Life history strategies of stream fishes linked to predictors of hydrologic stability

Nathaniel P. Hitt¹ | Andrew P. Landsman² | Richard L. Raesly³

1U.S. Geological Survey, U.S. Department of the Interior, Eastern Ecological Science Center, Kearneysville, West Virginia, USA
2National Park Service, U.S. Department of the Interior, Chesapeake and Ohio Canal National Historical Park, Williamsport, Maryland, USA
3Department of Biology, Frostburg State University, Frostburg, Maryland, USA

Abstract
Life history theory provides a framework to understand environmental change based on species strategies for survival and reproduction under stable, cyclical, or stochastic environmental conditions. We evaluated environmental predictors of fish life history strategies in 20 streams intersecting a national park within the Potomac River basin in eastern North America. We sampled stream sites during 2018–2019 and collected 3801 individuals representing 51 species within 10 taxonomic families. We quantified life history strategies for species from their coordinates in an ordination space defined by trade-offs in spawning season duration, fecundity, and parental care characteristic of opportunistic, periodic, and equilibrium strategies. Our analysis revealed important environmental predictors: Abundance of opportunistic strategists increased with low-permeability soils that produce flashy runoff dynamics and decreased with karst terrain (carbonate bedrock) where groundwater inputs stabilize stream flow and temperature. Conversely, abundance of equilibrium strategists increased in karst terrain indicating a response to more stable environmental conditions. Our study indicated that fish community responses to groundwater and runoff processes may be explained by species traits for survival and reproduction. Our findings also suggest the utility of life history theory for understanding ecological responses to destabilized environmental conditions under global climate change.

KEYWORDS
freshwater fish, hydrology, karst, life history, streams

TAXONOMY CLASSIFICATION
Community ecology

INTRODUCTION

Species face trade-offs between energetic investments in growth, reproduction, and survival that shape the evolution of life history strategies under different environmental conditions (Gadgil & Bossert, 1970; Levens, 1967; Southwood, 1977; Stearns, 1992). Stable or predictable environmental conditions can benefit long-lived species with delayed maturation and low fecundity (i.e., K-selected species), whereas unpredictable environmental conditions can benefit short-lived species with rapid maturation and low juvenile survivorship (i.e., r-selected species; Pianka, 1970). Environmental stability also shapes the evolution of iteroparous and semelparous reproduction in many taxonomic groups (Cole, 1954; Murphy, 1968) as well as the distribution and abundance of annual and perennial...
plants (Schaffer, 1974). Life history theory provides a fundamental framework to understand environmental change based on species strategies for survival and reproduction under stable, cyclical, or stochastic environmental conditions.

Fishes constitute an important model for life history research because they occupy diverse environmental conditions and have been undergoing natural selection since the Cambrian Period, longer than any other vertebrate group (Long et al., 2019). Freshwater and marine fishes exhibit life history strategies within a trilateral continuum defined by opportunistic, periodic, and equilibrium endpoints (Heino et al., 2013; Mims et al., 2010; Winemiller, 1992; Winemiller & Rose, 1992). Opportunistic strategies are demonstrated by short-lived, small-bodied species with early maturation, and low juvenile survivorship rates. Species that exhibit periodic strategies invest in growth and fecundity through delayed reproduction, whereas species exhibiting equilibrium strategies exhibit low fecundity but compensate for this with increased juvenile survivorship through parental care. Although some fish species exemplify a single life history strategy, most exhibit intermediate strategies between opportunistic, periodic, and equilibrium endpoints (Hitt et al., 2020; King & McFarlane, 2003; Winemiller & Rose, 1992). For example, fish species in the genus Etheostoma (Percidae) can exhibit early maturation as well as parental care (Frimpong & Angermeier, 2009; Winemiller & Rose, 1992), thus combining attributes of opportunistic and equilibrium strategies.

Life history theory has utility for understanding hydrologic controls on freshwater fish populations and communities. In lotic environments, flow regulation from dams and reservoirs can increase abundance of equilibrium strategist fishes (Kominoski et al., 2018; McManamay & Frimpong, 2015; Mims & Olden, 2013; Olden et al., 2006; Perkin et al., 2017), whereas hydrologic spates and droughts can increase abundance of opportunistic strategists (Hitt et al., 2020; Magoulick et al., 2021; Malone et al., 2021; Mims & Olden, 2013; Olden & Kennard, 2010). Strong seasonal fluctuations in flow, such as seasonal inundation of floodplains, are associated with periodic strategist fishes (Tedesco et al., 2008). Spatial patterns also indicate the importance of hydrologic controls on fish life history diversity: Species found in flashy headwater streams tend to have smaller bodies, shorter lifespans, and earlier maturation than species found in more stable conditions downstream (Schlosser, 1990). Similarly, large-bodied, long-lived fishes are more abundant where pool habitats are common and less abundant where turbulent riffle habitats are prevalent (Lamouroux et al., 2002).

Life history theory can also inform an ecological understanding of land use and climate change. Extreme precipitation events have increased over recent decades (Easterling et al., 2000; Gershunov et al., 2019), and many river systems show increasing flow variation in response (Coombs & Rahmstorf, 2012; Milly et al., 2008; Rahmstorf & Coombs, 2011; Ward et al., 2015). Urbanization can also increase flashiness and decrease stability of downstream flows (Anderson, 1970; O’Driscoll et al., 2010; Sauer et al., 1983), and therefore, cumulative effects of land use and climate change are expected to increase flow variation and decrease predictability of annual flow regimes (Miller & Hutchins, 2017; Zhou et al., 2016). However, groundwater inputs can moderate stream flow and temperature fluctuations (Kaandorp et al., 2019; Meisner et al., 1988; Poff & Ward, 1989; Snyder et al., 2015), and these effects may be particularly important in karst terrain where extensive aquifers permeate weathered carbonate bedrock materials (Bonacci et al., 2009). For instance, fish community composition can transition sharply where karst groundwater enters a stream (Coulter & Galarowicz, 2015), and temporal stability of stream fish communities has been attributed to the stabilizing effects of karstic groundwater inputs (Kolla et al., 2015; Magoullick et al., 2021).

In this study, we applied life history theory to evaluate the role of hydrologic stability on stream fish community composition in the Potomac River basin of eastern North America. We tested our expectations that anthropogenic land use and flashy stream flows benefit species with opportunistic life history strategies rather than equilibrium or periodic strategies because species with rapid development and extended spawning seasons can rebound quickly from environmental disturbances. We also hypothesized that groundwater inputs increase equilibrium life history strategies due to stabilized hydrologic conditions that benefit investment in parental care for juvenile survival.

2 | MATERIAL AND METHODS

2.1 | Study area and sampling design

Our study area encompassed streams intersecting the Chesapeake and Ohio Canal National Historical Park (C&O Canal), an administrative unit of the U.S. National Park Service located in the headwaters of the Chesapeake Bay in eastern North America (Figure 1). A primary management objective of the National Park Service and the C&O Canal is to support biological conservation and diverse natural ecosystems (NPS, 2006). The C&O Canal extends for nearly 300 km along the north bank of the Potomac River and is characterized as a narrow band of forest within watersheds of mixed forest, agricultural, and urban land cover. The study area extends through three physiographic regions (Ridge and Valley, Blue Ridge, and Piedmont) and includes areas of karst geology within the Ridge and Valley province (Doctor et al., 2014; Weary & Doctor, 2014). Karst groundwater flow paths in this region exhibit spatially and temporally complex patterns typically associated with faults and fractured rock layers (Evaldi et al., 2009; Kozar et al., 1991) rather than conduit-type flow paths characteristic of cave systems.

We selected 20 streams from across the length of the C&O Canal that represented each physiographic region (Figure 1; Table A1 in Appendix 1). We sampled stream sites during baseflow conditions between June and September of 2018 (n = 9) and 2019 (n = 11). We identified 75-m sample reaches at each site and used two-pass backpack electrofishing techniques (Smith-Root LR24) with one electrofishing unit for each 3–4 m of stream width (Heimbuch et al., 1997). Fishes captured during each pass were
placed in live wells, counted, identified to species, and returned to the stream. Fish unable to be identified in situ were euthanized with tricaine methanesulfonate and transported to the laboratory for identification. We estimated fish species abundance as the sum from the two electrofishing passes for each site. Fish were collected following U.S. National Park Service IACUC-approved standard operating procedures.

2.2 | Quantifying life history strategies

We compiled data on species life history traits to account for major sources of variation observed across North American freshwater fishes (Mims et al., 2010; Winemiller & Rose, 1992): maximum total body length (cm), spawning season length (months per year), age of female maturation (years), mean longevity (years), and fecundity (number of eggs per breeding female). We quantified parental care on an ordinal scale following Grabowska and Przybyliski (2015): (1) nonguarding species that do not select spawning substrates, (2) nonguarding species that hide their broods, (3) guarding species that select spawning substrates, and (4) guarding species that spawn in nests. Species life history data were compiled from Jenkins and Burkhead (1994) and Frimpong and Angermeier (2009). We also classified species as native or introduced from Jenkins and Burkhead (1994). Species life history data are given in Table A2 in Appendix 2.

We used nonmetric multidimensional scaling (NMS) and archetype analysis (AA) to quantify life history strategies for each observed species. First, we fit a 2-dimensional NMS ordination to log(x+1)-transformed traits data with Bray–Curtis distances. Alternative distance measures (Euclidean, Gower) produced similar results as Bray–Curtis distances (results not shown). Second, we used AA to quantify species locations within the trilateral continuum defined by opportunistic, periodic, and equilibrium-based endpoints (i.e., archetypes) following Pecuchet et al. (2017). AA is a technique used to quantify the location of observations in multidimensional space from their distance to extreme points (Cutler & Breiman, 1994), yielding a proportional life history strategy score for each species in our analysis. This approach is conceptually appropriate because most fish species exhibit some combination of life history strategies rather than a single strategy (Hitt et al., 2020; King & McFarlane, 2003; McManamay et al., 2015; Mims & Olden, 2012).

We then summed life history strategy scores from species presence/absence data for each site and scaled the cumulative site scores from 0 to 1 (Mims & Olden, 2012; Olden & Kennard, 2010; Pecuchet et al., 2017). This provided an index of the relative importance of opportunistic, periodic, and equilibrium-based life history strategies at each sampling site for use in statistical models described below.

We used R package “vegan” version 2.5-7 (Oksanen et al., 2020) for NMS analysis and R package “archetypes” version 2.2-0.1 (Eugster & Leisch, 2009) for AA.

2.3 | Linking life history and environmental conditions

We compiled six environmental variables, including attributes of habitat volume, land use, karst terrain, and soil type (Table 1). We estimated site elevation and upstream basin size using LiDAR-derived digital elevation models (1-m resolution) with the USGS StreamStats Batch Processing Tool version 5.03 (USGS, 2021). We calculated the percent of urban land cover and agricultural land cover in upstream watersheds from the 2019 National Land Cover Dataset (NLCD) (Yang et al., 2018). Urban land cover was calculated as the sum of all “developed” NLCD classes (categories 21, 22, 23, 24), and agricultural land cover included hay/pasture, cultivated crops, and shrubland classes (categories 52, 71, 81, 82). We calculated the percent carbonate bedrock (i.e., limestone and dolomite) within each watershed using a national karst atlas (Weary & Doctor, 2014) to index potential effects of groundwater discharge on stream temperature and
flow. We also used the STATSGO2 dataset (NRCS, 2021) to quantify the percent of soils in each watershed with the lowest infiltration rates and highest runoff potential (i.e., class D soils) (NRCS, 2007). Several highly correlated variables (Pearson $r > .7$) were excluded from further analysis (e.g., percent forest cover inversely related to percent agricultural land cover).

We evaluated environmental predictors of life history strategy scores among sites from beta regression models with AIC corrected for small sample size (AICc). Beta regression is appropriate for this analysis because the response variables (life history scores) are expressed as proportional data within sites (Douma & Weedon, 2019). We scaled environmental predictors to a mean of 0 and standard deviation of 1 to facilitate comparison of model coefficients. We then fit models using logit links for all additive combinations of environmental covariates (64 models per response variable). We evaluated AICc to rank the best models based on maximum likelihood estimation, and we considered models within 2.0 AICc units from the best model ($\Delta$AICc) to be insignificantly different from one another (Burnham & Anderson, 2002). We used the R package “betareg” version 3-1.4 to fit beta regression models (Cribari-Neto & Zeileis, 2010) and R package “MuMIn” version 1.43.17 (Barton, 2020) to facilitate model comparisons.

| Site code | Site name                          | ELE (m) | UBA (ha) | URB (%) | AGR (%) | KAR (%) | SCD (%) |
|-----------|------------------------------------|---------|----------|---------|---------|---------|---------|
| 1         | UNT to North Branch Potomac River  | 167     | 167      | 9.3     | 4.6     | 0.0     | 0.1     |
| 2*        | UNT to Potomac River at Lock 71    | 173     | 2701     | 6.0     | 12.9    | 54.8    | 1.3     |
| 3         | Town Creek                         | 156     | 40,647   | 4.4     | 13.1    | 19.4    | 0.8     |
| 4*        | UNT to Potomac River at Lock 62    | 151     | 130      | 1.6     | 0.5     | 0.0     | 0.0     |
| 5*        | UNT to Potomac River at Lock 61    | 170     | 281      | 8.4     | 4.0     | 0.0     | 0.0     |
| 6         | Sideling Hill Creek                | 144     | 26,916   | 6.1     | 18.2    | 0.0     | 0.3     |
| 7*        | UNT to Potomac River               | 142     | 846      | 1.9     | 8.4     | 0.0     | 1.5     |
| 8*        | UNT to Potomac River               | 140     | 503      | 6.6     | 24.4    | 55.2    | 0.7     |
| 9         | Little Tonoloway Creek             | 127     | 6526     | 8.7     | 19.1    | 14.7    | 1.9     |
| 10        | Tonoloway Creek                    | 131     | 29,513   | 6.5     | 28.7    | 6.1     | 1.8     |
| 11        | Green Spring Run                   | 117     | 909      | 10.7    | 10.3    | 49.8    | 0.9     |
| 12        | Little Conococheague Creek         | 112     | 4678     | 7.6     | 43.8    | 69.4    | 1.0     |
| 13*       | UNT to Potomac River               | 92      | 284      | 13.7    | 70.4    | 100.0   | 0.0     |
| 14        | Israel Creek                       | 78      | 3370     | 8.5     | 33.0    | 0.0     | 2.1     |
| 15        | Catoctin Creek                     | 73      | 31,207   | 12.6    | 48.5    | 0.0     | 1.2     |
| 16*       | Lander Branch                      | 77      | 513      | 7.7     | 41.0    | 0.0     | 1.6     |
| 17        | Tuscarora Creek                    | 70      | 5463     | 14.3    | 65.7    | 25.3    | 1.8     |
| 18*       | UNT to Potomac River               | 70      | 693      | 6.4     | 55.2    | 0.0     | 9.7     |
| 19*       | UNT to Potomac River               | 66      | 182      | 1.3     | 39.1    | 0.0     | 5.6     |
| 20        | Great Seneca Creek                 | 57      | 33,557   | 34.7    | 31.0    | 0.0     | 4.6     |

Note: Percent data are given as the percent of upstream watershed areas. Site codes area mapped in Figure 1. Unnamed tributaries are abbreviated UNT. Sites codes with * were sampled during 2018; Otherwise sites were sampled in 2019. Site location coordinates are given in Table A1 in Appendix 1.

3 | RESULTS

Sample sites ranged in elevation 57–173 m above sea level (NAVD 88) with mean 116 m ± 9 m standard error (SE). Upstream basin areas ranged 130–40,647 ha with mean 9454 ha ± 3031 ha SE (Table 1). Agriculture was the primary nonforest land use (mean 29% of watershed area), followed by urban land cover (mean 9% of watershed area) (Table 1). Agricultural and urban land cover were positively correlated (Figure A1 in Appendix 3) but not monotonically related. For example, the eastern-most site near Washington, D.C., showed the most extensive urbanization (Great Seneca Creek, site 20), whereas the greatest agricultural land cover was near the geographic center of the study area (an unnamed tributary near Shepherdstown WV, site 13). Class D soils (i.e., highest runoff potential) ranged from 0 to 10% of sampled watersheds.
and the percent watershed area with carbonate bedrock (i.e., karst terrain) ranged from 0 to 100% (Table 1). Karst terrain included areas defined by the Oriskany formation (western Ridge and Valley region), the Keyser and Tonoloway formations (central Ridge and Valley region), and the Conococheague formation (eastern Ridge and Valley region) (Weary & Doctor, 2014). Carbonate bedrock was not strongly associated with other environmental covariates in the analysis (Spearman \( r < |.3|, p > .2 \), respectively) (Figure A1 in Appendix 3).

We collected 3801 individuals from 51 species of which 32 species (63%) were considered native to the Potomac River basin (Table 2). Species richness in sampled streams ranged from 1 to 25 (mean 17 ± 2 species SE), and abundance ranged from 11 to 764 individuals (mean 190 ± 34 individuals SE) (Table A3 in Appendix 4). Among taxonomic families, Leuciscidae contained the greatest richness with 19 species and nearly 50% of total abundance, followed by Centrarchidae with 11 species that constituted approximately 25% of all collected individuals. Percids and catostomids each were represented by 5 species, constituting 8% and 3% of total abundance, respectively. Ictalurids included 4 species, and Cottidae was represented by 3 species (Table 2). Remaining families were represented by a single species: American eel (Anguillidae: Anguilla rostrata), banded killifish (Fundulidae: Fundulus diaphanus), eastern mosquitofish (Poeciliidae: Gambusia holbrooki), and rainbow trout (Salmonidae: Oncorhynchus mykiss).

Green sunfish (Lepomis cyanellus), bluntnose minnow (Pimephales notatus), and blacknose dace (Rhinichthys atratulus) were the most abundant species in the dataset, comprising 12%, 11%, and 11% of total abundance, respectively (Table 2). Green sunfish was also the most widely distributed species, occurring in 90% of the sample sites. Bluntnose minnow and white sucker (Catostomus commersoni) were the second-most widely distributed species, each occurring in 80% of the sites, followed by yellow bullhead (Ameiurus natalis) with occurrences in 75% of the sites (Table 2). Conversely, several species contained a single individual in the dataset: shorthead redhorse (Moxostoma macrolepidotum), black crappie (Pomoxis nigromaculatus), walleye (Sander vitreus), and rainbow trout. Cottid species included an undescribed sculpin (checkered sculpin, Cottus sp. cf. girardi) endemic to karst groundwater-dominated streams in the Ridge and Valley portion of the Potomac River basin (Albertson, 1995; Hitt et al., 2021; Welsh, 1996). Checkered sculpin was the only species observed in one site (site 13; Figure 1) and was negatively associated with abundance of other species in the dataset (Figure A2 in Appendix 5).

Spatial variation in fish community structure was represented by a 2-dimensional NMS ordination of fish abundance data (stress = 0.10; Figure 2). Axis 1 was primarily associated with karst geology (axis loading = 1.0; Table 3) but also corresponded to agricultural and urban land cover (axis loadings = 0.63 and 0.64, respectively; Table 3). By contrast, variation along axis 2 primarily was defined by elevation, watershed area, and class D soils (axis loadings > |0.96|, respectively; Table 3). Physiographic regions varied primarily along axis 2, and fish communities in the Ridge and Valley region exhibited more spatial variation than communities from other physiographic regions (Figure 2).

Life history traits exhibited substantial variation among study species (Table 4; Table A2 in Appendix 2). Maximum adult body size ranged from 4 to 155 cm total length with the smallest species including eastern mosquitofish (4 cm), fantail darter (Etheostoma flavellare, 8 cm), and mimic shiner (Notropis volucellus, 8 cm) and the largest species including flathead catfish (Pylodictus olivaris, 155 cm), American eel (154 cm), and channel catfish (Ictalurus punctatus, 132 cm). Fecundity ranged from 134 eggs per female in Potomac sculpin (Cottus girardi) to over \( 10^6 \) eggs per female in American eel, a catadromous species (Table 4; Table A2 in Appendix 2). Eastern mosquitofish matured at the youngest age (0.3 years) and exhibited the shortest lifespan (1 year) while American eel matured at 7 years and exhibited a mean lifespan of 25 years (Table 4; Table A2 in Appendix 2). The dataset included 16 species with the lowest level of parental care (nonguarding species that do not select spawning substrate) and 23 species with the highest level of parental care (guarding species that spawn in nests) (Table A2 in Appendix 2).

A 2-dimensional NMS ordination represented interspecific variation in life history strategies (stress = 0.08; Figure 3). Axis 1 primarily indicated variation in body size and associated traits (fecundity, maturation age, longevity), and axis 2 primarily indicated a gradient between spawning season length and parental care (Table 3). Use of species NMS scores in AA identified 3 end-member conditions (archetypes) representing opportunistic, periodic, and equilibrium life history strategies (Figure 3). Opportunistic strategies were typified by eastern mosquitofish (GAHO), which exhibit an extended spawning season, small body size, and low parental care. Periodic species were typified by walleye (SAVI), which exhibit large adult body size, high fecundity, late maturation, and long lifespan. Equilibrium species were characterized by checkered sculpin (COSP), which exhibit a short spawning season, small body size, and high parental care. Introduced species exhibited a range of opportunistic and periodic strategies, but only native species occupied the extreme equilibrium strategist space (Figure 3).

Most species represented intermediate locations within the life history ordination space (Figure 3), and this was similarly reflected in species life history strategy scores derived from AA (Figure 4). End-member species showed scores near 1.0 for opportunistic, periodic, and equilibrium-based strategies, indicating a life history strategy nearly entirely defined as opportunistic (GAHO), periodic (SAVI), or equilibrium (COSP) (Figure 4). Other species were characterized by a mix of two or three strategies. For example, central stoneroller (Campostoma anomum; CAAN) was located near the center of the life history space (Figure 3) and scored nearly evenly for each of the three strategies (Figure 4). By contrast, some species exhibited a combination of two of the three strategies: Golden shiner (Notemigonus crysoleucas; NOCR) was defined as a mix of opportunistic and periodic strategies but not equilibrium strategies (Figure 4) given its location in the NMS life history space (Figure 3). Alternatively, margined madtom (Noturus insignis; NOIN) showed a mix of opportunistic and equilibrium strategies but not periodic strategies (Figure 4).
TABLE 2
Fish species abundance and occurrence observed during 2018–2019 in the study area (Figure 1)

| Family         | Species             | Common name       | Total abundance (% of total) | Mean abundance per site (SE) | Count of occupied sites (% of total) |
|----------------|---------------------|-------------------|-----------------------------|------------------------------|-------------------------------------|
| Anguillidae    | Anguilla rostrata* (ANRO) | American eel      | 19 (0.5)                    | 1.0 (2.4)                    | 6 (30)                              |
| Catostomidae   | Catostomus commersoni* (CACO) | White sucker      | 83 (2.2)                    | 4.2 (4.7)                    | 16 (80)                             |
|                | Erimyzon oblongus* (EROB) | Creek chubsucker  | 10 (0.3)                    | 0.5 (1.1)                    | 5 (25)                              |
|                | Hypentelium nigricans* (HYNI) | Northern hogsucker | 6 (0.2)                    | 0.3 (1.1)                    | 2 (10)                              |
|                | Moxostoma erythrurum (MOER) | Golden redhorse    | 14 (0.4)                    | 0.7 (2.4)                    | 3 (15)                              |
|                | Moxostoma macrolepidotum* (MOMA) | Shorthead redhorse | 1 (<0.1)                    | 0.1 (0.2)                    | 1 (5)                               |
| Centrarchidae  | Ambloplites rupestris (AMRU) | Rock bass         | 25 (0.7)                    | 1.3 (2.8)                    | 9 (45)                              |
|                | Lepomis auritus* (LEAU) | Redbreast sunfish  | 68 (1.8)                    | 3.4 (5.9)                    | 9 (45)                              |
|                | Lepomis cyanellus (LECY) | Green sunfish      | 443 (11.7)                  | 22.2 (32.6)                  | 18 (90)                             |
|                | Lepomis gibbosus* (LEGI) | Pumpkinseed sunfish | 20 (0.5)                   | 1.0 (2.1)                    | 6 (30)                              |
|                | Lepomis gulosus (LEGU) | Warmouth           | 6 (0.2)                     | 0.3 (1.3)                    | 1 (5)                               |
|                | Lepomis macrochirus (LEMA) | Bluegill           | 303 (8.0)                   | 15.2 (32.1)                  | 13 (65)                             |
|                | Lepomis megalotis (LEME) | Longear sunfish    | 34 (0.9)                    | 1.7 (4.6)                    | 6 (30)                              |
|                | Lepomis microphus (LEMI) | Redear sunfish     | 4 (0.1)                     | 0.2 (0.9)                    | 1 (5)                               |
|                | Micropterus dolomieu (MIDO) | Smallmouth bass    | 22 (0.6)                    | 1.1 (1.5)                    | 10 (50)                             |
|                | Micropterus salmoides (MISA) | Largemouth bass   | 26 (0.7)                    | 1.3 (2.7)                    | 6 (30)                              |
|                | Pomoxis nigromaculatus (PONI) | Black crappie      | 1 (<0.1)                    | 0.1 (0.2)                    | 1 (5)                               |
| Cottidae       | Cottus caeruleomentum* (COCA) | Blue Ridge sculpin | 15 (0.4)                    | 0.8 (1.7)                    | 5 (25)                              |
|                | Cottus girardi* (COGI) | Potomac sculpin    | 154 (4.1)                   | 7.7 (10.6)                   | 10 (50)                             |
|                | Cottussp. cf. girardi* (COSP) | Checkered sculpin | 96 (2.5)                    | 4.8 (18.8)                   | 2 (10)                              |
| Fundulidae     | Fundulus diaphanus* (FUDI) | Banded killifish   | 11 (0.3)                    | 0.6 (1.4)                    | 5 (25)                              |
| Ictaluridae    | Ameiurus natalis* (AMNA) | Yellow bullhead    | 233 (6.1)                   | 11.7 (12.6)                  | 15 (75)                             |
|                | Ictalurus punctatus (ICPU) | Channel catfish    | 11 (0.3)                    | 0.6 (1.3)                    | 4 (20)                              |
|                | Noturus insignis* (NOIN) | Margined madtom    | 35 (0.9)                    | 1.8 (3.9)                    | 6 (30)                              |
|                | Noturus ornatus* (NOLE) | Bluehead chub      | 64 (1.7)                    | 3.2 (8.1)                    | 3 (15)                              |
|                | Notropis buccatus* (NOBU) | Silverjaw minnow   | 12 (0.3)                    | 0.6 (1.5)                    | 4 (20)                              |
|                | Notropis hudsonius* (NOHU) | Spottail shiner    | 142 (3.7)                   | 7.1 (16.8)                   | 7 (35)                              |
|                | Notropis rubellus* (NORU) | Rosyface shiner    | 4 (0.1)                     | 0.2 (0.7)                    | 2 (10)                              |
|                | Notropis volucellus (NOVO) | Mimic shiner       | 6 (0.2)                     | 0.3 (1)                      | 2 (10)                              |
|                | Pimephales notatus* (PINO) | Blunt nose minnow  | 401 (10.5)                  | 20.1 (55.3)                  | 16 (80)                             |
|                | Rhinichthys atratulus* (RHAT) | Blacknose dace     | 398 (10.5)                  | 19.9 (52.4)                  | 11 (55)                             |
|                | Rhinichthys cataractae* (RHCA) | Longnose dace     | 94 (2.5)                    | 4.7 (7.4)                    | 8 (40)                              |
|                | Semotilus atromaculatus* (SEAT) | Creek chub        | 202 (5.3)                   | 10.1 (15.3)                  | 12 (60)                             |
|                | Semotilus corporalis* (SECO) | Fallfish          | 38 (1.0)                    | 1.9 (4.2)                    | 7 (35)                              |
scores were near 50% in both cases, smallmouth bass (*Micropterus dolomieu*; MIDO) represented a greater proportion of periodic strategy than opportunistic strategy, whereas pumpkinseed sunfish (*Lepomis gibbosus*; LEGI) showed the opposite pattern (Figure 4). Leuciscids exhibited a large range of life history strategies among species. For instance, mimic shiner (*Novo*) and cutlip minnow (*Exoglossum maxilllingua*; EXMA) showed inverse trends for opportunistic and equilibrium strategies (Figure 4): The former was characterized as an opportunistic strategist (68% opportunistic score), while the latter was characterized as an equilibrium strategist (84% equilibrium score).

Site-level life history scores calculated as the proportional sum of strategy scores for observed species exhibited a mix of opportunistic, periodic, and equilibrium strategies for nearly all sites (Figure 5). The sole exception was site 13 where only a strong equilibrium strategist species was observed (checkered sculpin). Of the other 19 sites, the proportional score for opportunistic strategies ranged from 0.19 to 0.34 with a mean of 0.24, periodic strategies ranged from 0.22 to 0.42 with a mean of 0.31, and equilibrium strategies ranged from 0.19 to 0.53 with a mean of 0.45 (Figure 5). Equilibrium strategies comprised the largest share of life history scores among sites on average; however, periodic scores exceeded equilibrium scores in five of the 20 sites (Figure 5).

Beta regression models identified environmental predictors of fish life history strategies across sites (Table 5). The most parsimonious models for opportunistic strategies showed negative relationships with karst terrain and agriculture and positive relationships to elevation and class D soils, accounting for 44%–62% of the observed variation across sites. Periodic strategies also decreased with karst terrain, and no other terms were included in the best model which accounted for 51% of the observed variation (Table 5). By contrast, equilibrium strategies increased with karst terrain and agriculture and decreased with elevation in the best models which accounted for 52%–65% of the observation variation across sites. Among all models, karst terrain exhibited stronger effects than other covariates, as indicated by the greater absolute magnitude of standardized

---

**TABLE 2 (Continued)**

| Family       | Species                  | Common name          | Total abundance (% of total) | Mean abundance per site (SE) | Count of occupied sites (% of total) |
|--------------|--------------------------|-----------------------|------------------------------|-------------------------------|--------------------------------------|
| Percidae     | *Etheostoma blennioides* (ETBL) | Greenside darter      | 109 (2.9)                    | 5.5 (9.7)                     | 9 (45)                               |
|              | *Etheostoma caeruleum* (ETCA) | Rainbow darter        | 38 (1.0)                     | 1.9 (3.3)                     | 8 (40)                               |
|              | *Etheostoma flabellare* (ETFL) | Fantail darter        | 99 (2.6)                     | 5.0 (5.9)                     | 12 (60)                              |
|              | *Etheostoma olmsti* (ETOL)  | Tessellated darter    | 63 (1.7)                     | 3.2 (5.5)                     | 10 (50)                              |
|              | *Sander vitreus* (SAVI)     | Walleye               | 1 (<0.1)                     | 0.1 (0.2)                     | 1 (5)                                |
| Poeciliidae  | *Gambusia holbrooki* (GAHO) | Eastern mosquitofish  | 4 (0.1)                      | 0.2 (0.9)                     | 1 (5)                                |
| Salmonidae   | *Onchorhynchus mykiss* (ONMY) | Rainbow trout         | 1 (<0.1)                     | 0.1 (0.2)                     | 1 (5)                                |

Note: Standard error (SE) for abundance across sites is given in parentheses. Native species are indicated with an asterisk (Jenkins & Burkhead, 1994) with 2 exceptions as indicated in superscripts. Species codes are plotted in Figure 3, and species traits data are given in Table A2 in Appendix 2.

Jenkins and Burkhead (1994) classify *N. leptocephalus* "native but possibly introduced," and we consider it introduced.

Jenkins and Burkhead (1994) classify *P. notatus* "introduced but possibly native," and we consider it native.
model coefficients (Table 5). Basin size and urbanization were not included in the best models for any life history strategy.

4 | DISCUSSION

Our results indicate the utility of life history theory for understanding the ecological importance of environmental stability and stochasticity. First, we identified trade-offs between fecundity, spawning season duration, and parental care that organized species along a trilateral continuum of opportunistic-, periodic-, and equilibrium-type life history strategies, consistent with prior research (Hitt et al., 2020; McManamay et al., 2015; Mims & Olden, 2012; Winemiller & Rose, 1992). Second, we identified mechanistic effects of watershed hydrology: We showed that opportunistic life history strategies were more common where flashy runoff is expected and less common in karst terrain where groundwater inputs are expected to stabilize stream temperature and flow (Table 5). Prior research has demonstrated effects of flow regulation on life history diversity within riverine fish communities (Kominoski et al., 2018; McManamay & Frimpong, 2015; Mims & Olden, 2013; Olden et al., 2006; Perkin et al., 2017), and our study extends this perspective from regulated rivers into headwater streams. Our findings also suggest the utility of life history theory for understanding ecological responses to destabilized environmental conditions under global climate change.

The diversity of life history strategies we observed in the Potomac River basin was consistent with prior research at the continental scale (McManamay et al., 2015; Mims et al., 2010; Winemiller & Rose, 1992), indicating evolutionary processes that transcend zoogeographic boundaries. This is particularly noteworthy for the study area due to zoogeographic effects of Great Falls of the Potomac on fish species richness and endemism (Jenkins & Burkhead, 1994; Stauffer et al., 1995). For example, checkered sculpin, Potomac sculpin, and Blue Ridge sculpin (Cottus caeruleomentum) represented end-members for the equilibrium strategy due to their low fecundity, small body size, and investment in parental care (Figure 3). This pattern has been shown previously for freshwater sculpins (Winemiller, 2005) even though the species in our analysis are endemic to the region (Hitt et al., 2021; Kinziger et al., 2000; Robins, 1961). Other species in our analysis maintain larger geographic distributions and showed concordant life history

| Model | Covariate | NMS axis 1 | NMS axis 2 | $R^2$ | $p$ |
|-------|-----------|------------|------------|-------|-----|
| Fish assemblage structure | ELE | -0.287 | -0.958 | .246 | .081 |
| | UBA | 0.129 | 0.992 | .348 | .018 |
| | URB | 0.656 | 0.755 | .166 | .228 |
| | AGR | 0.624 | 0.781 | .514 | .003 |
| | KAR | 0.999 | -0.049 | .489 | .009 |
| | SCD | -0.101 | 0.995 | .281 | .079 |
| Life history strategy | TL | -0.996 | -0.093 | .503 | <.005 |
| | SS | 0.630 | 0.777 | .755 | <.005 |
| | MA | -0.953 | -0.304 | .636 | <.005 |
| | LO | -0.987 | -0.162 | .487 | <.005 |
| | FE | -0.921 | 0.389 | .373 | <.005 |
| | PC | 0.410 | -0.912 | .771 | <.005 |

Note: Covariates are defined in Table 1 (fish assemblage structure) and Table 4 (life history strategy). Goodness of fit is indexed by the squared correlation coefficient ($R^2$) and empirical type-1 error rate ($p$) from 1000 permutation tests.

FIGURE 3  Nonmetric multidimensional scaling (NMS) ordination representing fish life history diversity. Variables are represented as vectors for spawning season length (SS), fecundity (FE), longevity (LO), total length (TL), female maturation age (MA), and parental care (PC). Archetype analysis endpoints associated with periodic (PER), equilibrium (EQU), and opportunistic (OPP) strategies are shown as “X.” Filled circles indicate native species. Species codes are given in Table 2, and life history data are given in Table A2 in Appendix 2.
patterns with prior research. For example, Winemiller and Rose (1992) identified *Gambusia* sp. as an exemplar of the opportunistic strategy, corresponding with our results.

Karst terrain was an important predictor of life history strategies (Table 5), indicating the importance of groundwater–surface water interactions for stream fish community composition. Groundwater depth and volume influence the thermal resiliency of stream ecosystems (Briggs et al., 2018; Hare et al., 2021; Johnson et al., 2020; Snyder et al., 2015), and streams located in karst terrain are strongly influenced by losses from the surface to aquifers and the emergence of groundwater through springs and seeps (Bonacci et al., 2009). Our analysis demonstrated that karst terrain was associated with a life history strategy that capitalizes on stable environmental conditions, suggesting a stabilizing effect of karst groundwater dynamics on stream fish habitat conditions.

However, groundwater in karst terrain typically exhibits spatially and temporally complex flow and recharge dynamics rather than spatially uniform processes (Bonacci et al., 2009; Evaldi et al., 2009; Kozar et al., 1991), and this can affect streams in divergent ways. For instance, in their study of karst landscapes of the Ozark-Ouachita highlands region, Leasure et al. (2016) classified stream flow types as “groundwater stable” or “groundwater flashy,” and Magoulick et al. (2021) attributed seasonal structure in stream fish community composition to these hydrological differences. Vesper and Herman (2020) also recognized differences between limestone and dolomite springs in the study area based

---

**Table 4** Summary of life history variables across fish species (n = 51)

|        | TL  | SS  | MA  | LO  | FE   | PC  |
|--------|-----|-----|-----|-----|------|-----|
| Minimum| 4.0 | 0.5 | 0.3 | 1.0 | 134  | 1.0 |
| Maximum| 155.0 | 8.0 | 7.0 | 25.0 | 1,050,000 | 4.0 |
| Mean   | 39.6 | 2.7 | 2.2 | 7.1  | 60,522 | 2.6 |
| Standard deviation | 37.2 | 1.6 | 1.1 | 4.7 | 172,736 | 1.3 |

Note: Variables are maximum total length (TL) in cm, annual spawning season length (SS) in months, female maturation age (MA) in years, longevity (LO) in years, fecundity (FE) in eggs/female, and parental care (PC) indexed on an ordinal scale from 1–4 (see text). Species life history data are given in Table A2 in Appendix 2.
on their chemical composition. We cannot fully account for potential differences among karst types in our study because most of the sampled streams lacked flow gages, and mainstem river gages typically underrepresent variation observed in headwater streams (Evaluati et al., 2014; Kovach et al., 2019). However, one karst stream in our study area supports flow data (Antietam Creek, USGS gage 01619000), and flow in this site was less variable than in a nearby stream outside of karst terrain (Catoctin Creek, USGS gage 01619000) (Figure A3 in Appendix 6). This finding is consistent with prior research indicating the overriding importance of fractured rock layers for groundwater flow rather than conduits or caves within the study area (Evaluati et al., 2009; Kozar et al., 1991; White, 1977) because increased rock contact area facilitates conductive heat exchange processes and moderates quickflow storm responses (Bonacci et al., 2009).

Our study also indicates the importance of soil properties and runoff processes for fish life history strategies. In contrast to karst terrain, we found that streams draining watersheds with high runoff potential were associated with opportunistic life history strategies (Table 5), suggesting the importance of an extended spawning period and short generation time to facilitate recovery from repeated disturbance events (i.e., discrete high or low flow events; Resh et al., 1988). Schlosser (1990) observed longitudinal variation in opportunistic life history strategies and attributed this to flashy flows in headwater areas versus the comparative stability of larger rivers. In contrast, we found that basin size (i.e., an index of stream volume) was less important than soil type in our best models, suggesting an overriding effect of soil properties and runoff dynamics. Hydrologic soil classification data are available globally (Ross et al., 2018), and this provides opportunities to evaluate the patterns observed here within other zoogeographic and physiographic regions.

In contrast to our expectation, nonforest land use did not increase opportunistic life history strategies. Instead, agricultural development showed no relationship to opportunistic strategies and was positively associated with equilibrium strategies. Moreover, we found no effect of urbanization in the best models, despite evidence that impervious land cover increases downstream peak flows (Anderson, 1970; O’Driscol et al., 2010; Sauer et al., 1983) and evidence that increasing peak flows promotes opportunistic life history strategies in Potomac River fish communities (Hitt et al., 2020). This result may be due to the spatial arrangement of our sample sites (see below) or due to moderating effects of karstic groundwater on stream ecosystem responses to land use practices. For example, Kollaus et al. (2015) attributed temporal stability of fish communities in an urbanizing landscape to moderating effects of karst terrain and associated groundwater processes.

Alternatively, our index of parental care may indicate avoidance of substrate embeddedness or other physical habitat alternations associated with agricultural development (Diana et al., 2006). For instance, bluehead chub (Nocomis leptopephalus; NOLE) exhibits high levels of parental care due to nest construction and maintenance, and this behavior enables population persistence in agricultural
landscapes by clearing fine substrates from spawning areas (Hitt & Roberts, 2012; Peoples et al., 2011). We also observed this species in streams draining watersheds with extensive agricultural development (sites 14, 15, and 17), suggesting that parental care may compensate for potentially adverse environmental conditions. Likewise, checkered sculpin exhibits nest cleaning behaviors to remove fine sediments (R. Hagerty, U.S. Fish and Wildlife Service; personal communication), and this species was observed in sites with extensive agricultural development (sites 12 and 13; Table A3 in Appendix 4).

The spatial arrangement of sample sites has implications for the interpretation of our results. The sites encompassed a large range of environmental conditions (i.e., large and small streams within 3 physiographic regions), which facilitated generalizations about the observed environmental effects. However, site elevation was inversely correlated to the percent of soils with high runoff potential, and therefore we could not fully partition effects of air temperature or other attributes associated with site elevation versus runoff processes associated with soil type. In addition, site elevation was inversely related to the size of the Potomac River near stream confluences, so we could not partition effects of elevation from fish dispersal from riverine source populations (i.e., mass effects; Leibold et al., 2004). Dispersal from riverine source populations has been demonstrated in many zoogeographic regions (Gorman, 1986; Hitt & Angermeier, 2008, 2011; Osborne & Wiley, 1992; Paukert et al., 2006), and 8 of the 51 species in our dataset (16%) were previously classified as “riverine specialists” (Hitt & Angermeier, 2011): flathead catfish, walleye, channel catfish, mimic shiner, ros冶face shiner (Notropis rubellus), greenside darter, longear sunfish (Leopomis megalotis), and spotfin shiner (Cyprinella spiloptera). Moreover, stream confluences can create unique physical habitat features (Benda et al., 2004), and we were unable to account for such potential effects in our sampling design.

Our use of AA demonstrated its utility for quantifying species life history as composites of disparate strategies, and this was appropriate given the mix of life history traits that most fishes exhibit (Hitt et al., 2020; King & McFarlane, 2003; Winemiller & Rose, 1992). However, our use of AA was facilitated by the large range of life history traits among species in our dataset which permitted us to interpret meaningful end-members for each life history strategy. For instance, eastern mosquitofish represented the opportunistic strategy, and the absence of this species in the dataset would have established an opportunistic endpoint relative to banded killifish and mimic shiner rather than the more extreme traits of eastern mosquitofish. Applications of AA therefore can enable quantitative interpretation of species life history as combinations of strategies (Pecuchet et al., 2017) but require interpretation relative to patterns observed across large geographic regions (Mims et al., 2010; Winemiller & Rose, 1992).

A central tenet in climate change research is that biological responses will be more sensitive to extreme environmental conditions than average conditions (Turner et al., 2020), and our study indicates the utility of life history theory for understanding these mechanisms (Lancaster et al., 2017). Many river systems have shown increased flow variation over recent decades (Coumou & Rahmstorf, 2012; Milly et al., 2008; Rahmstorf & Coumou, 2011; Ward et al., 2015) in response to extreme precipitation events (Easterling et al., 2000; Gershunov et al., 2019). Prior research has demonstrated the importance of scouring flows for fish population dynamics (Blum et al., 2018; Kanno et al., 2015), and our study extends this perspective to the community level through the analysis of life history traits that transcend zoogeographic boundaries. Our results also suggest that groundwater processes in karst terrain stabilize environmental conditions in receiving streams, but the sensitivity of these systems will depend in part on groundwater depth (Hare et al., 2021), spatially complex flow pathways (Kozar et al., 1991), and temporal lags in precipitation response (Schreiner-McGraw & Ajami, 2021) that control stream habitat resiliency to atmospheric change.

ACKNOWLEDGMENTS
We thank S. Faulkner, C. Snyder, K. Rogers, K. Kessler, T. O’Connell, S. Phillips, K. Hyer (U.S. Geological Survey), K. Stanfield (National Park Service), D. Healey, E. Myers, J. Shaffer, M. Stum, and M. White (Frostburg State University) for collaboration on this study. This work was supported by the US Geological Survey Chesapeake Bay studies, the USGS Ecosystems Mission Area, the USGS Eastern Ecological Science Center, the National Park Service (P18AC00652), and Frostburg State University Department of Biology. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST
The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS
Nathaniel P. Hitt: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review & editing (lead). Andrew P. Landsman: Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review & editing (supporting). Richard L. Raesly: Data curation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review & editing (supporting).

OPEN RESEARCH BADGES
This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at [https://irma.nps.gov/DataStore/Reference/Profile/2288619].

DATA AVAILABILITY STATEMENT
Data are available from the U.S. National Park Service’s Integrated Resource Management Applications data portal: [https://irma.nps.gov/DataStore/Reference/Profile/2288619].
### APPENDIX 1

| Site code | Site name                                      | Site coordinates in decimal degrees (NAD83) |
|-----------|-----------------------------------------------|---------------------------------------------|
| 1         | UNT to North Branch Potomac River             | 39.538883, -78.650270                       |
| 2         | UNT to Potomac River at Lock 71               | 39.541512, -78.617686                       |
| 3         | Town Creek                                    | 39.523621, -78.544266                       |
| 4         | UNT to Potomac River at Lock 62               | 39.571003, -78.453110                       |
| 5         | UNT to Potomac River at Lock 61               | 39.584040, -78.459903                       |
| 6         | Sideling Hill Creek                           | 39.639885, -78.334251                       |
| 7         | UNT to Potomac River                          | 39.631583, -78.308974                       |
| 8         | UNT to Potomac River                          | 39.651125, -78.242464                       |
| 9         | Little Tonoloway Creek                        | 39.697782, -78.183025                       |
| 10        | Tonoloway Creek                               | 39.697782, -78.157477                       |
| 11        | Green Spring Run                              | 39.607730, -77.970462                       |
| 12        | Little Conococheague Creek                    | 39.604222, -77.909207                       |
| 13        | UNT to Potomac River                          | 39.430468, -77.764586                       |
| 14        | Israel Creek                                  | 39.328337, -77.683076                       |
| 15        | Catoctin Creek                                | 39.311602, -77.569350                       |
| 16        | Lander Branch                                 | 39.303171, -77.557221                       |
| 17        | Tuscarora Creek                               | 39.244011, -77.474710                       |
| 18        | UNT to Potomac River                          | 39.193828, -77.470232                       |
| 19        | UNT to Potomac River                          | 39.159348, -77.516609                       |
| 20        | Great Seneca Creek                            | 39.090286, -77.329515                       |

**Table A1** Sample site coordinates. Site locations are mapped in **Figure 1.** Unnamed tributaries are abbreviated UNT.
### APPENDIX 2

**TABLE A2**  Species traits data. Life history variables are maximum total length (TL) in cm, annual spawning season length (SS) in months, female maturation age (MA) in years, longevity (LO) in years, fecundity (FE) in eggs per female, and parental care (PC) indexed from 1 to 4 (see text). Data sources are Jenkins and Burkhead (1994) and Frimpong and Angermeier (2009)

| Family            | Species name          | Code | Common name            | TL  | SS  | MA  | LO  | FE    | PC |
|-------------------|-----------------------|------|------------------------|-----|-----|-----|-----|-------|----|
| Anguillidae       | Anguilla rostrata     | ANRO | American eel           | 152 | 2.7 | 7.0 | 25.0 | 1,050,000 | 1  |
| Catostomidae      | Catostomus commersoni | CACO | White sucker           | 64  | 1.8 | 3.0 | 8.0 | 50,000 | 1  |
|                   | Erimyon oblongus       | EROB | Creek chub sucker      | 36  | 2.3 | 2.0 | 5.5 | 83,013 | 1  |
|                   | Hyphentelium nigricans | HYNI | Northern hogsucker     | 61  | 1.5 | 3.0 | 11.0 | 30,000 | 1  |
|                   | Moxostoma erythrurum   | MOER | Golden redhorse        | 78  | 2.0 | 3.5 | 8.0 | 23,350 | 1  |
|                   | Moxostoma macrolepidotum | MOMA | Shorthead redhorse     | 75  | 1.3 | 3.5 | 12.0 | 44,000 | 1  |
| Centrarchidae     | Ambloplites rupestris | AMRU | Rock bass              | 43  | 3.0 | 3.0 | 8.0 | 11,000 | 4  |
|                   | Lepomis auritus       | LEAU | Redbreast sunfish      | 31  | 2.3 | 2.0 | 6.0 | 10,000 | 4  |
|                   | Lepomis cyanellus     | LECY | Green sunfish          | 31  | 4.0 | 2.0 | 8.0 | 10,000 | 4  |
|                   | Lepomis gibbosus      | LEGI | Pumpkinseed sunfish    | 40  | 7.0 | 2.0 | 8.0 | 14,000 | 4  |
|                   | Lepomis gulosus       | LEGU | Warmouth               | 31  | 3.8 | 1.5 | 8.0 | 63,000 | 4  |
|                   | Lepomis macrochirus   | LEMA | Bluegill               | 41  | 6.0 | 2.0 | 10.0 | 50,000 | 4  |
|                   | Lepomis megalotis     | LEME | Longear sunfish        | 24  | 2.5 | 2.0 | 7.0 | 22,119 | 4  |
|                   | Lepomis microlophus   | LEMI | Redear sunfish         | 43  | 4.0 | 2.0 | 5.0 | 80,000 | 4  |
|                   | Micropterus dolomieu  | MIDO | Smallmouth bass        | 69  | 2.3 | 3.5 | 15.0 | 27,000 | 4  |
|                   | Micropterus salmoides | MISA | Largemouth bass        | 97  | 3.0 | 2.5 | 16.0 | 109,314 | 4  |
|                   | Pomoxis nigromaculatus | PONI | Black crappie          | 49  | 2.3 | 2.5 | 8.0 | 188,000 | 4  |
| Cottidae          | Cottus caeruleomentum | COCA | Blue Ridge sculpin     | 15  | 1.3 | 2.0 | 6.0 | 176   | 4  |
|                   | Cottus girardi        | COGI | Potomac sculpin        | 14  | 2.0 | 2.0 | 5.0 | 134   | 4  |
|                   | Cottussp. cf. girardi | COSP | Checkered sculpin      | 9   | 0.5 | 2.0 | 5.0 | 689   | 4  |
| Fundulidae        | Fundulus diaphanus    | FUDI | Banded killfish        | 10  | 6.0 | 1.0 | 4.0 | 252   | 1  |
| Ictaluridae       | Amelius natalis       | AMNA | Yellow bullhead        | 47  | 1.5 | 2.5 | 7.0 | 7000  | 4  |
|                   | Ictalurus punctatus   | ICPU | Channel catfish        | 132 | 1.5 | 3.5 | 10.0 | 10,600 | 4  |
|                   | Noturus insignis      | NOIN | Margined madtom        | 15  | 2.0 | 2.0 | 4.0 | 223   | 4  |
|                   | Pyloicus olivarius    | PYOL | Flathead catfish       | 155 | 1.5 | 4.5 | 23.0 | 100,000 | 4  |
| Leuciscidae       | Campostoma anomalum   | CAAN | Central stoneroller    | 22  | 2.5 | 2.5 | 5.0 | 4800  | 2  |
|                   | Carassius auratus    | CAAU | Goldfish               | 59  | 3.0 | 3.5 | 10.0 | 400,000 | 1  |
|                   | Clinostomus funduloides | CLFU | Rosside dace           | 11  | 1.0 | 2.0 | 4.0 | 560   | 1  |
|                   | Cyprinella analostana | CYAN | Satinfin shiner        | 11  | 2.8 | 1.5 | 4.0 | 3628  | 2  |
|                   | Cyprinella piloteca   | CYSP | Spotfin shiner         | 12  | 2.8 | 2.0 | 5.0 | 7474  | 2  |
|                   | Exoglossum maxilligia | EXMA | Cutlip minnow          | 16  | 1.0 | 2.0 | 4.5 | 1177  | 4  |
|                   | Luxilus cornutus      | LUCO | Common shiner          | 18  | 2.0 | 2.0 | 6.0 | 1950  | 2  |
|                   | Nocomis leptoccephalus | NOLE | Bluehead chub          | 26  | 1.5 | 1.5 | 2.5 | 800   | 4  |
|                   | Nocomis micropogon    | NOMI | River chub             | 32  | 1.5 | 2.0 | 5.0 | 1000  | 2  |
|                   | Notemigonus crysoleucus | NOCR | Golden shiner          | 30  | 3.5 | 1.0 | 8.0 | 4700  | 1  |
|                   | Notropis buccatus     | NOBU | Silverjaw minnow      | 10  | 3.5 | 1.5 | 3.0 | 1762  | 1  |
|                   | Notropis hudsonius    | NOHU | Spottail shiner        | 15  | 1.3 | 1.5 | 4.5 | 3709  | 1  |
|                   | Notropis rubellus     | NORU | Rosyface shiner        | 9   | 3.0 | 1.5 | 3.0 | 1500  | 2  |
|                   | Notropis volucellus   | NOVO | Mimic shiner           | 8   | 6.5 | 1.0 | 3.0 | 1000  | 1  |
### TABLE A2 (Continued)

| Family        | Species name         | Code  | Common name           | TL  | SS  | MA  | LO  | FE   | PC  |
|---------------|----------------------|-------|-----------------------|-----|-----|-----|-----|------|-----|
|               | Pimephales notatus   | PINO  | Bluntnose minnow      | 11  | 3.3 | 1.0 | 3.5 | 4195 | 4   |
|               | Rhinichthys atratulus| RHAT  | Blacknose dace        | 10  | 3.0 | 1.5 | 3.5 | 2674 | 2   |
|               | Rhinichthys cataractae| RHCA | Longnose dace         | 22  | 2.0 | 2.5 | 5.0 | 10,000 | 3 |
|               | Semotilus atromaculatus| SEAT | Creek chub            | 30  | 1.5 | 2.0 | 5.0 | 7157 | 2   |
|               | Semotilus corporalis| SECO  | Fallfish              | 51  | 1.0 | 2.5 | 9.0 | 12,000 | 2 |
| Percidae      | Etheostoma biennisoides| ETBL | Greenside darter      | 17  | 1.8 | 1.5 | 5.0 | 2000 | 1   |
|               | Etheostoma caeruleum| ETCA  | Rainbow darter        | 8   | 3.0 | 1.0 | 4.0 | 1462 | 2   |
|               | Etheostoma flavellare| ETFL | Fantail darter        | 8   | 2.0 | 1.0 | 4.0 | 467  | 4   |
|               | Etheostoma olmstedii| ETOL  | Tessellated darter    | 11  | 3.0 | 1.0 | 3.0 | 1435 | 4   |
|               | Sander vitreus       | SAVI  | Walleye               | 90  | 1.0 | 3.0 | 14.0 | 600,000 | 1 |
| Poeciliidae   | Gambusia holbrooki   | GAHO  | Eastern mosquitofish  | 4   | 8.0 | 0.3 | 1.0 | 315  | 1   |
| Salmonidae    | Oncorhynchus mykiss  | ONMY  | Rainbow trout         | 120 | 4.0 | 4.0 | 7.0 | 27,000 | 2 |

*aData from mottled sculpin (Cottus bairdii).*

*bData from slimy sculpin (Cottus cognatus).*

### APPENDIX 3

**FIGURE A1** Spearman correlations in environmental variables across sites. Variables are abbreviated as elevation (ELE), upstream basin area (UBA), urban land cover (URB), agricultural land cover (AGR), carbonate parent material in karst terrain (KAR), and class D soils (SCD). Land cover and geological variables are expressed as the percent of upstream basin area.
### APPENDIX 4

**Table A3** Species abundance by site. Site codes are given in Table 1, and species codes are given in Table 2.

| Site code | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|-----------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|
| AMNA      | 0 | 2 | 6 | 0 | 0 | 9 | 0 | 27 | 24 | 7 | 21 | 5 | 0 | 1 | 6 | 22 | 20 | 49 | 13 | 21 |
| AMRU      | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 13 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 |
| ANRO      | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 11 |
| CAAN      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 1 | 9 | 7 | 16 | 4 | 0 | 12 | 11 | 3 |
| CAAU      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 |
| CACO      | 3 | 1 | 1 | 0 | 0 | 3 | 0 | 1 | 9 | 7 | 16 | 4 | 0 | 12 | 1 | 1 | 13 | 6 | 3 | 2 |
| CLFU      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 12 | 6 | 1 | 2 | 0 | 0 | 0 | 0 |
| COCA      | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 |
| COGI      | 0 | 2 | 9 | 0 | 0 | 5 | 0 | 19 | 13 | 11 | 28 | 38 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 19 |
| COSP      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 86 | 0 | 0 | 0 | 0 | 0 | 0 |
| CYAN      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| CYSP      | 1 | 0 | 7 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 4 | 0 |
| EROB      | 0 | 0 | 0 | 4 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| ETBL      | 0 | 0 | 8 | 0 | 0 | 5 | 0 | 0 | 1 | 21 | 20 | 37 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 12 |
| ETCA      | 0 | 0 | 2 | 0 | 0 | 6 | 0 | 0 | 2 | 2 | 6 | 13 | 0 | 6 | 1 | 0 | 0 | 0 | 0 | 0 |
| ETFL      | 0 | 8 | 7 | 0 | 0 | 4 | 12 | 4 | 0 | 6 | 3 | 8 | 0 | 23 | 3 | 15 | 0 | 0 | 0 | 6 |
| ETOL      | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 1 | 14 | 20 | 1 | 0 | 1 | 0 | 0 | 8 | 0 | 0 | 11 |
| EXMA      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| FUDI      | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 1 | 2 |
| GAHO      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| HYNI      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 |
| IPCU      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 |
| LEAU      | 0 | 0 | 6 | 0 | 0 | 7 | 0 | 1 | 14 | 10 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 4 | 0 | 23 |
| LECY      | 7 | 3 | 19 | 4 | 70 | 5 | 0 | 40 | 39 | 21 | 14 | 2 | 0 | 5 | 7 | 12 | 21 | 144 | 22 | 8 |
| LEGI      | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 |
| LEGU      | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LEMA      | 0 | 114 | 20 | 0 | 0 | 8 | 1 | 0 | 20 | 2 | 0 | 0 | 0 | 1 | 15 | 4 | 12 | 105 | 2 | 9 |
| LEME      | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 21 | 0 | 1 |
| Species code | Site code | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|--------------|-----------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|
| LEMI         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 4  | 0  | 0  |    |    |    |    |
| LUCO         |           | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 0  | 0  | 0  | 0  | 5  | 2  | 11 | 0  | 0  |    |    |    |    |
| MIDO         |           | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 3  | 6  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 3  | 0  | 3  |    |
| MISA         |           | 0 | 7 | 0 | 0 | 0 | 0 | 1 | 0 | 0  | 0  | 0  | 0  | 2  | 0  | 10 | 0  | 1  | 5  | 0  |    |    |
| MOER         |           | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 11 | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |    |    |
| MOWA         |           | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |    |    |    |    |    |
| NOBU         |           | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 0  | 6  | 0  |    |    |    |
| NOCR         |           | 0 | 0 | 4 | 0 | 1 | 3 | 0 | 0  | 3  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 3  | 0  |    |
| NOHU         |           | 0 | 0 | 38 | 0 | 0 | 28 | 0 | 0  | 0  | 1  | 0  | 0  | 0  | 5  | 1  | 3  | 0  | 66 | 0  |    |    |
| NOIN         |           | 0 | 0 | 9 | 0 | 0 | 8 | 1 | 1  | 1  | 0  | 15 | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |    |
| NOLE         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 25 | 28 | 0  | 11 | 0  | 0  |    |    |    |    |
| NOMI         |           | 0 | 0 | 8 | 0 | 0 | 3 | 0 | 0  | 2  | 8  | 3  | 0  | 0  | 0  | 70 | 0  | 2  | 6  | 1  |    |    |
| NORU         |           | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |    |    |    |
| NOVO         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 4  | 0  | 0  | 0  | 0  | 2  |    |
| OXMY         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |    |
| PONI         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  |
| PYOL         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |    |
| RHAT         |           | 229 | 3 | 0 | 0 | 4 | 0 | 0 | 95 | 1  | 0  | 15 | 8  | 5  | 7  | 1  | 30 | 0  | 0  | 0  |    |    |
| RHAC         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 0  | 0  | 2  | 18 | 9  | 8  | 21 | 1  | 0  | 0  | 0  | 18 |    |
| SAVI         |           | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |    |
| SEAT         |           | 35 | 36 | 0 | 0 | 0 | 0 | 0 | 13 | 6  | 0  | 8  | 58 | 9  | 0  | 14 | 0  | 15 | 1  | 0  | 6  | 1  |
| SECO         |           | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0  | 1  | 0  | 0  | 19 | 2  | 0  | 0  | 4  | 4  | 0  | 0  | 4  | 0  |
APPENDIX 5

FIGURE A2  Spearman correlations in species abundance across sites. Species codes are given in Table 2 and Table A1 in Appendix 1.

APPENDIX 6

FIGURE A3  Comparison of stream flow variability in karst terrain vs nonkarst terrain within the study area. The karst site is located at Antietam Creek near Waynesboro, Pennsylvania (U.S. Geological Survey gage #01619000), and the nonkarst site is located at Catoctin Creek near Middletown, Maryland (U.S. Geological Survey gage #01637500). Flow data were adjusted for upstream basin area in each site (karst site = 93.5 mi²; nonkarst site = 66.9 mi²). The nonkarst site exhibited greater variance in basin area-adjusted flow (Conover squared ranks test p < .0001) in this sample of over 497,000 observations from 7/1/2005 to 7/1/2020. This test statistic provides a nonparametric version of Levene’s test for homogeneity of variance among groups.