosystems, Inc.) in GeneMarker version 2.4.0 (Soft Genetics, LLC, State College, PA, USA).We screened a total of 48 microsatellite markers in 4 to 8 individuals (not including the individual from which the genomic library was constructed) and a negative control.All reactions were performed with an initial denaturation at 94^{o}C for 5 min, followed by 30 cycles of 94°C for 30 s, 56°C for 45 s (annealing temp), 72°C for 45 s, followed by 8 cycles of 94°C for 30 s, 53°C for 45 s and 72°C for 45 s, then final extension at 72°C for 10 min. We amplified each primer at annealing temperatures of 59 ^{o}C, 57 ^{o}C and 62^{o}C. Of the 48 markers, 69% (33/48) did not amplify consistently, 6% (3/48) were monomorphic, and 25% (12/48) were polymorphic. Of the 12 polymorphic markers, 3 demonstrated consistent amplification of fragments in an additional 8–12 individuals.Forward primers for these three markers were then ordered using fluorescent dyes (HEX and FAM) and used in population genetic analysis.

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