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Natal and intergenerational dispersal of riverine smallmouth bass (*Micropterus dolomieu*)

Robert Humston, Eric Hallerman, Scott Smith, Juli Sorenson, and Garrett Muckleroy

Abstract: Quantifying the scale of offspring dispersal is essential for understanding demographic connectivity across landscapes and rates of population spread. However, characterizing natal dispersal in fishes is complicated by the difficulties of tracking origins and movement during early life-history stages. We combined direct observation of natal dispersal based on otolith chemistry with indirect estimates of dispersal from population genetics to quantify intergenerational dispersal of smallmouth bass (*Micropterus dolomieu*) inhabiting a river network. Average parent–offspring dispersal was estimated as 7.7 km from genetic isolation-by-distance and demographic population data. Otolith chemistry indicated that adults were captured an average of 8.3 km from their natal tributary, supporting the genetics-based estimate. Our estimate of intergenerational dispersal is higher than previous estimates for lotic fishes and considerably higher than estimates for smallmouth bass in lake systems. Differences in availability of seasonal habitats for smallmouth bass may account for the contrasting scales of dispersal between lake and river populations. The large intergenerational dispersal distance of riverine smallmouth bass should be considered in conservation of fisheries or efforts to control invasive populations in river networks.

Résumé : La quantification de l'échelle de la dispersion de la progéniture est nécessaire pour comprendre la connectivité démographique des paysages et les taux de propagation des populations. La caractérisation de la dispersion natale chez les poissons est toutefois compliquée par les difficultés que pose la détermination des origines et des déplacements durant les premières étapes du cycle biologique. Nous avons combiné l'observation directe de la dispersion natale basée sur la chimie des otolites à des estimations indirectes de la dispersion reposant sur la génétique des populations afin de quantifier la dispersion intergénérationnelle d'achigans à petite bouche (*Micropterus dolomieu*) dans un système fluvial. La dispersion parent–progéniture moyenne est estimée à 7,7 km à partir de données sur l'isolement par la distance et de données démographiques sur la population. La chimie des otolites indique que les adultes ont été capturés en moyenne à 8,3 km de leur affluent natal, ce qui appuie l'estimation basée sur la génétique. Notre estimation de la dispersion intergénérationnelle est plus élevée que les estimations antérieures pour des poissons lotiques et considérablement plus élevée que les estimations pour des achigans à petite bouche dans des systèmes lacustres. Des différences de disponibilité d'habitats saisonniers pour l'achigan à petite bouche pourraient expliquer les différentes échelles de dispersion des populations de lacs et de rivières. La grande distance de dispersion intergénérationnelle des achigans à petite bouche de rivière devrait être prise en compte dans la conservation des ressources halieutiques et dans les efforts de contrôle de populations envahissantes dans les réseaux fluviaux. [Traduit par la Rédaction]

Introduction

Understanding the scale of intergenerational dispersal in populations provides important information for species management and conservation planning. While natal dispersal is the movement of an individual from its birth site to its breeding site (Stenseth and Lidicker 1992), intergenerational dispersal is the spatial extent of natal dispersal of all offspring of a breeding pair. The dispersal process determines the effective connectivity of habitats and subpopulations and has important implications for projecting the effects of spatially directed management actions, such as the desired recruitment "spillover" from protected areas to fished or hunted areas (Kininmonth et al. 2011; Palumbi 2004) or conservation of metapopulations (Hanski 1999; Botsford et al. 2001). Determining the extent of intergenerational dispersal also can be useful for predicting rates of gene flow and colonization of new habitats, as might be the case for anticipating the spread of introduced species (e.g., Stoeckel et al. 1997) or recolonization of previously degraded habitats following restoration (Bond and Lake 2003; Hughes 2007).

Measuring intergenerational dispersal is difficult for most wild populations. This is particularly true for fish populations due to the challenges of tracing movement through early life history, when locating or marking individuals may be impossible. Natural tags, such as chemical signatures recorded in fish "hard parts" like otoliths, can provide inference on natal origins under appropriate conditions of spatial heterogeneity, temporal persistence, and reliable incorporation of site-specific chemistry (Elsdon et al. 2008; Pracheil et al. 2014; Carlson et al. 2017). Spatial variation in elemental isotopic ratios such as $^{87}Sr/^{86}Sr$ often provide

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conditions that allow retrospective reconstruction of individual movement histories by comparison of chemical records with spatial maps (isoscapes) of isotopic variation (Bataille and Bowen 2012; Hegg et al. 2013). This approach can provide an opportunity to observe and estimate natal dispersal, including average extent and individual variation in dispersal distance — both of which are important for understanding short- and long-term rates of population expansion and connectivity (Clobert et al. 2009). However, this approach cannot provide direct inference on genetically effective dispersal and gene flow unless it can be coupled with knowledge of individual reproductive success.

Genetic approaches such as kinship or parentage analysis as well as differentiation-by-distance can provide inference on gene flow and indirect measures of natal or intergenerational dispersal. Kinship and parentage analysis may provide substantial information on the scale and variation of dispersal among offspring of a parent or mating pair (Hudy et al. 2010; Morrissey and Ferguson 2011; Roberts et al. 2016). However, this approach may provide limited insight on average gene flow and intergenerational dispersal if relatively few sibling cohorts or generations are analyzed or if the spatial extent of the study area is too narrow. Patterns of pairwise genetic differentiation between populations or individuals across a range of distances can provide direct inference on gene flow and, when coupled with data on density of reproductive adults, can provide an indirect estimate of average intergenerational dispersal distance across the study area (Rousset 2000). Combining direct estimates of natal dispersal with an indirect estimate of intergenerational dispersal potentially can provide comprehensive insight into the individual and population scales of parent–offspring dispersal.

Smallmouth bass (*Micropterus dolomieu*) is an important gamefish across eastern North America and elsewhere that has been widely introduced (Brewer and Orth 2015). Its spatial ecology provides an interesting system for study of intergenerational dispersal. Adult smallmouth bass migrate annually between warm- and cold-season home ranges, which typically do not overlap with adult nesting sites (Ridgway et al. 2002). Males build nests in suitable substrate, attract females to lay their eggs there, and after fertilization guard the eggs and fry through yolk-sac resorption and dispersal of the young. Males may exhibit strong nest-site fidelity, nesting within 20 m of their previous year's nest (Ridgway et al. 1991; Barthel et al. 2008). Inference from genetic analyses suggest that smallmouth bass may be philopatric, and males may nest in close proximity to their natal location via natal site homing (Gross et al. 1994; Stepien et al. 2017). Ridgway et al. (2002) suggest that establishment of adult home ranges is strongly influenced by density-dependent processes and dispersal during the mid-juvenile period (termed the "Juvenile Transition Hypothesis"). Much of the evidence documenting this spatial ecology is derived from studies in lake or adfluvial populations. Smallmouth bass in river networks are known to move among habitat types both seasonally (Todd and Rabeni 1989; Langhurst and Schoenike 1990; Westhoff et al. 2016) and ontogenetically (Probst et al. 1984; Sabo and Orth 1994; Humston et al. 2010, 2017). Smallmouth bass in river systems may migrate upstream to tributaries to minimize risks of nest failure due to washout in high flows or to nest predation (Lyons and Kanehl 2002). Reproductive homing of smallmouth bass in river systems, however, is as yet uncharacterized.

Spatially directed management of fisheries tends to be oriented around jurisdictional and geographic (e.g., lake or river) boundaries; however, the spatial ecology of a population may not be similarly constrained. Demographic connectivity of populations in mainstem–tributary networks is increasingly recognized as important in conservation of lotic fisheries and river biodiversity (Pracheil et al. 2013; Spurgeon et al. 2018). Likewise, management of invasive or expanding populations must consider spatial ecology for predicting impacts or directing control measures. Loppnow and Venturelli (2014) demonstrated that interventions to control invasive smallmouth bass populations should focus on removals of young-of-the-year — thus the spatial structure of recruitment connectivity and intergenerational dispersal among river networks is of paramount importance for directing such efforts and determining their potential effects on population growth and expansion.

In this study, we combine natural trace-element and genetic markers to estimate the scale of natal and intergenerational dispersal in smallmouth bass inhabiting a river–tributary network. These two methods provide complementary insight into population connectivity (Lowe and Allendorf 2010); population genetics integrates movement over intergenerational timescales, while otolith microchemistry documents movement patterns within the lifespan of an individual. Our study area in the James River basin of Virginia provides an opportunity to assess genetic structure in an established population, while the geologic heterogeneity of the basin provides a unique setting for analyzing otolith microchemistry to discern natal origins using strontium isotopic ratios (Humston et al. 2017).

Materials and methods

Study system and fish collections

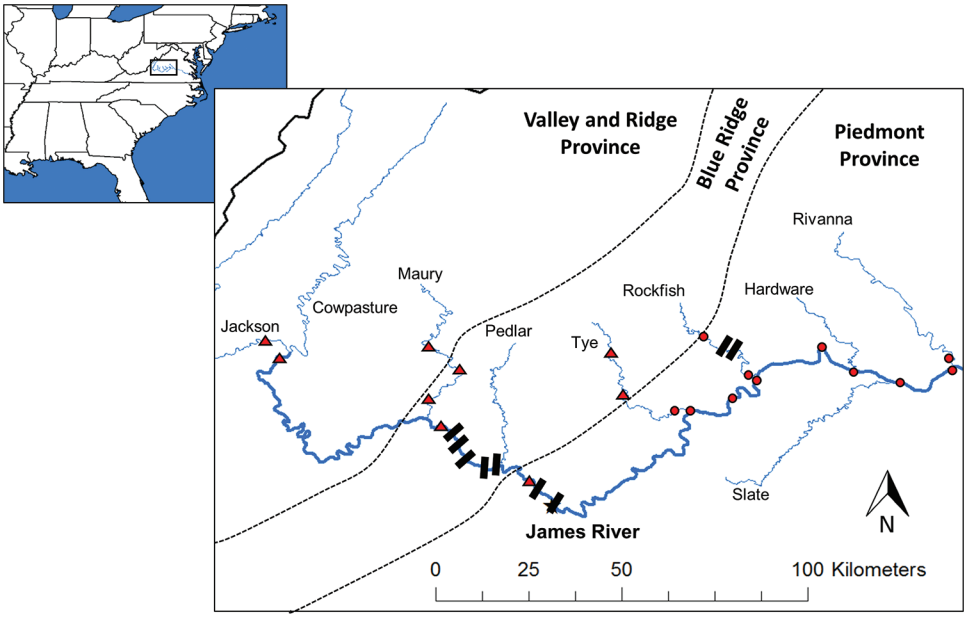
Our study system was the non-tidal region of the James River basin within the Commonwealth of Virginia in the eastern United States. The James River is formed by the confluence of the Jackson and Cowpasture rivers in the western Valley and Ridge physiographic province of Virginia. The river flows eastward through the Blue Ridge and Piedmont provinces for roughly 360 km before passing through the "fall line" demarcating the upper Coastal Plain and tidal-influenced reaches of the river. Several run-of-river dams coinciding with the eastern slope of the Blue Ridge Mountains separate what are commonly referred to as the upper (montane) and middle (Piedmont) sections of the basin, with the lower section beginning at the fall line. Smallmouth bass were introduced into this basin in 1871 (Jenkins and Burkhead 1994) and now support highly popular fisheries throughout the river and its larger tributaries. The mainstem James River population is managed to provide trophy fishing opportunities and ranks among the state's flagship recreational fisheries.

Smallmouth bass were collected from seven locations in the middle James River and from four tributaries (Fig. 1) using boat-mounted electrofishing equipment in 2011–2013. Tissue samples (pelvic fin clips) were collected from all fish and preserved by freezing at −80 °C; otoliths also were removed and stored dry in polyethylene vials after cleaning. All collections were conducted in accordance with protocols approved by the Washington and Lee University Institutional Animal Care and Use Committee and under scientific collection permit number 60033 issued by the Virginia Department of Wildlife Resources. Additional tissue samples from earlier collections from three mainstem sites and two tributaries in the upper basin (Hallerman et al. 2015) expanded the spatial coverage of the genetic analysis.

Genetic analysis and indirect estimate of dispersal

We digested tissue samples and extracted DNA using DNeasy Blood and Tissue Kits (Qiagen, Inc., Germantown, Maryland, USA). Extracts were examined by ultraviolet spectrophotometer (Nanodrop 1000, Thermo Fisher Scientific, Waltham, Massachusetts, USA) to quantify DNA and determine quality. Samples were screened at fifteen microsatellite loci: *Mdo1*, *Mdo2*, *Mdo3*, *Mdo4*, *Mdo5*, *Mdo6*, *Mdo7*, *Mdo9*, *Mdo10*, and *Mdo11* from Malloy et al. (2000) and *MiSaTPW011*, *MiSaTPW057*, *MiSaTPW060*, *MiSaTPW076*, and *MiSaTPW096* from Lutz-Carrillo et al. (2008). PCR and fragment-size analysis were completed at the University of Arizona Genetics Core Laboratory (Tucson, Arizona, USA). Microsatellite loci were visualized using an ABI3730 DNA Analyzer (Applied Biosystems, Foster City, California, USA) and scored using Genemarker

Fig. 1. Study area, with sampling locations, major tributaries, and approximate boundaries of physiographic provinces. Dams are indicated as black rectangles oriented perpendicular to rivers. Circles indicate sampling locations where genetic and otolith samples were collected; triangles indicate collections of tissue samples only. Inset map shows the geographic location of the study area. Maps prepared using ArcMap 10.4 (Esri 2011) with data from the National Hydrography Dataset (USGS 2019) and the Esri US states boundaries map (Esri 2018). Physiographic province boundaries are approximated from US Geological Survey digital geologic map data for Virginia (Dicken et al. 2005). Sampling and dam locations were mapped from field data.



1.85 software (SoftGenetics, State College, Pennsylvania, USA). All allele scores were checked for accuracy by eye prior to compilation for data analysis. Genotype data were assessed for errors and presence of null alleles using Micro-Checker software (Van Oosterhout et al. 2004). In addition, data were examined for deviations from Hardy–Weinberg equilibrium and linkage equilibrium using GENEPOP (Raymond and Rousset 1995; Rousset 2008) at the $\alpha = 0.05$ level with appropriate Bonferroni correction for multiple tests.

We analyzed genotype data using the program STRUCTURE (Pritchard et al. 2000) to assess multilocus genotypic clusters within the data within mainstem and tributary collections. We used the Admixture model with the LOCPRIOR option applied; each model run utilized a burn-in of 10 000 runs and 30 000 replicate run length. This was repeated five times for all values of K between 1 and 10. The best-supported number of clusters (K) in the data was evaluated based on inference from the Ln $P(D|K)$ metric in STRUCTURE output as well as the delta-K metric (Evanno et al. 2005) as implemented in the program STRUCTURE HARVESTER (Earl and Von Holdt 2012). Individual assignments were used to assess the spatial distribution of clusters (i.e., spatial population structure) within the basin.

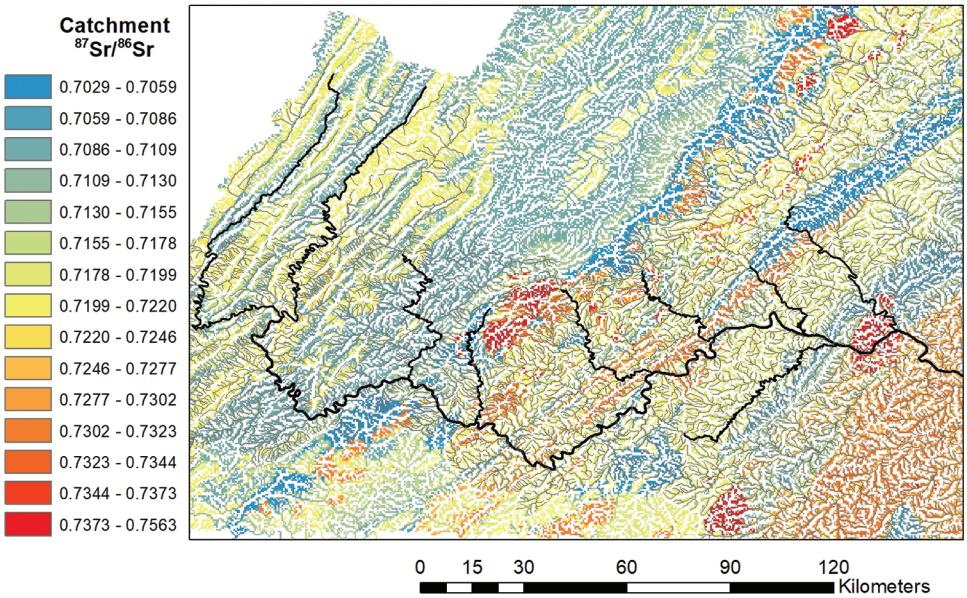
We also analyzed genotype data for evidence of isolation-by-distance by regressing estimated genetic distance on geographic distance (watercourse distance in km) between sampling locations. Pairwise genetic distances between collection locations were quantified as $F_{st}/(1 - F_{st})$ using methods implemented in the program GENEPOP (Raymond and Rousset 1995; Rousset 2008). The correspondence of pairwise genetic and geographic distance matrices was assessed using Mantel tests in the R package VEGAN, calculated using the Spearman rank-based statistic and with significance assessed by permutation (Oksanen et al. 2019; R Core Team 2019). The slope of the relationship between genetic and geographic distances was calculated by linear regression. This slope was used to estimate the scale of natal dispersal (or parent–offspring dispersal) using the method described for linear habitats by Rousset (1997) and applied in recent studies (e.g., Puebla et al. 2009; Comte and Olden 2018). The average parent–offspring dispersal distance σ can be estimated by

$$(1) \qquad \sigma = \sqrt{\frac{1}{4D_e m}}$$

where D_e is the effective population density (breeding adult density), and m is the slope of the relationship between genetic and geographic distances determined by regression. We were able to obtain direct estimates of smallmouth bass adult population density from quantitative sampling conducted by the Virginia Department of Wildlife Resources (VDWR; formerly Virginia Department of Game and Inland Fisheries) in the James River (Odenkirk and Smith 2005). Multiple-pass removal sampling was conducted at four specific locations in the middle and upper James River in 2002 and 2007 (VDWR, unpublished data). To calculate an average population density ($N \cdot km^{-1}$), we first averaged density between years at each depletion sampling location. We then calculated the mean and standard deviation of average density across all sampling locations.

To estimate the density of breeding adults D_e, we used age and growth data collected annually by VDWR in 1997–2001 and again in 2005 to determine the proportion of adults in the population. In the James River, smallmouth bass typically reach reproductive maturity at age 3 (VDWR, unpublished data). We further assumed a 50:50 sex ratio in the population. However, adult breeding activity and success in smallmouth bass populations is modulated by interacting biotic and abiotic factors, which makes it difficult to estimate the mean proportion of breeding adults (Pr_{breed}) annually. Raffetto et al. (1990) observed that the percentage of adults breeding in Nebish Lake ranged from 11%–33% annually for males and 16%–45% for females. However, this may be strongly influenced by density-dependent competition (Ridgway et al. 1991). Moreover, recent research suggests smallmouth bass mating is primarily monogamous (Franckowiak et al. 2017); therefore, Pr_{breed} may be determined primarily by male nesting success.

Fig. 2. Map of the study area with a superimposed $^{87}Sr/^{86}Sr$ isoscape generated using information on geologic composition following Bataille and Bowen (2012). The sections of the James River and major tributaries considered in this study are depicted by bold black lines. Map prepared using ArcGIS 10.1 (Esri 2011) with river mapping data from the National Hydrography Dataset (USGS 2019) and geologic data for Virginia (Dicken et al. 2005).



Streamflow has a strong influence on nest success in rivers, and flow variation during the spawning season can cause high rates of nest failure (Winemiller and Taylor 1982; Lukas and Orth 1995; Knotek and Orth 1998). Cooke et al. (2003) summarized previous studies reporting nest success rates ranging from 0%–83% in river populations with a mean of 51.8% (±SD = 9.9%). To capture the potential range of average Pr_{breed} in the James River system, we calculated D_e based on low (Pr_{breed} = 0.15), mid-range (Pr_{breed} = 0.3), and high (Pr_{breed} = 0.6) estimates for proportion of breeding adults. Respectively, these correspond roughly to high density–dependence and average flow-induced nest failure; mid-range density dependence and average nest failure; and low density dependence and average nest failure.

To assess how parameter uncertainty may influence our estimate of σ, we applied a resampling approach of generating random values for each parameter and recalculating σ in eq. 1 repeatedly. The slope parameter m was resampled from a normal distribution using the mean and standard error of the slope coefficient estimated from the genetic-geographic distance regression described above. Population density was resampled from a normal distribution using the mean and standard deviation of density observed from depletion sampling. Resampled parameter values were then applied to low, mid-range, and high estimates of Pr_{breed} to calculate σ. Resampling was repeated 10 000 times to generate a range of corresponding values of σ for each estimate of Pr_{breed}.

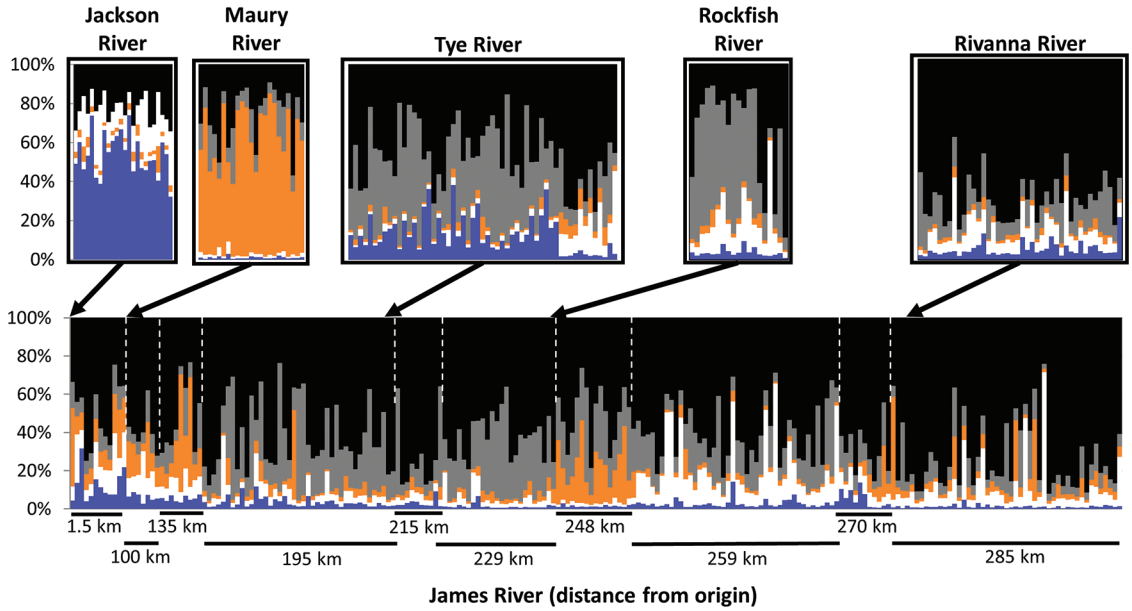
Direct estimates of dispersal distance

In a previous study (Humston et al. 2017), otolith samples from our collections in the middle basin were used to assess the degree of recruitment exchanged between the mainstem James River and its major tributaries in the Blue Ridge and Piedmont physiographic provinces. That study documented significant differences in strontium isotopic composition between tributaries and mainstem locations, characterized by higher levels of radiogenic ^{87}Sr in tributaries and thus higher $^{87}Sr/^{86}Sr$ ratios. Mainstem sampling locations were highly consistent in $^{87}Sr/^{86}Sr$, and thus only tributary–mainstem distinctions were possible. This contrast allowed straightforward determination of whether a specific fish was spawned in a tributary or mainstem habitat. That study also utilized methods proposed by Bataille and Bowen (2012) and Bataille et al. (2014) to map the $^{87}Sr/^{86}Sr$ "isoscape" of the basin and estimate the $^{87}Sr/^{86}Sr$ of a given sub-basin and waterbody (Fig. 2). The isoscape map provided a resource for approximating the likely origin of fish when their otolith $^{87}Sr/^{86}Sr$ could not be matched with any known isotopic composition of rivers from water sample analysis.

For the current analysis, we leveraged this methodology to generate observations on individual natal dispersal using otoliths from individual smallmouth bass collected from the middle James River. We first identified all smallmouth bass captured from the mainstem sampling locations whose otolith core $^{87}Sr/^{86}Sr$ indicated natal origins in tributary habitats ($^{87}Sr/^{86}Sr > 0.712$, as described in Humston et al. 2017). Age was estimated from otolith annuli, and sex was determined by visual inspection of gonads in mature adults. Next, we attempted to match their otolith core $^{87}Sr/^{86}Sr$ with a corresponding value from the major tributaries analyzed in water samples; a match was considered suitable when water $^{87}Sr/^{86}Sr$ fell within ±0.0005 of otolith $^{87}Sr/^{86}Sr$. Where a matching tributary could not be found among known water $^{87}Sr/^{86}Sr$, or when the best-matching tributary was a significant distance from the collection location (>10 km), we used an $^{87}Sr/^{86}Sr$ isoscape map overlain with polylines of persistent tributaries to identify the potential rivers of origin for each fish proximate to the collection location. In each case, we took the conservative approach of choosing the tributary *closest* to the sampling location with a reasonably matching $^{87}Sr/^{86}Sr$ when approximating natal origins. Smallmouth bass are known to utilize smaller tributaries for spawning (Lyons and Kanehl 2002); therefore, we considered any persistent tributary of Strahler order 2 or higher to be potential spawning locations. Ephemeral and intermittent streams were excluded from consideration.

Dispersal distance was calculated as watercourse distance (km) between the putative natal river and the collection location of the fish. This conservative approach provided inference on the scale of movement undertaken by an individual since birth. We

Fig. 3. Individual assignment results from analysis of microsatellite data using STRUCTURE for the best-supported (K = 5) number of multilocus genotypic clusters. Tributary samples are shown in separate panels above the James River samples, ordered from upstream to downstream (left to right) with arrows indicate their approximate position relative to sampling sites on the James River. Vertical dashed lines in the James River sample indicate separation of sampling locations. The dominant cluster (black) has its strongest presence in the mainstem James River and the downstream-most tributary Rivanna River. The gray cluster is most associated with the middle tributaries Rockfish River and Tye River, with significant admixture in the mainstem James River. The orange and blue clusters correspond to Maury and Jackson river collections, respectively.



separated juveniles and adults during analyses; collections took place shortly after the spawning season, so adult capture locations likely were influenced by the location of their spawning site, and thus this approach provides inference on natal dispersal. The dispersal distance of juveniles would not be considered an estimate of natal dispersal and is provided for comparative purposes. As $^{87}Sr/^{86}Sr$ of the mainstem James River does not vary consistently across our study area, we could not use this method to assess dispersal distance of fish spawned in the mainstem river. However, the estimates of individual dispersal afforded by otolith isotope data provide an opportunity for comparing our indirect estimate of average parent–offspring distance σ with direct observations on natal dispersal within the same study area (e.g., Broquet et al. 2006).

We also reviewed other studies on smallmouth bass population genetics as well as mark–recapture and telemetry studies in riverine habitats for comparison of our results to observations from other systems. Smallmouth bass are known to occupy different habitats for spawning (spring), summer, and winter seasons (Lyons and Kanehl 2002; Ridgway et al. 2002) and in some cases undertake substantial migrations between seasonal habitats (Langhurst and Schoenike 1990; Lyons and Kanehl 2002; Westhoff et al. 2016). Therefore, we restricted our review of movement studies to only those where movement was observed over a period that encompassed these three seasons.

Results

We obtained otolith and tissue samples from 220 smallmouth bass age 1 and older collected from the middle James River and four of its major tributaries (Rivanna, Hardware, Rockfish, and Tye rivers; see Fig. 1). As described in Humston et al. (2017), most of these collections were located within 2 km of mainstem–tributary confluences to maximize likelihood of observing evidence of exchange between these rivers in otolith isotopic chemistry. Three mainstem sampling sites were located several kilometres from confluences. A total 169 additional fin-clips were collected from sampling (this study) in the upper Tye River and from historical collections (Hallerman et al. 2015) in the upper James River and tributaries (Maury and Jackson rivers). Thus, a total of n = 389 tissue samples was processed for microsatellite amplicon length analysis across the upper and middle James River basin. A subset of otolith samples (n = 209) was analyzed for inference on natal origins and dispersal between rivers (Humston et al. 2017).

Genetic analyses

Screening of genetic data with MicroChecker did not indicate the segregation of null alleles, while GENEPOP analyses indicated that genotype frequencies at three loci (*Mdo1*, *Mdo11*, and *MisaTPW011*) did not conform to expectations of Hardy–Weinberg equilibrium. We analyzed the data with and without these loci and the results were not substantively different, and therefore present the outcomes of analyses with these loci retained. STRUCTURE analyses indicated best support for K = 5 admixed genetic "clusters" within our study area, as determined by both the $\mathrm{Ln}P(D|K)$ and ΔK metrics. These clusters appear to correspond to differentiated populations in the respective tributaries, with admixture of different contributions from these clusters in the mainstem samples (Fig. 3). The degree of admixture from tributary-specific clusters in mainstem samples generally diminishes with distance from tributary confluences. Thus, our results present evidence for tributary–mainstem differentiation in genetic structure spatially along the basin. The longitudinal genetic structure in the mainstem river is apparent as intra-river dispersal and admixture of tributary and mainstem demes. Mantel tests indicated a positive correspondence between matrices of genetic and geographic distances between sampling locations (P = 0.048; r = 0.2652). Regression results further revealed a pattern of weak genetic isolation by geographic distance (Fig. 4; P = 0.013; R^2 = 0.032); the slope of the regression line was $m = 9.98 \times 10^{-5}$ ($\pm$SE = 3.98×10^{-5}).

Fig. 4. Pairwise genetic and geographic distances between sampling locations, with dashed line showing the regression line, $y = (9.98 \times 10^{-5})x + 0.03$ ($P = 0.013$; $R^2 = 0.032$).

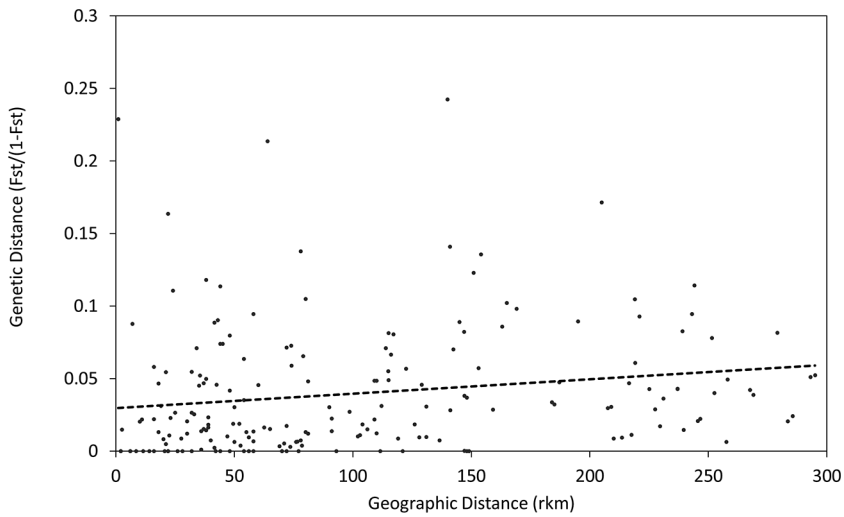


Table 1. Variables estimated in this and other studies that were used in calculation of intergenerational dispersal.

Variable (symbol)	Estimated value	SD or SE
IBD regression slope (m)	9.98×10^{-5}	3.98×10^{-5} SE
Smallmouth bass density	756.8 per km	318.9 SD
Percentage of adults (≥age 3) in population	19.1%	10.4% SD
Percentage of adults breeding annually (Pr_{breed})	Low = 15% Mid-range = 30% High = 60%	

Estimates of dispersal distance

Population estimates indicated that average abundance across all ages was 756.8 (±SD = 318.9) smallmouth bass per kilometre (Odenkirk and Smith 2005; VDWR, unpublished data) and age-structure data indicated that on average 19.1% (±SD = 10.4%) of the population was age 3 or greater. This indicates average D_e values of 21.7, 43.4, and 86.7 breeding adults per kilometre corresponding with our low, mid-range, and high estimates of Pr_{breed}. These values of D_e combined with the slope from the regression of pairwise genetic–geographic distances between collection locations ($m = 9.98 \times 10^{-5}$), allow us to estimate mean parent–offspring dispersal distance of σ = 10.8, 7.6, and 5.4 km. Resampling parameter values (Table 1) and recalculating to address uncertainty produced σ values ranging from 1.7–979.1 km (Fig. 5). The distribution of σ values calculated in this resampling approach was asymmetrical with positive skewness.

Otolith chemistry analyses revealed a substantial amount of inter-river movements within the middle James River basin, as detailed in Humston et al. (2017). Among 146 smallmouth bass collected from mainstem sampling locations analyzed, 39 were spawned in tributaries based on otolith core $^{87}Sr/^{86}Sr$. We selected 8 adults and 19 juveniles for which the tributary of natal origin could be determined with reasonable confidence. In some cases, uncertainty in exact $^{87}Sr/^{86}Sr$ natal signature resulted from ablation rasters that were oriented slightly off-center from the otolith core, or where fissures in the polished surface led to ablation of material below the polished surface; see Humston et al. (2017) for details. The distance between the known collection location and each adult's putative natal tributary ranged from 0.5–25 km, with mean 8.3 km (SD = 9.1 km). For juveniles, this distance ranged from 1–30 km with a mean of 13.1 km (SD = 8.8 km); comparison by t test indicated no significant difference in average dispersal distance between juveniles and adults.

Discussion

Our indirect and direct estimates of dispersal distance agree well and indicate substantial intergenerational dispersal in this riverine smallmouth bass population. Genetic analysis demonstrated spatial structure among smallmouth bass populations of the James River basin influenced by tributary–mainstem differentiation and a pattern of isolation-by-distance. The latter suggests that the average parent–offspring dispersal distance (σ) is on the order of 8 km. This corresponds well with the scale of natal dispersal observed (and conservatively estimated) from otolith $^{87}Sr/^{86}Sr$ in adults in our sample (mean = 8.3 km). Previous studies monitoring smallmouth bass movement reported mean dispersal distance from 0.5–24.6 km (mean = 4.9 km, SD = 7.7 km) and maximum observed movements ranging from 3.5–118.0 km (mean = 25.4 km, SD = 38.3 km; Table 2). Thus, our direct and indirect estimates of dispersal distance are squarely within the range of smallmouth bass dispersal distances reported from other river systems. The timescale underlying average parent–offspring dispersal distance is the population generation time (sensu Caughley 1977). Lacking life-table data to calculate generation time, a rough estimate based on our assumed age at maturity (age 3) and observed maximum age in our data (age 8) would indicate generation time is on the scale of approximately 4 years in this population.

The results of STRUCTURE analysis indicated a pattern of genotypic clustering in certain tributaries such as in the Jackson, Maury, and Rockfish rivers, with admixture of these clusters in the mainstem James River (Fig. 3). This finding agrees with those of a previous analysis which found that 26%–30% of smallmouth bass collected in the James River originated from spawning in tributaries (Humston et al. 2017). Generally, the degree of admixture appears to attenuate with distance from the corresponding tributary (e.g., as for the Jackson River "blue" cluster). However, the Maury River (orange) cluster makes up a significant proportion of individual assignments at mainstem sampling locations located at 135, 248, and 285 rkm. This discrete pattern is suggestive of "nascent foci" resulting from past long-distance dispersal by a relatively small number of individuals, rather than a long-term pattern of multi-generational geneflow from this tributary (Moody and Mack 1988). This supports the view that dispersal distances within the mainstem James River can be substantial. These mainstem

Fig. 5. Violin plots with inset boxplots summarize the distribution and range of values calculated for parent–offspring dispersal distance (σ) using resampling approaches to address parameter uncertainty. Outlier points are removed from boxplots to avoid obscuring upper extent of violin plots. The solid gray horizontal line indicates the mean dispersal distance estimated from otolith chemistry for adult smallmouth bass; the dashed line indicates the dispersal distance estimated for juveniles.

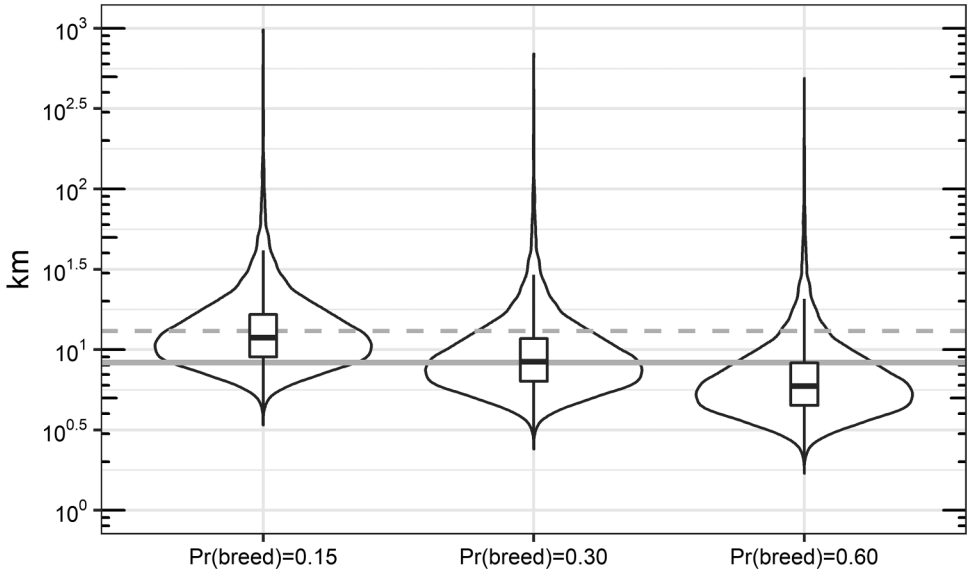


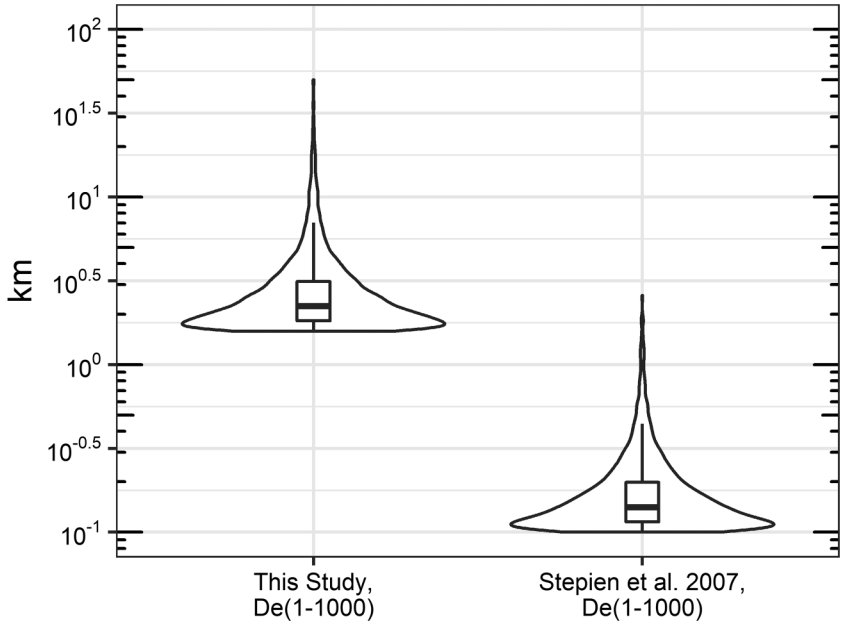
Table 2. Mean and maximum dispersal distance reported in mark–recapture and radio telemetry studies on smallmouth bass movement ("—" indicates not reported).

Study method	Length of study (days)	Sample Size	Mean dispersal distance (km)	Maximum dispersal distance (km)	Reference
Telemetry	361	24	0.43	29.44	Altena 2003
	365	29	—	42.50	Westhoff et al. 2016
	365	15	0.40	3.50	Gunderson VanArnum et al. 2004
	365	39	5.30	23.40	Gunderson VanArnum et al. 2004
	722	14	0.05	0.37	Beam 1990
	311	4	4.10	7.10	Bunt et al. 2002
	365	84	24.6	118.0	Schall et al. 2019
Mark–recapture	214	130	0.28	—	Munther 1970
	3650	109	5.39	—	Funk 1957
	326	66	—	0.87	Fajan 1962
	449	18	3.79	30.58	Brown 1961

locations where the Maury River cluster appears are separated from the Maury River confluence by seven run-of-river dams (Fig. 1). This also suggests that these barriers are passable in the downstream direction by smallmouth bass. Downstream passage potential is supported by observations of downstream passage by muskellunge (*Esox masquinongy*) in an ongoing mark–recapture study in the James River basin (VDWR, unpublished data).

Our analysis represents the first documentation of isolation-by-distance and corresponding estimate of σ for smallmouth bass in an exclusively lotic system. Previous studies of lacustrine populations (Stepien et al. 2007, 2017; Euclide et al. 2020) reported much stronger patterns of isolation-by-distance, suggesting smaller scales of intergenerational dispersal. These studies considered broader geographic scales encompassing native populations in the Great Lakes and upper Mississippi basin with varying degrees of connectivity among populations. All three studies revealed patterns of isolation-by-distance at scales ranging from a single lake basin (Lake Erie, Lake Michigan) to multiple lake and river collections encompassing broader areas. For comparison with this study, only the analysis by Stepien et al. (2007) that focused solely on Lake Erie offers similar distance and connectivity among sampling locations as well as information sufficient to calculate an estimate of σ (see figure 3*b* in Stepien et al. 2007). Their regression of geographic and genetic distances showed a slope of m = 0.0119, which is roughly two orders of magnitude greater than that found in our study ($m = 9.98 \times 10^{-5}$; SE = 3.98×10^{-5}). Their slope estimate can be applied in calculations for dispersal in two-dimensional habitats (Rousset 1997) to generate an estimate of σ for comparison with ours. Lacking data on adult density in their study system, we follow the example of previous authors (Kinlan and Gaines 2003; Comte and Olden 2018) and calculate σ using a range of values for D_e randomly selected from a uniform distribution from 1 and 1000 individuals per kilometre. Applying this approach to their estimate of slope and ours allows for direct comparison of the resulting distribution of dispersal distances (Fig. 6). This produced values for σ between 0.08 and 1.83 km with a mean of 0.15 km using the slope value m = 0.0119 estimated by Stepien et al. (2007). By comparison, our estimate of slope $m = 9.98 \times 10^{-5}$ produced σ values between 1.6 and 50.1 km with a mean of 3.1 km. This suggests that the scale of intergenerational dispersal is

Fig. 6. Violin plots with inset boxplots comparing σ calculated from slope parameter (m) estimates determined in this study and in Stepien et al. (2007) using values of adult density randomly selected from a uniform distribution ranging from 0–1000 adults·km^{-1}.



significantly smaller for smallmouth bass populations in lake systems than in rivers. Alternatively, this observation could also be a result of differences between native and nonnative populations. Lake Erie falls within the native range of smallmouth bass and the study by Stepien et al. (2007) focused on indigenous populations with no known history of stocking from hatcheries. By contrast, the James River basin falls outside the native range of smallmouth bass and the population was established through stocking within the last 170 years (Jenkins and Burkhead 1994). Thus, the weaker pattern of isolation-by-distance in the James River in part may be a result of a lack of time for spatial differentiation to fully develop within the system.

Our study highlights a potential difference between riverine and lacustrine natal and intergenerational dispersal in smallmouth bass populations despite evidence of large dispersal distances in both systems. One hypothesis to explain the contrast in patterns between lake and river population genetics is that natal site fidelity is less common in lotic smallmouth bass and therefore does not act as a constraint upon natal and intergenerational dispersal distance as postulated for lake populations. Both Stepien et al. (2007) and Euclide et al. (2020) noted that the degree of differentiation documented in their respective systems was unexpected given previous observations on long-range movements (e.g., Ridgway and Shuter 1996; Kaemingk et al. 2011) and the high degree of connectivity among their sampling sites. Both studies hypothesized that a combination of patchily distributed spawning habitat and high site fidelity among adults contributed to the pattern of differentiation they observed. Stepien et al. (2007) further suggested this could be reinforced by a tendency for adults to return to their natal sites for spawning. Natal homing also was suggested by Gross et al. (1994) as a mechanism underlying the pattern of philopatry inferred from DNA "fingerprinting" of smallmouth bass from Lake Opeongo, Ontario. To our knowledge, natal homing has not been confirmed by direct observation of smallmouth bass movement.

In the James River basin, spawning habitat is widespread and would not be considered a limiting resource; therefore, it may not be a strong factor structuring spatial ecology and movement patterns in this and other river populations. Dispersal and migratory movements in rivers may be influenced by a combination of seasonal changes in hydrology (e.g., Hafs et al. 2010) and heterogeneous distribution of thermal habitat (particularly overwintering habitat; Westhoff et al. 2016). Seasonal habitats may be more sparsely distributed than spawning habitat, and therefore may be more important for determining spatial structure. Studies in river systems have demonstrated that smallmouth bass may undertake substantial annual migrations between seasonal habitats (Langhurst and Schoenike 1990; Lyons and Kanehl 2002). Westhoff et al. (2016) documented movements as far as 42.5 km between winter and spring habitats, and Schall et al. (2019) observed seasonal movements up to 118 km between tributary and mainstem habitats. Thus, while spawning habitat may be patchily distributed in lakes (as suggested by Stepien et al. 2007), other seasonal habitats may be more widely distributed and thus require less migration distance between them — or shorter dispersal distances to locate them when an individual first establishes its seasonal home ranges. In contrast, an abundance of spawning sites in rivers might discourage natal site fidelity, while heterogeneous distribution of other seasonal habitats could lead to greater "ranging" distances in search of seasonal habitats and subsequently higher rates of natal dispersal and greater parent–offspring dispersal distances in riverine populations.

A recent synthesis by Comte and Olden (2018) reviewed direct and indirect measures of dispersal distance across a variety of riverine fishes and noted that the indirect measure σ tended to be lower than estimates from direct measures. Comte and Olden (2018) noted that downward bias in σ could be attributed to uncertainty in estimates of effective density, which they assumed ranged from 1–1000 per kilometre following Kinlan and Gaines (2003). Increasing the estimate of effective density D_e would decrease the estimate of dispersal distance σ and vice-versa. Our estimate of D_e is derived from demographic data rather than genetic data, which we feel is a strength of this study. The data requirements for estimating effective population size (N_e) with narrow confidence intervals are substantial, and genetic models for calculation have strict assumptions which are often violated in practice (Wang et al. 2016). The sensitivity of σ to the corresponding estimate of effective density suggests that this should

be an area of priority for any study attempting to estimate dispersal distance using these indirect methods.

Introduced riverine smallmouth bass populations may be uniquely problematic for control measures due to their potential for rapid expansion relative to other species. Our estimate of σ for smallmouth bass exceeds the 75th percentile of bootstrapped estimates of this parameter for all fish taxa considered in the meta-analysis by Comte and Olden (2018), including their estimate for Centrarchiformes (median value $\sigma \approx 1.75$ km). The rate of population expansion in smallmouth bass is of concern, as they have been widely introduced outside their native range and are likely to expand into new systems as thermal regimes are altered by climate change (Wenger et al. 2011; Lawrence et al. 2012; Loppnow et al. 2013). Control strategies will need to consider this potential for spatial expansion, as the spatial scale of any control and mitigation efforts will therefore need to be substantial. These efforts should also address the role of tributaries as recruitment sources for mainstem river habitats at significant distances (Loppnow and Venturelli 2014; Bestgen and Hill 2016).

The results of our study underscore the point that combining inferences from population genetics and direct movement observation can provide a more comprehensive understanding of dispersal dynamics. Direct observation of movement often is used to determine the potential scale of dispersal in fishes; however, it is difficult to extrapolate "effective dispersal" (sensu Nathan et al. 2003) from data obtained using traditional mark–recapture or telemetry methods. While an individual may migrate or range annually across a large area of standing water or length of river, their adult spawning site(s) may not necessarily be far from their natal site. Otolith chemistry holds promise for determining natal origins of smallmouth bass in river networks (Humston et al. 2010, 2017), but spawning location (and success) are more difficult to connect with an individual's spatial history. Indirect estimates of dispersal distance therefore provide an important complement to direct observations on movement for understanding population expansion rates, particularly in the context of introduced populations. The comparison of our results with those from lentic systems suggests that smallmouth bass movement ecology may be fundamentally different in lake versus river settings. This may have to do with patchy distribution of seasonal habitats required prior to reproductive maturity (e.g., winter, summer habitats), which in turn could structure dispersal ecology differently between these systems. Future studies should seek to elucidate the role of spatial arrangement of seasonal and spawning habitats in structuring dispersal among lentic and lotic fish populations (Fausch et al. 2002).

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