Transactions of the American Fisheries Society, 2025, **00**, 1–18
https://doi.org/10.1093/tafafs/vnae001
Advance access publication: March 18 2025
Article

Decadal stability in stream fish communities and contemporary ecological drivers of species occupancy in two Appalachian U.S. National Parks

Morgan B. Stum[1]*, Caleb J. Tzilkowski[2], Matthew R. Marshall[2], Frances E. Buderman[3], and Tyler Wagner[4]

[1]Pennsylvania Cooperative Fish and Wildlife Research Unit, Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania, USA
[2]National Park Service, Eastern Rivers and Mountains Network, University Park, Pennsylvania, USA
[3]Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania, USA
[4]U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, Pennsylvania, USA

*Corresponding author: Morgan B. Stum. Email: morganstum5@gmail.com

ABSTRACT

Objective: Although conserving fish biodiversity in lotic systems is challenging, protected areas can provide refuge from certain environmental stressors. In the Appalachian region, USA, the National Park Service manages the Delaware Water Gap National Recreation Area and New River Gorge National Park & Preserve, which contain abundant and diverse freshwater resources. To assess the effectiveness of these protected areas in conserving stream fishes, we evaluated decadal changes and ecological drivers of species occupancy and detection.

Methods: Using fish assemblage data from backpack electrofishing surveys conducted in both parks during 2013–2014 and 2022–2023, we quantified temporal differences in species occupancy and detection probabilities using a Bayesian hierarchical multispecies occupancy modeling approach. For the 2022–2023 survey, we included habitat variables as predictors of occupancy and detection.

Results: Community composition and occupancy probabilities for species in both parks remained similar through time, with the most recent occupancy estimates ranging from 0.07 (90% CI = 0.02, 0.14) for Variegate Darter *Etheostoma variatum* and Rainbow Darter *E. caeruleum* to 0.73 (90% credible interval = 0.59, 0.85) for Blacknose Dace *Rhinichthys atratulus*. Changes in occupancy were more prominent at Delaware Water Gap National Recreation Area than New River Gorge National Park & Preserve, with Yellow Perch *Perca flavescens* having a posterior mean difference of −0.17 [90% credible interval = −0.35, −0.01] and American Eel *Anguilla rostrata* having a high posterior probability (>80%) of occupancy increasing by at least 1%. Habitat variables were related to community structure, but effects varied in significance, magnitude, and direction among species and parks. Conversely, species-specific detection probabilities were comparatively less affected by environmental and sampling effort predictors.

Conclusions: Between 2013 and 2023, occupancy estimates for 44 fish species across two protected, ecologically diverse landscapes remained relatively stable. Furthermore, we highlight the efficacy of national parks in maintaining freshwater fish biodiversity amidst rapid global change.

KEYWORDS: habitat, multispecies occupancy modeling, national park, occupancy, protected areas, stream fish

LAY SUMMARY

Stable estimates of stream fish occupancy over approximately 10 years in two Appalachian U.S. national parks suggest effective conservation of freshwater biodiversity.

INTRODUCTION

Protected areas (PAs) have become a crucial and widely used conservation strategy in response to the global biodiversity crisis (Pringle, 2017; Watson et al., 2014). By reducing human pressure and habitat loss, PAs help maintain abundance and can provide critical protection for threatened and endangered species (Geldmann et al., 2015; Watson et al., 2014). Unfortunately,

Received: July 11, 2024. **Revised:** November 8, 2024. **Accepted:** November 12, 2024
© The Author(s) 2025. Published by Oxford University Press on behalf of American Fisheries Society. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

global biodiversity has continued to decline, and the efficacy of PAs in stemming the loss of biodiversity has lately come under scrutiny (Geldmann et al., 2015; Pringle, 2017). Due to the recent areal expansion of PAs and their increasing contact with human activity, levels of anthropogenic pressure and land use change within some PAs have equaled those in unprotected areas (Visconti et al., 2019; Watson et al., 2014). Additionally, PAs are often subject to conflicting management objectives, such as implementing conservation practices while providing benefits to local communities through ecotourism, recreation, and sustainable resource use (Pringle, 2017; Watson et al., 2014). Because the designation of PAs alone does not guarantee reduction or mitigation of biodiversity decline (Geldmann et al., 2015), the importance of effectively managing natural resources within PAs has more recently been emphasized (Visconti et al., 2019; Watson et al., 2014).

Frequent inventorying and long-term monitoring of species and environmental conditions in PAs is a crucial yet sometimes overlooked aspect of conservation because it allows managers to identify outside ecological threats and assess the effectiveness of the PA over time and compared to the surrounding landscape. Proactive monitoring and risk assessment is particularly important in the context of freshwater environments (Acreman et al., 2020; Hermoso et al., 2016), which are dynamic and broadly connected systems that can be heavily influenced by factors originating beyond PA boundaries, such as land use change, pollution, habitat fragmentation, and invasive species (Arthington et al., 2016; Reid et al., 2019). Due to the complexity of freshwater habitats and the large spatial scale required to fully address environmental stressors they face, contemporary management strategies designed for terrestrial PAs are often not adequate for freshwater ecosystems and do not ensure protection for aquatic species (Hermoso et al., 2016; Lawrence et al., 2011). Moreover, conservation objectives in terrestrial PAs often do not include measures of freshwater biodiversity, leading to knowledge gaps, underfunding, and subsequent mismanagement of important aquatic resources (Acreman et al., 2020; Hermoso et al., 2016). In an assessment of the effectiveness of PAs in conserving inland waters, Acreman et al. (2020) found that nearly half of the reviewed PA case studies failed to preserve freshwater biodiversity. Consequently, the authors identified increased quantitative research across a broad range of aquatic taxa and ecological processes as a primary and necessary step forward to evaluate whether PAs are meeting freshwater conservation goals (Acreman et al., 2020).

Although over 16% of terrestrial and 7% of marine areas are currently under some form of protection (United Nations Environment Programme World Conservation Monitoring Center and International Union for the Conservation of Nature, 2021), less attention has been given to implementing and managing freshwater PAs. This is particularly concerning because freshwater ecosystems contain disproportionally high levels of biodiversity and yet are declining at comparatively much faster rates (Darwall & Freyhof, 2016; Su et al., 2021). For example, freshwater habitats make up less than 1% of earth's surface area yet contain over 51% of global fish diversity, of which approximately one-third are at risk of extinction (Hughes, 2021). Specifically in North America, nearly 40% of freshwater fish species are considered imperiled, with several already going extinct during the past century (Burkhead, 2012; Walsh et al., 2011). Although in their infancy, freshwater PAs have potential to curb this decline in North American freshwater fishes, especially if management strategies were tailored to freshwater habitats already contained within terrestrial PAs (Acreman et al., 2020; Hermoso et al., 2016). In the United States, a large network of federal PAs (>34 million ha; National Park Service [NPS], 2023) managed by the NPS represents the potential for increased and efficient freshwater protection (Lawrence et al., 2011). Despite many national parks being designated primarily to conserve terrestrial habitats and cultural landmarks, they contain approximately two-thirds of the U.S. native freshwater fish diversity and thus have dual capacity to serve as freshwater PAs (Lawrence et al., 2011). Additionally, the NPS Inventory and Monitoring (I&M) Program's robust framework for long-term monitoring of ecological "vital signs" ensures that parks are meeting conservation goals and maintaining "unimpaired" natural resources (Marshall & Piekielek, 2007). Specifically, NPS staff can prioritize research and management of fish and other aquatic taxa in I&M network parks with considerable freshwater resources, which is necessary to detect freshwater biodiversity decline and mitigate habitat loss within and adjacent to PAs (Marshall & Piekielek, 2007).

This study utilized the stream fish monitoring program established by the NPS Eastern Rivers and Mountains I&M Network (ERMN) to evaluate spatiotemporal differences in fish communities of two member parks: Delaware Water Gap National Recreation Area (DEWA) and New River Gorge National Park and Preserve (NERI). Because these parks are centered around notable Appalachian rivers and contain some of the most significant freshwater resources in the U.S. National Park System (>1,000 km of waterways; Marshall & Piekielek, 2007), ERMN research staff designed the I&M programs for DEWA and NERI to include various aspects of freshwater biological integrity, such as benthic macroinvertebrates; riparian vegetation; streamside birds; and, more recently, stream fish (Faulk & Weber, 2017; Marshall & Piekielek, 2007). As a preliminary assessment of the effectiveness of these parks in meeting NPS management goals for fish in wadeable streams, we quantified differences in estimates of species occupancy and detection probabilities over approximately a decade using DEWA and NERI stream fish assemblage data sets from an initial survey conducted in 2013–2014 (Faulk, 2015) combined with a survey in 2022–2023. To identify potential environmental threats to the stream fish in these parks and account for biases of imperfect detection, we also examined how site- and watershed-scale habitat factors are currently influencing estimates of species occupancy and detection probabilities. Together, this information can provide early warning signs of native species decline, or an increase in nonnative species, and can aid in developing proactive management strategies to protect and restore critical aquatic habitat in PAs. This study also provides a benchmark for potential changes in fish community occupancy in unprotected areas within the Appalachian region of the United States, which are likely to become more degraded as stressors and demands on freshwater ecosystems continue to increase.

METHODS

Study area

The study area encompassed the two largest ERMN parks, DEWA and NERI (Figure 1). The Delaware Water Gap National

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

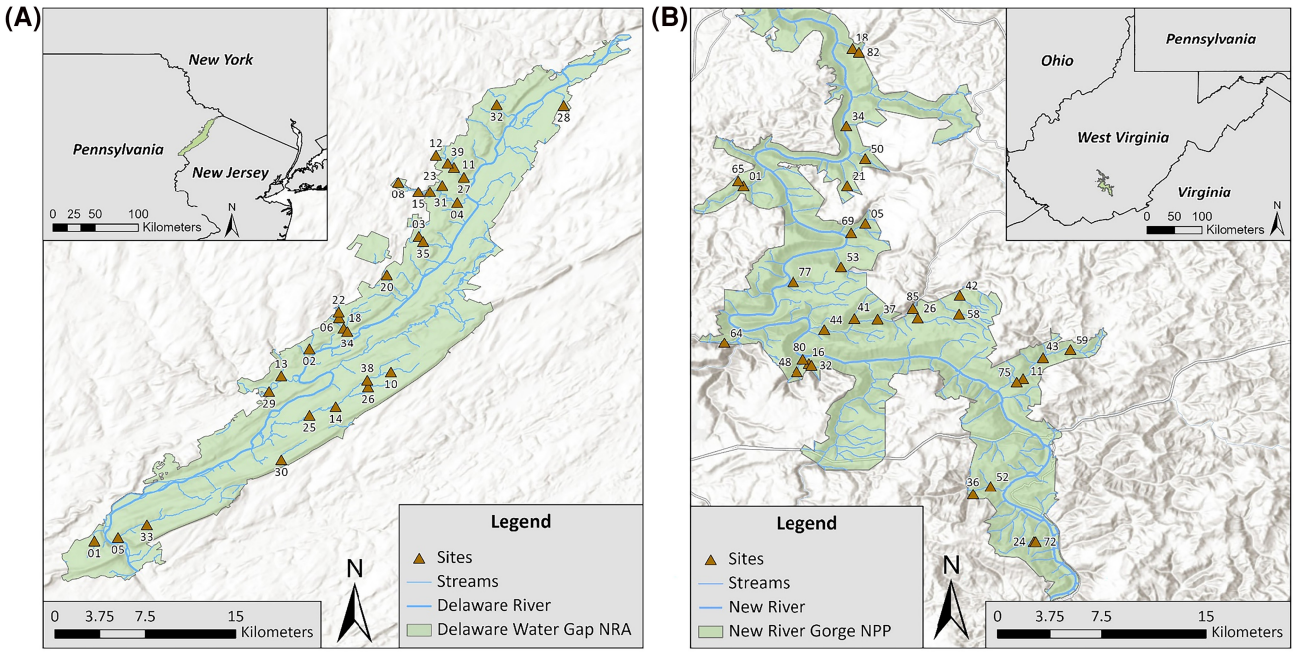

Figure 1. Site maps for (A) Delaware Water Gap National Recreation Area (NRA) and (B) New River Gorge National Park and Preserve (NPP). Stream study reaches (triangles) are labeled with a Short ID code defined in Supplement Tables S.1 and S.2.

Recreation Area is located between Pennsylvania and New Jersey along 70 km of the middle Delaware River and encompasses over 28,000 ha of land, nearly 25 km of smaller rivers, and more than 80 km of wadeable streams (Marshall et al., 2016). As the longest undammed major river in the eastern United States, the Delaware River is home to a diverse fish community, including several species of conservation interest and migratory species with unique, diadromous life histories (Horwitz et al., 2014). Historic industrial and agricultural land use in the Delaware River valley heavily impacted DEWA aquatic ecosystems and fish communities, and both changing forest dynamics within DEWA and increasing residential development in the surrounding area are ongoing environmental threats (Marshall & Piekielek, 2007).

The New River Gorge National Park and Preserve is located in southern West Virginia along 90 km of the New River and contains over 100 km of wadeable streams (Marshall et al., 2016). The New River system is geologically unique, flowing north from its headwaters in the Blue Ridge province of North Carolina, across the Ridge and Valley province of Virginia, and into the Appalachian Plateau in West Virginia. Due to glaciation across the region, New River fishes were repeatedly displaced and isolated, resulting in a comparatively few native species but many endemic species (Jenkins & Burkhead, 1994; Stauffer et al., 1995). Unfortunately, the New River also has the largest proportion of nonnative fish species among major eastern U.S. drainages (Cincotta et al., 1999). In addition to the threat of introduced species, historic and continued land use practices such as logging, mining, agriculture, and inadequate wastewater treatment have resulted in deforestation, habitat loss, and poor water quality in and adjacent to NERI (Marshall & Piekielek, 2007).

Site selection

Fish sampling sites were located on "wadeable" tributaries—those with drainage areas <100 km^2 (Tzilkowski et al., 2016). Wadeable streams were targeted because they represent the most abundant type of surface water throughout the parks, can be safely accessed on foot, and require less intensive survey methods than larger rivers (Marshall et al., 2016; Tzilkowski et al., 2016). Additionally, other agencies sample and manage fish in the main stems of the Delaware River and New River, making their inclusion redundant (Marshall et al., 2016). There were 61 sampling sites (DEWA $n = 30$, NERI $n = 31$; Figure 1) that were randomly selected by ERMN research staff (Marshall et al., 2016). Each site consisted of a 100-m stream reach that had previously been established for benthic macroinvertebrate monitoring to prioritize safety and spatially align the core wadeable stream vital signs monitored by the ERMN (Faulk & Weber, 2017; Tzilkowski et al., 2016). At DEWA, five sites from the 2013–2014 survey were not resampled in 2022–2023 due to changes in habitat that made sampling ineffective or unsafe, but one new site was added (see Table S.1 [see online Supplementary Material] for differences in site locations between sampling periods). Similarly for NERI, five original sites were removed from sampling with the addition of two new sites in 2022–2023 (Table S.2).

Sampling design

Sites were sampled following a two-panel design where approximately half of the sites in both DEWA and NERI were sampled each year such that all sites are sampled once across 2 years (see Tables S.1 and S.2 for site panel distinctions for DEWA and NERI, respectively; Tzilkowski et al., 2016). New River Gorge National Park & Preserve Panel 1 sites were sampled from May 2 to June 13, 2022, (with the exceptions of two sites, which were sampled in 2023 due to logistics and unfavorable sampling conditions in 2022), and Panel 2 sites were sampled from May 15 to June 22, 2023. Likewise, DEWA Panel 1 sites were sampled from June 16 to July 26, 2022, and Panel 2

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafs/vnae001/8081928 by guest on 19 March 2025

sites were sampled from July 6 to August 11, 2023. This differed from the 2013–2014 survey, where all DEWA sites were sampled in a single season from May 20 to August 8, 2013, and all NERI sites were sampled from April 3 to June 22, 2014 (Faulk, 2015). For statistical analysis purposes, the combined sampling effort in each park from 2022–2023 was considered to be one sampling "period" and hereafter referred to as the 2023 survey, whereas the 2013–2014 sampling period is referenced as the 2013 survey.

To account for imperfect detection and estimate species occupancy and detection probabilities, sites were sampled three times in a single season (i.e., 2022 or 2023), with as few days as logistically possible between each "visit" in an attempt to meet the closure assumption—that there were no changes in occupancy between visits (MacKenzie & Royle, 2005). For the 2023 survey, the average time between visits at both DEWA and NERI was 9 d (range = 3–24 d and 1–23 d, respectively), whereas the 2013 survey average was 29 d (range = 15–62 d) between visits at DEWA and 23 d (range = 2–57 d) at NERI. If fish were not captured on the first visit in 2023 at sites considered "fishless" during the 2013 survey, these sites were considered "low priority" and were not revisited.

Fish sampling

Each site (100-m reach) was sampled in an upstream direction using single-pass, pulsed-DC backpack electrofishing (EF) with a Smith-Root LR 24 unit (Smith-Root, Vancouver, Washington). The frequency (Hz) and duty cycle (%) were set to 60 Hz with 12% duty, which are suitable and effective EF settings when targeting fish communities in wadeable streams (Rabeni et al., 2009). The applied voltage (V) ranged from 90 to 800 V and was adjusted according to the specific conductance (μS) of stream water at the time of sampling following methods by Wofford and Demarest (2018). Prior to sampling, EF settings were tested and refined downstream of the reach by observing the physiological reactions of fish to maximize efficiency (Reynolds & Kolz, 2013). Sampling crews typically consisted of one backpack EF operator and two netters, while a second EF backpack was used at a few larger streams with up to eight netters. Block nets were placed at the upstream reach boundary (Faulk, 2015), and a block net was placed at the downstream boundary only if the reach start was deep with low water velocity, where fish could easily escape as EF began. Occasionally, block nets were not used where obvious natural barriers (e.g., waterfalls, dry streambed, etc.) occurred at either end of the reach. All captured fish were counted and identified to species before redistributing them throughout the reach. At least one specimen from each species, sex (when distinguishable), and age-class (i.e., young of year, juvenile, or adult) was photographed using a digital camera after being placed in a clear viewing Photarium (Wild Fish Conservancy, Duvall, Washington) or on a measuring board. Any fishes not easily identified in the field were photographed extensively for key morphological characteristics, and a taxonomical decision was determined after examining the photos and consulting with an ichthyologist. However, this rarely occurred, and most fish were successfully identified in the field.

Habitat data collection and summarization (2023)

To evaluate ecological drivers of fish occupancy and detection, a suite of environmental data was collected at each site during the 2023 survey. Habitat variables were chosen based on their documented effects in structuring aquatic communities (Infante & Allan, 2010) and measured following methods from the U.S. Environmental Protection Agency (USEPA) Wadeable Stream Assessment Protocol (USEPA, 2004). At five evenly spaced transects along the sampling reach (0 [beginning of the reach], 25, 50, 75, and 100 m [end of the reach]), we recorded aspects of stream morphology, including channel wetted width (m) and five cross-sectional measurements (left bank, one-fourth of the width, center, three-fourths of the width, right bank) of channel depth (cm), substrate size-class, and substrate embeddedness (%). We quantified the percentage of canopy cover using a spherical densiometer (model A, convex type; Lemmon, 1957) and placed the dominant riparian vegetation into qualitative categories ("deciduous," "coniferous," "broadleaf evergreen," "mixed," or "none"). We visually estimated areal fish cover by assigning percentage classes (0% ["Absent"], 0–10% ["Sparse"], 10–40% ["Moderate"], 40–75% ["Heavy"], or >75% ["Very Heavy"]) to various cover categories, which were averaged and summed to the proportional area of natural concealment features (Kaufmann et al., 1999). We enumerated large woody debris (LWD) pieces (dead wood >1.5 m length with a small-end diameter >10 cm) between each transect and placed them in categories based on length and diameter. We then estimated the reach total cubic volume of LWD, assuming the volume of a cylinder using mean lengths and diameters from the size-classes and summarized it to LWD density (m^3/m^2) to account for variations in reach area and their capacity to accumulate LWD (Kaufmann et al., 1999). Lastly, we conducted a visual-based rapid habitat assessment of the entire reach and surrounding area by scoring 10 habitat components from 0 to 20 or 0–10 within general quality categories ("poor," "marginal," "suboptimal," or "optimal"), following the USEPA Rapid Bioassessment Protocol for high-gradient, riffle/run prevalent streams (USEPA, 2004), which we then summarized as the percentage of points earned out of the maximum possible. We considered these habitat characteristics to be constant across the sampling period and therefore only measured them once at each site, usually on the first visit.

Because water quality is an important driver of fish distributions, (Jackson et al., 2001; Wang et al., 2006) and can affect EF efficiency (Reynolds & Kolz, 2013), we also measured select water chemistry variables prior to fish sampling on each visit. Instantaneous measurements of water temperature (°C), dissolved oxygen (DO; mg/L and % saturation), specific conductance (μS/cm), and pH were taken using a Eureka Water Probes Manta 2 multiparameter instrument (Eureka Water Probes, Austin, Texas) and averaged across the three visits (unless only visited once) to characterize each site's water quality conditions. Because water clarity could affect detection probabilities, we also indirectly quantified stream turbidity on each visit as distance of visibility (cm) in the water column using a 120-cm Secchi tube. Lastly, we measured water velocity using a Marsh McBirney FlowMate 2000

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

(Marsh-McBirney, Frederick, Maryland) at a location in or near the reach with the most uniform channel and then calculated stream discharge (m^3/s) following the cross-sectional area method (USEPA, 2004).

To provide additional insights into fish community structure in response to long-term stream temperature patterns, hourly temperature data (°C) was collected by deploying Onset HOBO temperature loggers (Onset Computer Corporation, Bourne, Massachusetts) at each site for the duration of the study (March 2022–October 2023; Tzilkowski, 2024). To account for annual variation in thermal regimes and short temporal gaps in readings due to displaced loggers, we averaged the daily mean and maximum water temperatures over both years. Temperature summary statistics included the maximum daily mean temperature during the sampling period for each site; the annual maximum temperature; and, as metrics pertaining to coldwater classification, the number of annual days where the daily mean and maximum temperatures exceeded 20°C (Heck et al., 2018). Some temperature readings were missing from late fall through early spring in both 2022 and 2023 at several NERI sites. Because these gaps were outside of the sampling period for NERI, as well as the typical range for peak summer temperatures, we deemed the temperature summary statistics for these sites acceptable for analysis.

Habitat characteristics at the landscape or watershed scale are often important determinants of stream fish community structure due to their influence shaping local aquatic environments (Infante & Allan, 2010; Jackson et al., 2001; Wang et al., 2006). For this study, watershed-scale variables of interest included upstream catchment area (km^2); Strahler stream order; the percentage of agricultural, developed, and forested land use in the upstream catchment; distance (m) from the sample site to the confluence with either the Delaware River or New River; mean reach slope (%); and reach elevation (m). Watershed variables were derived (ESRI, Redlands, California) from spatial data sets, including the National Hydrology Dataset Plus High Resolution (U.S. Geological Survey, 2018a, 2018b), and the 2019 National Landcover Database (Dewitz & U.S. Geological Survey, 2021). We standardized all habitat variables to a mean of zero with a standard deviation of one before analysis due to the wide range of scales across predictors. Prior to standardization, we also $\log_e$ transformed highly skewed predictors where appropriate or logit transformed skewed predictors, which were measured as proportions.

Statistical analysis

Occupancy modeling framework

Bayesian hierarchical occupancy modeling was used to estimate species-specific occupancy and detection probabilities as well as their relationships to habitat variables (Kéry & Royle, 2016; MacKenzie et al., 2018). Applying an occupancy modeling framework to fish community data sets is a useful method to estimate species occupancy while accounting for imperfect detection (Faulk, 2015; Lamothe et al., 2023; White et al., 2020). Occupancy models use repeat sampling visits to estimate the probability of detecting a species given that it occupies a site (p) and the probability that a site is occupied by the species (ψ). In these models, the latent occupancy state (z) is defined as the outcome of a Bernoulli trial with probability ψ, where if species k is present at site i, $z_{ik} = 1$, and if the species is truly absent, $z_{ik} = 0$. Thus, the species presence is modeled as a function of the probability of occupancy (ψ_{ik}): $z_{ik} \sim \text{Bernoulli}(\psi_{ik})$. Subsequently, the observation of a species y_{ijk} is conditional both on the probability that the species occupies the site and on the probability that it is detected on visit j, which also follows a Bernoulli distribution such that $y_{ijk} \sim \text{Bernoulli}(z_{ik} \times p_{ijk})$.

A multispecies occupancy model (MSOM) was used instead of multiple, single-species models to improve the precision of estimated occupancy and detection probabilities using partial-pooling with species-specific random effects, which are informed by a common prior distribution governed by community-level hyperparameters (Kéry & Royle, 2016; White et al., 2020). Specifically, each species was assumed to have a baseline logit-scale probability of occupancy (β_0) and detection (α_0) across sites, which came from a normal distribution with an overall mean and variance describing the heterogeneity in species occupancy and detection such that $\beta_{0k} \sim N(\mu_\psi, \sigma^2_\psi)$ and $\alpha_{0k} \sim N(\mu_p, \sigma^2_p)$, where μ_ψ and μ_p represent the community-level occupancy and detection probabilities, respectively, and σ^2_ψ and σ^2_p represent the variance among species. Thus, for intercept-only models used to estimate unconditional species-specific occupancy and detection probabilities, we modeled occupancy and detection on the logit scale as $\text{logit}(\psi_{ik}) = \beta_{0k}$ and $\text{logit}(p_{ijk}) = \alpha_{0k}$, respectively.

The unconditional models were modified to include habitat variables, which varied by site or visit, as linear predictors of occupancy and detection probability. We assumed that the effect of a habitat variable c on occupancy probability (β_c) varied by species and came from a normal distribution with some mean ($\mu_{\beta c}$) and variance ($\sigma_{\beta c}$), representing the community-level average response and variation among species. For example, a model of occupancy for species k at site i with the effects of stream depth (β_1) and percent forest (β_2) would be expressed as $\text{logit}(\psi_{ik}) = \beta_{0k} + \beta_{1k} \times \text{depth}_i + \beta_{2k} \times \text{forest}_i$. Similarly, species-specific random effects were used for the detection response to habitat or sampling effort variables (α_c), which came from a normal distribution with a community-level mean and variance ($\alpha_{ck} \sim N[\mu_{\alpha c}, \sigma_{\alpha c}]$) such that a model for the detection of species k at site i with effects of discharge (α_1) and sampling effort (α_2) on visit j would be expressed as $\text{logit}(p_{ijk}) = \alpha_{0k} + \alpha_{1k} \times \text{discharge}_{ij} + \alpha_{2k} \times \text{effort}_{ij}$.

All intercept and slope parameters were assigned normal prior distributions with a 0 mean and 0.5 variance following recommendations from Northrup and Gerber (2018), and variance parameters were given uniform priors ($\sigma^2_\psi \sim U[0,5]$; $\sigma^2_p \sim U[0,3]$; $\sigma_{\beta c}$ and $\sigma_{\alpha c} \sim U[0,10]$). All models were fitted using Markov chain–Monte Carlo simulations in the program JAGS (Plummer, 2003) by using the package jagsUI (Kellner, 2021) in the R Statistical Software environment version 4.2.1 (R Core Team, 2022). For the unconditional models, three Markov chain–Monte Carlo chains were run for 200,000 iterations, thinning every two samples, and a burn-in of the first 150,000 iterations, resulting in 75,000 samples used to summarize the posterior distribution. For the habitat models, 250,000 iterations with the same amount of burn-in and thinning were used for a total of 150,000 samples used to summarize the posterior distribution. Convergence was assessed

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

using trace plots of the posterior distributions and the potential scale reduction factor (<1.1; Gelman et al., 2013).

Quantifying change in occupancy and detection

Due to differences in sampling site location and the amount of time between sampling periods (8–10 years), we assumed species occupancy for each period to be independent (Guillera-Arroita & Lahoz-Monfort, 2012; MacKenzie et al., 2018). Therefore, we fit an unconditional, single-season MSOM to each sampling period within each park. We removed species that were uniquely detected in only one sampling period from analysis due to lack of parameter convergence for the sampling period in which they were not detected, resulting in occupancy and detection parameters being estimated for 29 and 15 species at DEWA and NERI, respectively. To evaluate changes in species occupancy and detection over time, we subtracted the 2013 posterior distributions for estimated occupancy and detection parameters from the respective 2023 parameter posterior distributions and reported the difference as posterior means with 90% and 80% credible intervals (CIs). Given the NPS management objective of "no decline in the condition of park resources" (Marshall et al., 2016; Tzilkowski et al., 2016) and the potential severity of not detecting a decline in occupancy when there was one for a species of concern, a change in occupancy or detection between time periods was deemed significant if the 80% CI for the posterior mean difference did not overlap zero as a precautionary threshold. However, because defining a CI is arbitrary, we also examined the posterior probability of species occupancy changing by at least ±0.01. This threshold is relevant since a 1% decline in resource condition is a key metric for both the ERMN streamside bird and benthic macroinvertebrate monitoring protocols (Marshall et al., 2016; Tzilkowski et al., 2016), which aim to meet NPS standards for maintaining natural resources. Species that had >80% of their posterior distributions for estimated occupancy probability being greater than or equal to a ±0.01 difference were considered to have a high probability of changing by at least ±1%. Additionally, we reported the probability of direction for the difference in posterior distributions such that the probability of a strictly negative or positive change in species occupancy and detection is available for interpretation at various levels (available in Tables S.3 and S.4 for DEWA and NERI, respectively; Makowski et al., 2019).

Quantifying effects of habitat (2023)

Due to differing habitat data collection methods between sampling periods, only the 2023 survey data set was used to estimate contemporary effects of habitat variables on species occupancy and detection at each park (see Faulk, 2015, for habitat effects on occupancy and detection for the 2013 survey). To avoid multicollinearity issues, we did not include habitat variables with Pearson correlation coefficient values >0.6 in models of occupancy or detection. We chose which correlated variables to remove based on low variation across sites and/or values within ranges not expected to affect occupancy or detection (means, standard deviations, and ranges of all measured and derived habitat and sampling effort variables are available in Tables S.5 and S.6 for DEWA and NERI, respectively). For example, DO (mg/L) was removed because it was highly correlated with stream temperature metrics and all values fell between 8 and 11 mg/L, which are normal levels of oxygenation for stream environments and suitable for all species observed (Bulbul Ali & Mishra, 2022). Because elucidating relationships with species occupancy and detection probabilities and habitat variables at the park scale was of more importance than a parsimonious model for predicting site-specific species occupancy, we retained all remaining uncorrelated habitat covariates and fit full models to avoid spurious removal of potentially important variables. The DEWA model of occupancy included 11 habitat predictors that varied by site: mean number of annual days with maximum stream temperature >20°C, maximum stream depth, mean substrate embeddedness (%), substrate larger than fine gravel (%), natural fish cover (%), $\log_e$LWD density (m^3/m^2), USEPA rapid habitat score (%), reach slope (%), $\log_e$distance to Delaware River (m), $\log_e$upstream catchment area (km^2), and the developed land use (%) in the upstream catchment. Additionally, the DEWA model of detection included six predictors for detection that varied by visit ($n=3$) and site ($n=3$): sampling effort standardized to reach area (s/m^2), $\log_e$stream discharge (m^3/s), $\log_e$specific conductance (μS/cm), natural fish cover (%), $\log_e$LWD density (m^3/m^2), and maximum stream depth (cm). Similar to DEWA, the NERI model of occupancy included 11 habitat predictors: annual maximum stream temperature (°C), mean stream depth (cm), substrate larger than fine gravel (%), mixed riparian vegetation (%), logit-canopy cover (%), natural fish cover (%), $\log_e$LWD density (m^3/m^2), USEPA rapid habitat score (%), logit-reach slope (%), $\log_e$-distance to New River (m), and the forested land use (%) in the upstream catchment area. The NERI model of detection included eight habitat and sampling effort variables, including those from the DEWA detection model as well as turbidity (Secchi depth [cm]) and number of netters standardized to stream width (netters/m). We reported habitat effects on species occupancy and detection as posterior means with 90% and 80% CIs. A habitat effect on species occupancy or detection was deemed significant if the 80% CI for the posterior mean did not overlap zero.

RESULTS

Catch summary and comparison

During the 2023 survey at DEWA, fish were captured at 29 of 30 sites, with one site remaining "fishless" as documented during the 2013 survey (Faulk, 2015). Across all DEWA sites and visits, there were 11,531 individual fish captured (see Table S.7 for DEWA species-specific counts) representing nine families and 30 species, which was two fewer species than the total number observed in 2013 (Faulk, 2015). Species recorded in 2013 (Faulk, 2015) that were not observed in the 2023 survey included Black Crappie *Pomoxis nigromaculatus*, Comely Shiner *Notropis amoenus*, and a hybrid tiger trout (Brown Trout *Salmo trutta* × Brook Trout *Salvelinus fontinalis*), whereas Rock Bass *Ambloplites rupestris* was a newly detected species in 2023. However, given that these species were all captured at rates of less than five individuals across one to three sites and that Rock Bass was recorded in DEWA streams in prior studies (Horwitz et al., 2014), it is likely that these species were present

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafs/vnae001/8081928 by guest on 19 March 2025

in the park but not observed during both sampling periods. The five most abundant (total *n* over three visits) DEWA species in 2023 were Blacknose Dace *Rhinichthys atratulus* ($n=5{,}637$), Brown Trout ($n=1{,}267$), American Eel *Anguilla rostrata* ($n=1{,}073$), Longnose Dace *R. cataractae* ($n=786$), and Brook Trout ($n=688$), which remained the most abundant species since 2013 observations despite shifts in their relative order and raw abundance (see Table S.7 for differences in species counts from 2013 to 2023; Faulk, 2015).

During the 2023 survey at NERI, fish were detected at 21 of 31 sites, with eight sites remaining "fishless" as documented during the 2013 survey (Faulk, 2015). Across all sites and visits, there were 5,648 individual fish captured (see Table S.8 for NERI species-specific counts) from five families and 16 species, which was five fewer species than the total number observed in 2013 (Faulk, 2015). Six species observed only in the 2013 survey (Faulk, 2015) included Bluegill *Lepomis macrochirus*, Smallmouth Bass *Micropterus dolomieu*, Fathead Minnow *Pimephales promelas*, White Shiner *Luxilus albeolus*, Whitetail Shiner *Cyprinella galactura*, and White Sucker *Catostomus commersonii*, whereas Largemouth Bass *M. nigricans* was a newly observed species in 2023. However, given that these species were all captured at rates of less than seven total individuals across one to four sites and that Largemouth Bass was recorded in NERI streams in prior studies (Wellman, 2004), these species were likely present in the park but not observed during both sampling periods. Similar to DEWA, the five most abundant NERI species in 2023—Blacknose Dace ($n=2{,}488$), Fantail Darter *Etheostoma flabellare* ($n=825$), Rosyside Dace *Clinostomus funduloides* ($n=701$), Creek Chub *Semotilus atromaculatus* ($n=625$), and Central Stoneroller *Campostoma anomalum* ($n=515$)—remained the same since 2013, though their relative order of abundance shifted (Table S.8; Faulk, 2015). Interestingly, Creek Chub were observed at one site where fish were not detected in 2013 (Faulk, 2015). Conversely, no fish were found at two sites where Brook Trout were observed in low numbers during the 2013 survey (Faulk, 2015).

Changes in occupancy and detection (2013–2023)

From the unconditional MSOMs, the 2023 DEWA posterior mean for the community-level occupancy hyperparameter was low ($\mu_\psi=0.20$ [90% CI = 0.14, 0.27]), although several species occurred at roughly half or more sites. Blacknose Dace was the most widely distributed species, followed by American Eel, Brown Trout, and Brook Trout (Table 1). The remaining 25 species each occupied ≤40% of sites, with the Redfin Pickerel *Esox americanus* having the most restricted range (Table 1). The posterior mean for community-level detection in 2023 was relatively high ($\mu_p=0.78$ [90% CI = 0.66, 0.87]), and estimated detection probabilities were moderate ($p\geq0.50$) to high ($p\geq0.80$) for most species (Table 1). Differences in estimated occupancy probabilities between sampling periods at DEWA varied in direction and magnitude among species, although only three species had significant differences in mean occupancy (Figure 2): Yellow Perch (posterior mean occupancy probability difference = −0.17 [90% CI = −0.35, −0.01]), Bluegill, (posterior mean occupancy probability difference = −0.19 [80% CI = −0.35, −0.03]), and Pumpkinseed (posterior mean occupancy probability difference = −0.20 [80% CI = −0.35, −0.05]). One species of interest, American Eel, had >80% posterior probability of increasing in occurrence by 1% or greater, while seven species (five native: Brook Trout, Redbreast Sunfish, Golden Shiner, Pumpkinseed, and Yellow Perch; two introduced: Rainbow Trout and Bluegill), showed high probability of declining in occurrence by at least 1% (Figure 3). Although differences in estimated mean detection probabilities between sampling periods at DEWA varied in direction among species, the magnitude of change was greater than estimates of occupancy, with several species having significantly higher probabilities of detection in 2023 than in 2013 (Figure 2).

At NERI, the posterior mean for the 2023 community-level occupancy hyperparameter was also relatively low ($\mu_\psi=0.16$ [90% CI = 0.10, 0.25]), with only a few species being widely distributed. Two native minnow species, Blacknose Dace and Creek Chub, occurred at half the sites, but the remaining 13 species each occupied ≤30% of sites, with two nonnative darter species, Rainbow Darter *Etheostoma caeruleum* and Variegate Darter *E. variatum*, having the most restricted ranges (Table 2). Like at DEWA, estimated detection probability in 2023 was high for the community ($\mu_p=0.87$ [90% CI = 0.70, 0.95]) and for most species (Table 2). Differences in estimated occupancy probabilities between sampling periods varied in direction across species, but none were significant (Figure 2). Additionally, no species had >80% posterior probability of occupancy changing by at least ± 1% (Figure 3). Differences in estimated detection probabilities between sampling periods also varied in direction and magnitude among species, but only Blacknose Dace was significantly more likely to be detected in 2023 (posterior mean detection probability difference = 0.08 [90% CI = 0.01, 0.15]; Figure 2).

Habitat effects on occupancy and detection (2023)

Of the habitat predictors included for the 2023 DEWA occupancy model, seven had significant effects on occupancy for at least one species (Figure 4). Species responses were strongly unidirectional to the landscape variables upstream catchment area (+) and reach slope (−). Similarly, most species, including the highly migratory American Eel, were more likely to be found close to the Delaware River, although Creek Chub was more likely to occur farther from the river. The community, on average, as well as five species, including warmwater obligates (e.g., Largemouth Bass and Bluegill), had a higher probability of occurrence at sites with maximum stream temperatures frequently exceeding 20°C, whereas Brown Trout occupancy was negatively affected by increased frequency of warm water temperatures. The percentage of developed land use in the upstream catchment area had comparatively little impact on occupancy for most species, although notable exceptions included two salmonids (Brook Trout and Rainbow Trout) that were less likely to occupy sites with increasing developed land use (>5–10%; see Stum, 2024, for species-specific predicted occupancy response curves), and a leuciscid and an ictalurid (Blacknose Dace and Margined Madtom) that were more likely to occupy sites with higher levels of development (20–30%; Stum, 2024). Likewise, occupancy for most species was unaffected by USEPA rapid habitat score, except for

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafs/vnae001/8081928 by guest on 19 March 2025

Table 1. Estimated posterior means (90% credible intervals in parentheses) of occupancy and detection probabilities for species observed in Delaware Water Gap National Recreation Area in 2023. Native species are shown in bold. Rock Bass was not included in model estimates because it was not detected during the 2013 survey. Species are sorted descending based on posterior mean occupancy probabilities.

Species	Occupancy	Detection
Blacknose Dace *Rhinichthys atratulus*	**0.73 (0.59, 0.85)**	**0.98 (0.96, 1.00)**
American Eel *Anguilla rostrata*	**0.60 (0.45, 0.74)**	**0.78 (0.68, 0.86)**
Brown Trout *Salmo trutta*	0.49 (0.35, 0.64)	0.96 (0.91, 0.99)
Brook Trout *Salvelinus fontinalis*	**0.44 (0.30, 0.58)**	**0.87 (0.78, 0.94)**
Creek Chub *Semotilus atromaculatus*	**0.38 (0.24, 0.52)**	**0.93 (0.85, 0.98)**
Bluegill *Lepomis macrochirus*	0.34 (0.21, 0.50)	0.60 (0.43, 0.75)
Largemouth Bass *Micropterus nigricans*	0.33 (0.18, 0.53)	0.42 (0.24, 0.62)
Margined Madtom *Noturus insignis*	**0.32 (0.20, 0.46)**	**0.85 (0.74, 0.94)**
White Sucker *Catostomus commersonii*	**0.29 (0.17, 0.42)**	**0.91 (0.81, 0.98)**
Pumpkinseed *Lepomis gibbosus*	**0.29 (0.16, 0.44)**	**0.59 (0.39, 0.76)**
Longnose Dace *Rhinichthys cataractae*	**0.20 (0.10, 0.32)**	**0.92 (0.80, 0.99)**
Green Sunfish *Lepomis cyanellus*	0.18 (0.05, 0.45)	0.26 (0.05, 0.61)
Rainbow Trout *Oncorhynchus mykiss*	0.18 (0.09, 0.30)	0.71 (0.50, 0.88)
Brown Bullhead *Ameiurus nebulosus*	**0.18 (0.06, 0.39)**	**0.37 (0.11, 0.68)**
Chain Pickerel *Esox niger*	**0.18 (0.06, 0.37)**	**0.37 (0.11, 0.67)**
Cutlip Minnow *Exoglossum maxillingua*	**0.17 (0.08, 0.29)**	**0.95 (0.86, 1.00)**
Tessellated Darter *Etheostoma olmstedi*	**0.15 (0.07, 0.26)**	**0.81 (0.61, 0.95)**
Fall Fish *Semotilus corporalis*	**0.15 (0.07, 0.26)**	**0.81 (0.61, 0.95)**
Bluespotted Sunfish *Enneacanthus gloriosus*	**0.13 (0.03, 0.35)**	**0.32 (0.03, 0.77)**
Golden Shiner *Notemigonus crysoleucas*	**0.13 (0.03, 0.36)**	**0.32 (0.04, 0.77)**
Northern Hog Sucker *Hypentelium nigricans*	**0.13 (0.05, 0.24)**	**0.64 (0.34, 0.87)**
Yellow Bullhead *Ameiurus natalis*	**0.12 (0.05, 0.23)**	**0.75 (0.50, 0.94)**
Redbreast Sunfish *Lepomis auritus*	**0.12 (0.05, 0.22)**	**0.85 (0.64, 0.98)**
Common Shiner *Luxilus cornutus*	**0.12 (0.05, 0.22)**	**0.85 (0.64, 0.98)**
Shield Darter *Percina peltata*	**0.12 (0.05, 0.22)**	**0.93 (0.79, 1.00)**
Sea Lamprey *Petromyzon marinus*	**0.11 (0.04, 0.21)**	**0.63 (0.28, 0.90)**
Yellow Perch *Perca flavescens*	**0.10 (0.03, 0.19)**	**0.79 (0.50, 0.97)**
Smallmouth Bass *Micropterus dolomieu*	0.10 (0.03, 0.19)	0.79 (0.49, 0.97)
Redfin Pickerel *Esox americanus*	0.07 (0.02, 0.15)	0.86 (0.55, 0.99)

Bluegill, which was more likely to occupy sites with lower habitat scores. The negative response to the amount of fish cover across all species was unexpected, but mean effect sizes were relatively small with high uncertainty. The remaining habitat variables did not significantly affect occupancy for any species (see Stum, 2024, for estimated effect sizes of nonsignificant occupancy predictors). For the 2023 DEWA model of detection, all habitat and effort predictors except maximum stream depth significantly affected the detection probability of at least one species (Figure 5). However, detection for most species was unaffected by any of the variables and the effect sizes were relatively small (see Stum, 2024, for estimated effect sizes of nonsignificant detection predictors and species-specific predicted detection response curves).

Of the habitat predictors included in the 2023 NERI occupancy model, seven had significant effects on occupancy for at least one species (Figure 6). Two variables associated with stream morphology—reach slope and average stream depth—had a unidirectional and significant impact on the community, on average, with species being more likely to occupy lower gradient, deeper reaches. Although the effects of annual maximum stream temperature on species occupancy showed more variability in direction, a group of seven species, which included all observed leuciscids, were more likely to occupy sites with higher stream temperatures. The community average occupancy response to USEPA rapid habitat score was positive, although only two species, Blacknose Dace and Green Sunfish, were significantly more likely to occupy sites with higher habitat scores. Surprisingly, distance to the New River had little impact on estimated occupancy for most species compared to its effect at DEWA. However, like at DEWA, Creek Chub was the only species at NERI more likely to be found farther from the river. The amount of mixed riparian vegetation and natural fish cover did not significantly affect occupancy for the community on average, despite several species responding positively to both variables, and the remaining habitat predictors included in the model did not significantly affect occupancy for any species (see Stum, 2024, for estimated effect sizes of nonsignificant occupancy predictors and species-specific predicted occupancy response curves). Only three habitat and sampling effort predictors for the NERI model of detection had significant effects for at least one species, although the number of significant responses among species was greater than at DEWA (Figure 7). As expected, most species were more likely to be detected at higher stream conductivity levels, whereas the negative detection response to an increasing proportion of netters for several species was surprising. The mean effect sizes of maximum stream depth on species detection were comparatively small and only significant for one species. The remaining included habitat and effort predictors did not significantly affect detection probabilities

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafs/vnae001/8081928 by guest on 19 March 2025

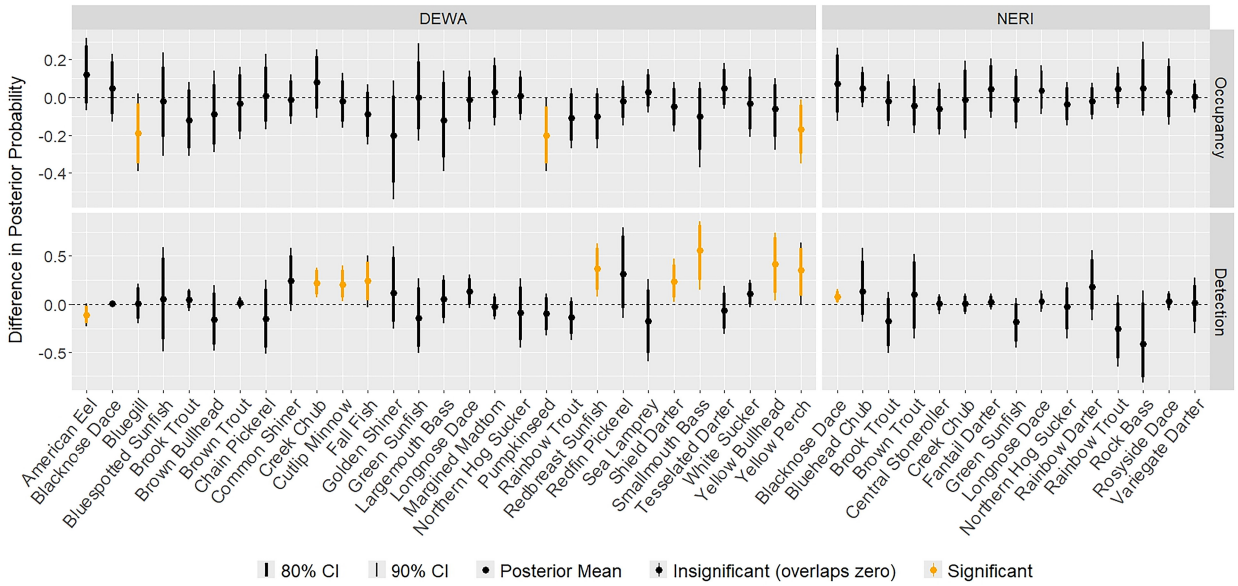

Figure 2. Posterior mean differences (2013 estimates subtracted from 2023 estimates) in posterior occupancy probabilities (top) and detection probabilities (bottom) with credible intervals (CIs) for species observed at Delaware Water Gap National Recreation Area (DEWA; left) and New River Gorge National Park and Preserve (NERI; right). Species encountered in only one sampling period were not included in model estimates. See Tables 1 and 2 for DEWA and NERI species scientific names, respectively.

for any species (see Stum, 2024, for estimated effect sizes of nonsignificant detection predictors and species-specific predicted detection response curves).

DISCUSSION

There were few significant decadal differences in estimated mean occupancy probabilities for stream fishes at either DEWA or NERI. Although some species exclusively at DEWA had significant, negative differences in mean occupancy or high probability (>80%) of declining in occupancy by at least 1%, these results were not entirely unexpected or concerning when considering the specific circumstances of occurrence for those species. Specifically, several of the DEWA species estimated to be in decline are considered either lacustrine or warmwater species (Redbreast Sunfish, Golden Shiner, Bluegill, Pumpkinseed, and Yellow Perch; Halliwell et al., 1999), which are not typical occupants of headwater streams. While the above-mentioned species are native to the Delaware River watershed (except Bluegill; Horwitz et al., 2014), their presence in our study reaches was likely the result of historical stocking in upstream lakes and ponds and subsequent flushing events (Schultz et al., 2003). Thus, observations of decline in occupancy for these species in headwater streams are not cause for ecological concern since headwater streams do not provide suitable instream conditions for their population growth and the individuals detected during the 2013 survey were likely transient residents from upstream sources. Additionally, the apparent decline in nonnative Rainbow Trout (>80% probability of 1% occupancy decline) was possibly due to a change in the state-regulated trout stocking program, which discontinued Rainbow Trout stocking at four DEWA sites after 2021 (Pennsylvania Fish and Boat Commission [PFBC], 2021, 2022) and, therefore, was not representative of natural processes.

Similar to Rainbow Trout, Brook Trout, a native species of conservation concern in the eastern USA, showed a high probability of declining in occupancy by at least 1%, yet it remained one of the most common species at DEWA in both raw abundance and relative estimated occupancy. While a potential decline in the distribution of Brook Trout would align with literature detailing its native range reduction due to anthropogenic impacts such as land use change, sedimentation, and elevated water temperatures (Hudy et al., 2008; Kanno et al., 2015), more than two annual survey periods with consistent sampling locations will be necessary to elucidate a true negative trend in Brook Trout occupancy, as neutral population and landscape dynamics could be driving the observed differences. Consequently, the possibility of a slight decline in Brook Trout occupancy highlights the need for targeted population monitoring as a precautionary measure. Specifically, because Brook Trout were less likely to occupy sites with higher levels of upstream development, special attention could be given to monitoring potential impacts of upstream residential development on coldwater habitat in DEWA (Marshall et al., 2016), especially as climate change is expected to exacerbate stressors associated with land use change (Kanno et al., 2015; Kirk et al., 2022). A future significant decrease in Brook Trout occupancy combined with an increase in species that are comparatively more tolerant to warm water, pollution, and siltation, such as Blacknose Dace, Margined Madtom, and Bluegill (Grabarkiewicz & Davis, 2008; Halliwell et al., 1999), which were also more likely to occupy DEWA sites with higher levels of upstream development or lower USEPA rapid habitat scores, could serve as an indicator for habitat degradation. However, there is currently no supporting evidence for any of the above-mentioned tolerant species significantly increasing in occupancy. Ultimately, the lack of substantial decline in species occupancy from 2013 to 2023 indicates that a consistent level

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafs/vnae001/8081928 by guest on 19 March 2025

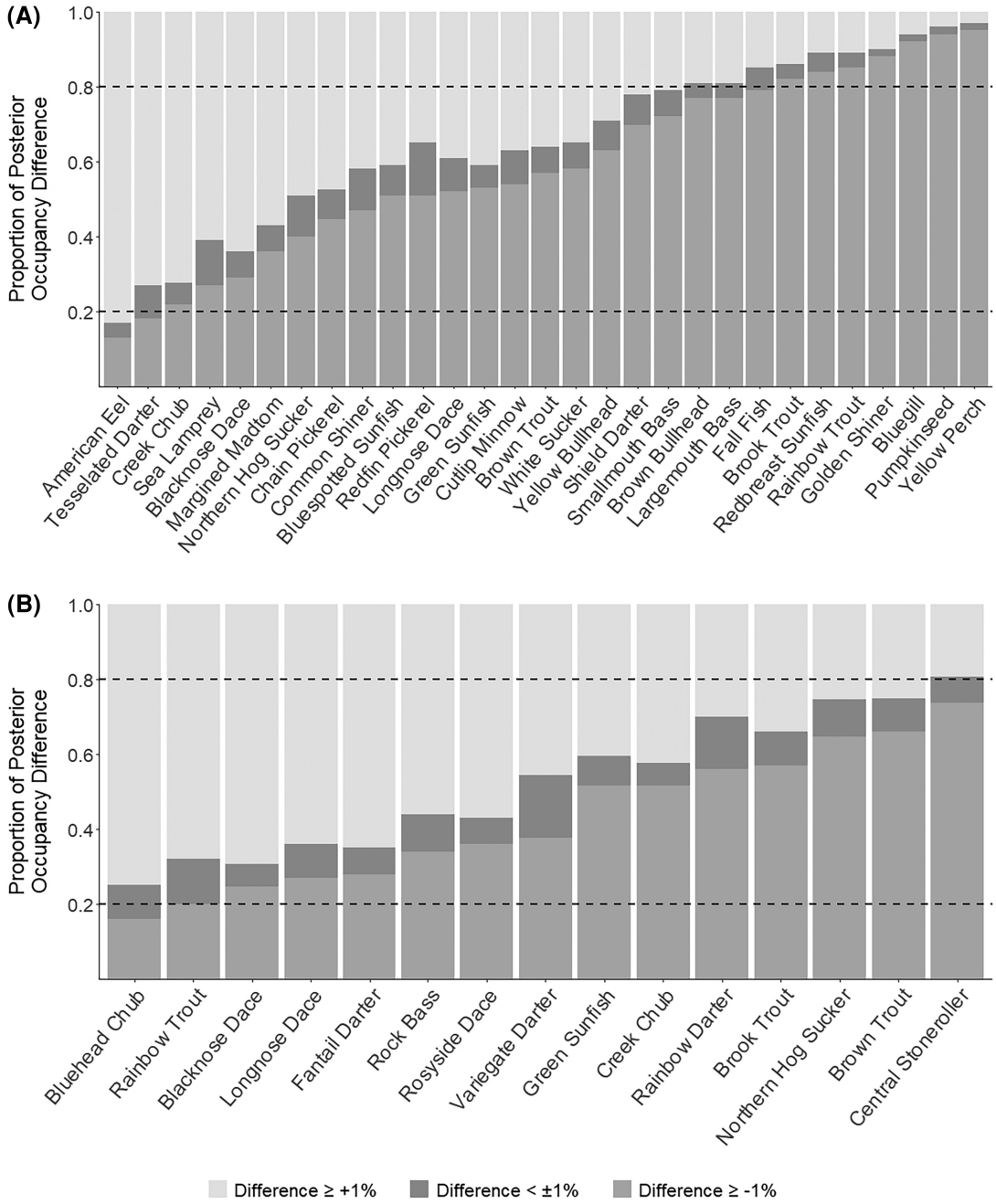

Figure 3. Proportions of the posterior distribution for difference in estimated occupancy from 2013 to 2023 that are ≥1% occupancy increase, ≥1% occupancy decrease, and an occupancy difference <±1% for species at (A) Delaware Water Gap National Recreation Area and (B) New River Gorge National Park and Preserve. Bars that cross the reference lines at 0.2 (for ≥1% increase) or 0.8 (or ≥1% decrease) indicate >80% of the posterior distribution. See Tables 1 and 2 for species scientific names.

of freshwater fish biodiversity was maintained within park boundaries during this period and suggests that DEWA and NERI are currently meeting the NPS management objective of "no decline in the condition of park resources" pertaining to wadeable stream fish.

Beyond simply maintaining species occupancy, our research indicates high probability (>80%) for American Eel to have increased in occupancy by at least 1% at DEWA, which is encouraging given its globally endangered status (Pike et al., 2023). As a highly migratory species and the only catadromous fish in North America, the American Eel has consequently suffered significant stock reductions across its range due to widespread dam construction and habitat fragmentation (Dittman et al., 2009; Fenske et al., 2011). However, due to the absence of major dams along the main stem of the Delaware River, American Eels have remained abundant throughout the basin compared to neighboring mid-Atlantic drainages such as the Potomac and Susquehanna, which each have several large dams for water supply, flood control, and producing hydroelectricity (Dittman et al., 2009; Horwitz et al., 2014). Additionally, our results are consistent with another study documenting increased American Eel

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

Table 2. Estimated posterior means (90% credible intervals in parentheses) of occupancy and detection probabilities for species observed in New River Gorge National Park and Preserve in 2023. Native species are shown in bold. Largemouth Bass was not included in model estimates because it was not detected during the 2013 survey. Species are sorted descending based on posterior mean occupancy probabilities.

Species	Occupancy	Detection
Blacknose Dace *Rhinichthys atratulus*	**0.50 (0.36, 0.65)**	**0.99 (0.95, 1.00)**
Creek Chub *Semotilus atromaculatus*	**0.50 (0.35, 0.65)**	**0.88 (0.79, 0.95)**
Rosyside Dace *Clinostomus funduloides*	**0.30 (0.18, 0.44)**	**0.95 (0.87, 0.99)**
Fantail Darter *Etheostoma flabellare*	**0.25 (0.14, 0.37)**	**0.98 (0.91, 1.00)**
Green Sunfish *Lepomis cyanellus*	**0.19 (0.09, 0.32)**	**0.63 (0.39, 0.83)**
Longnose Dace *Rhinichthys cataractae*	**0.16 (0.08, 0.27)**	**0.97 (0.88, 1.00)**
Central Stoneroller *Campostoma anomalum*	**0.14 (0.06, 0.24)**	**0.96 (0.86, 1.00)**
Brook Trout *Salvelinus fontinalis*	**0.13 (0.05, 0.25)**	**0.63 (0.32, 0.88)**
Rock Bass *Ambloplites rupestris*	0.13 (0.02, 0.38)	0.31 (0.02, 0.80)
Bluehead Chub *Nocomis leptocephalus*	0.12 (0.04, 0.21)	0.86 (0.65, 0.98)
Brown Trout *Salmo trutta*	0.10 (0.03, 0.21)	0.63 (0.26, 0.91)
Rainbow Trout *Oncorhynchus mykiss*	0.10 (0.03, 0.21)	0.63 (0.26, 0.91)
Northern Hog Sucker *Hypentelium nigricans*	**0.09 (0.03, 0.18)**	**0.81 (0.50, 0.98)**
Rainbow Darter *Etheostoma caeruleum*	0.07 (0.02, 0.14)	0.90 (0.61, 1.00)
Variegate Darter *Etheostoma variatum*	0.07 (0.02, 0.14)	0.90 (0.61, 1.00)

densities in the Upper Delaware River watershed during the same period (2013–2023; Morrill et al., 2024). American Eels at DEWA in our study were also more likely to occupy sites with larger watersheds, closer to the Delaware River, further emphasizing that habitat connectivity with the river is crucial for this highly migratory species. Together, these findings suggest that this regional stock of American Eel, a species of widespread conservation concern, is benefiting from the protection and management of over 75% of the nontidal main stem of the Delaware River as "free-flowing" under the National Wild and Scenic Rivers Act (including DEWA and other NPS park units; Dittman et al., 2009; NPS, 2012).

In addition to the important ecological drivers of occupancy already mentioned, aspects of stream morphology and instream habitat were important predictors for many species. Specifically, most species in both parks were more likely to occupy lower gradient stream reaches, many species were more likely to inhabit tributaries near a large river, and species at NERI were more likely to occur at sites with greater average depth. In areas with steep topography and frequent natural habitat disturbances from floods and droughts (Wellman, 2004), which are prevalent throughout the Appalachian region, stream reaches with lower slopes and deeper pools provide habitat stability for community persistence, and connectivity with a stable source population (i.e., the riverine communities) allows for recolonization (Grossman et al., 1998; Grossman & Sabo, 2010). Conversely, the only species more likely to occupy sites farther from a major river confluence at both parks was Creek Chub, which is a common pioneer species in many headwater streams due to its ability to persist in intermittent environments and tolerate a wide range of conditions (Fitzgerald et al., 1999; Walker & Adams, 2016). It is also possible that Creek Chub existed in headwater reaches due to human translocation (i.e., bait bucket releases; Nielsen, 1982; PFBC, 2022), given the prevalence of steep slopes and natural barriers in the mid-reaches of many DEWA and NERI streams that would typically prohibit Creek Chub movement (Boizard et al., 2009; Faulk, 2015). Despite the illegality of transferring baitfish between waterways in both parks per the respective state regulations (PFBC, 2022; West Virginia Division of Natural Resources, 2022), the potential anthropogenic movement of aquatic species within, into, and out of parks remains a challenge when managing freshwater PAs for both resource preservation and recreational use. However, considering that Creek Chub was a common and widely distributed native species in both parks, their presence in headwater steams does not necessarily warrant ecological concern.

The mixed response of occupancy to percentage of natural fish cover between parks was unexpected, as occupancy was hypothesized to increase with higher levels of fish cover, regardless of location. However, because most sites had comparatively intact habitat, even the minimum values of fish cover observed in this study were likely suitable for most species. Therefore, a spurious distribution of species skewed toward sites with lower fish cover values may be responsible for the negative association between species occupancy and fish cover at DEWA. Conversely, several NERI species were more likely to occupy sites with metrics indicative of higher quality habitat (i.e., USEPA rapid habitat score, percentage of mixed riparian vegetation, and natural fish cover), which further underscores the importance of stable, aquatic habitat in a frequently disturbed environment, even for species that are considered tolerant to a wide range of conditions (e.g., Blacknose Dace, Creek Chub, and Green Sunfish; Grabarkiewicz & Davis, 2008; Halliwell et al., 1999).

Unsurprisingly, communities throughout both parks were dominated by diverse groups of cool- to warmwater species (Faulk, 2015; Halliwell et al., 1999) that responded positively to different measures of stream temperature, indicating that the current upper range of stream temperatures in both parks are suitable for species in these thermal guilds. Although Brown Trout at DEWA were more likely to occupy sites that did not frequently exceed 20°C, there is evidence to suggest that even coldwater obligate species like trout can tolerate exposures to temperatures above their thermal optimal range for short periods of time (Carline & Machung, 2001). Additionally, the

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

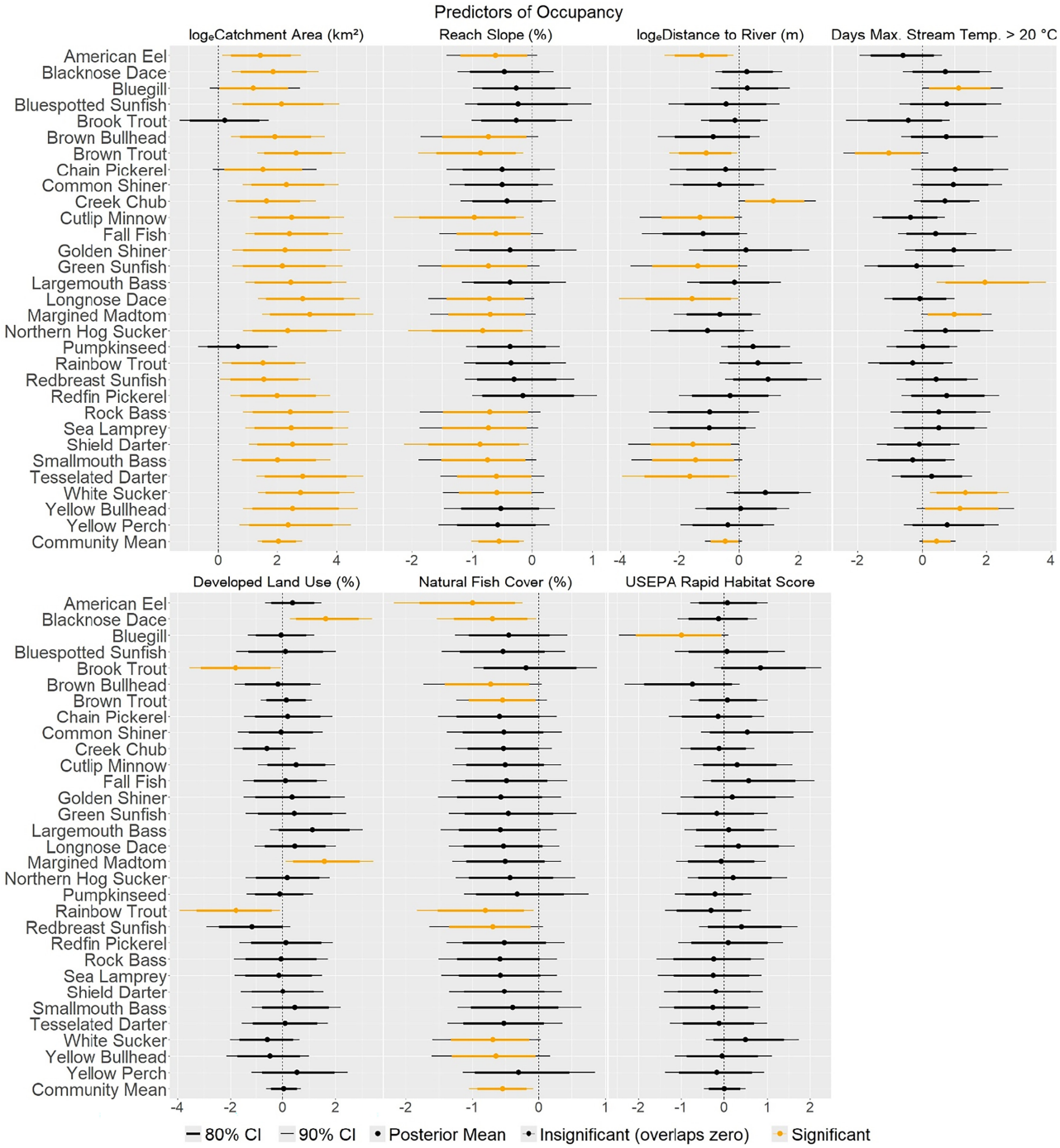

Figure 4. Estimated posterior mean effects with credible intervals (CIs) of habitat variables on species occupancy probabilities at Delaware Water Gap National Recreation Area in 2023. See Table 1 for species scientific names.

relatively high occupancy probabilities of both Brown Trout and Brook Trout at DEWA indicate that the stream temperatures are currently tolerable and that the park contains areas of thermal refugia, which will become increasingly important as climate change threatens coldwater species (Kirk et al., 2022; Reid et al., 2019).

Interestingly, estimates of detection differed for more species between sampling periods than estimates of occupancy. Significant differences in detection probabilities were possibly due to observer bias between sampling periods, as previous studies have found significant heterogeneity in detection probabilities estimated from surveys with differing observers (Schmidt et al., 2023). However, the two-panel sampling design used during the 2023 survey may have contributed to greater species detection by decreasing the average time between repeat visits from 29 d during the 2013 survey to 9 d, therefore reducing the possibility of violating the closure assumption of the occupancy modeling framework. This is consistent with recommendations that repeat surveys for occupancy studies be conducted in as quick succession as possible (MacKenzie & Royle, 2005) and also demonstrates that the improved sampling design is an accurate method for continuing to monitor

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

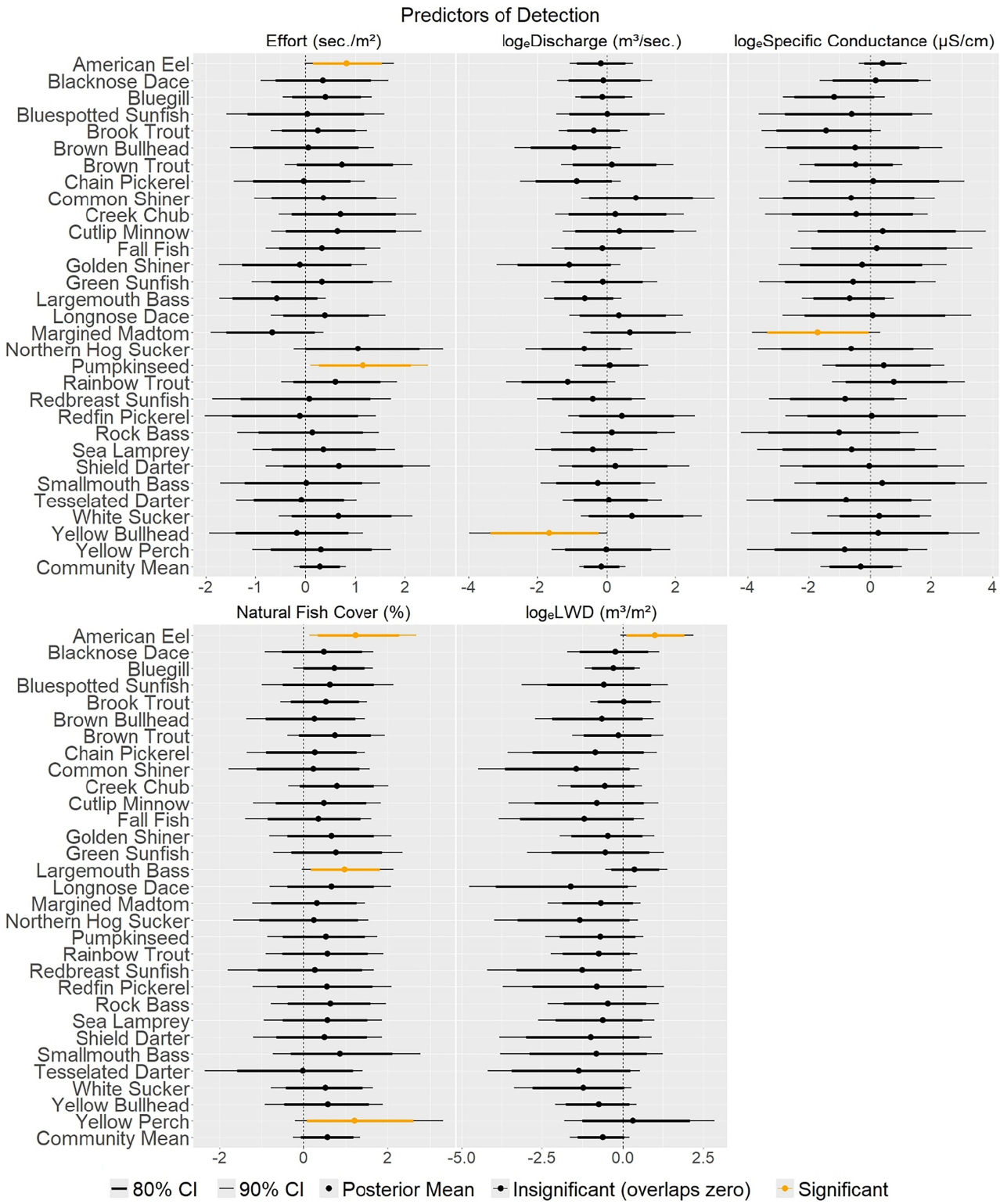

Figure 5. Estimated posterior mean effects with credible intervals (CIs) of habitat and effort variables on species detection probabilities at Delaware Water Gap National Recreation Area in 2023. See Table 1 for species scientific names.

stream fish species occupancy and detection in the ERMN, which is necessary to assess if these PAs are meeting freshwater biodiversity conservation goals (Acreman et al., 2020; Geldmann et al., 2015; Hermoso et al., 2016).

Compared to predictors of occupancy, habitat variables and measures of sampling effort did not strongly influence detection for most species at either park. The lack of significant effects of either EF effort or stream conductivity on detection for many species suggests that effort was similar throughout the study and that voltage settings were effectively standardized to specific conductance. Of those species whose detection was significantly influenced by specific conductance,

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

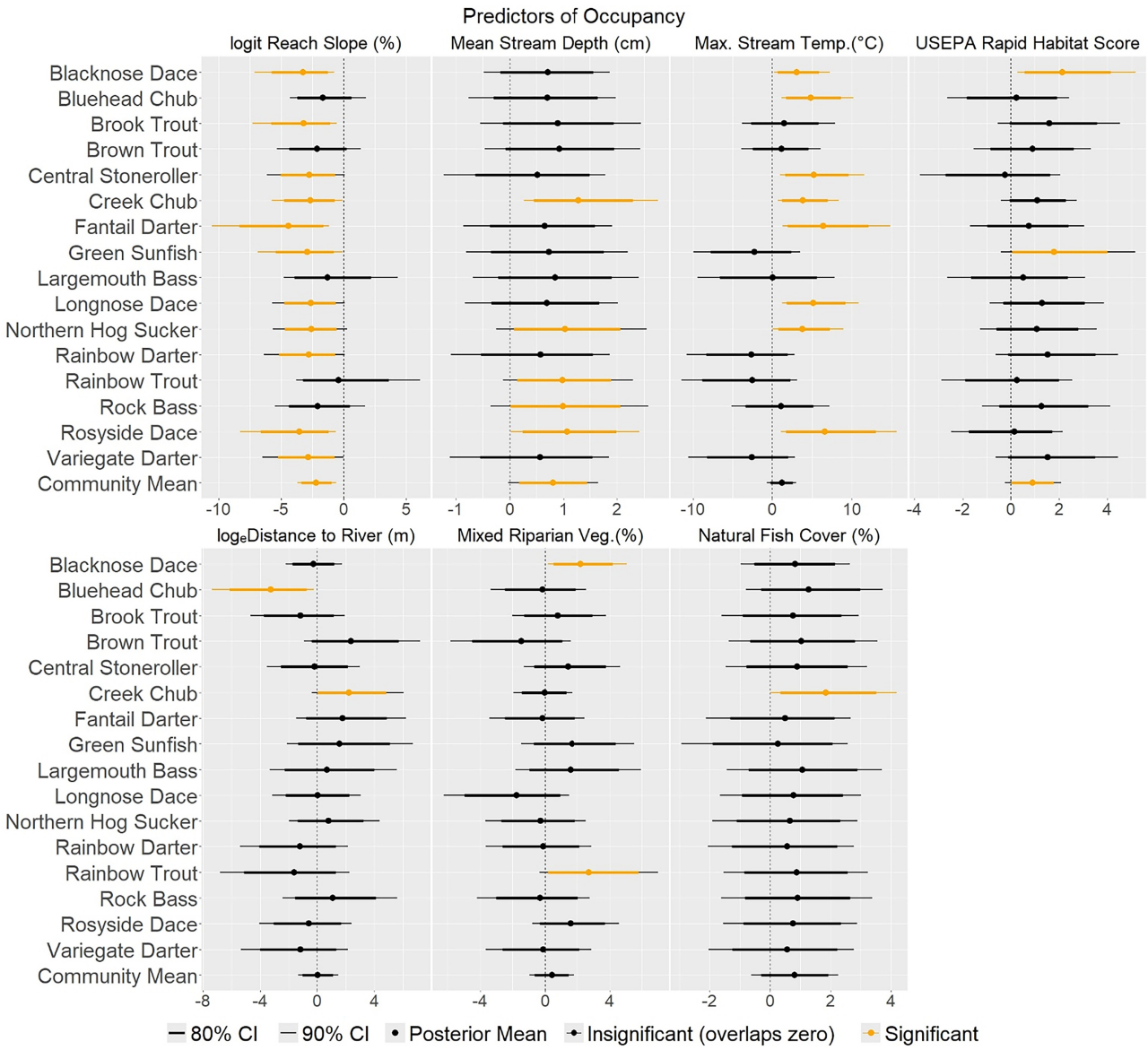

Figure 6. Estimated posterior mean effects with credible intervals (CIs) of habitat variables on species occupancy probabilities at New River Gorge National Park and Preserve in 2023. See Table 2 for species scientific names.

most were more likely to be detected in higher conductivity streams, which is consistent with the EF principle that reduced resistance with increasing specific conductance contributes to increased catchability (Reynolds & Kolz, 2013). Although detection for few species did respond contradictorily to this principle, some studies have reported a similar negative correlation (White et al., 2020), but the mechanism behind this relationship remains unclear. Additionally, we targeted most sampling visits during baseflow conditions for crew safety and EF efficiency, which limited instances of high discharge, turbid waters, and stream depths that were not easily wadeable. As a result, the effects of these environmental variables on detection for most species were reduced. The negative effect of number of netters per meter of stream width on the detection probabilities for several species at NERI was counterintuitive to suggestions for effective backpack EF (Reynolds & Kolz, 2013). However, the number of netters during this study was usually three, with additional netters who were often much less experienced than the primary EF crew only helping at a few larger sites. This suggests that more netters during backpack EF surveys may not always be beneficial, depending on the skill level of the additional surveyors, and that effective monitoring of stream fish communities in the ERMN parks can be conducted with small but experienced field crews, which is beneficial considering that budgetary constraints often limit research strategies for managers of PAs. Overall, the ERMN wadeable stream fish monitoring program, and more generally the NPS I&M Program, provides an example for robust research and sampling designs, which are necessary to ensure that PAs are meeting conservation goals.

This case study of decadal stability in the stream fish communities of two U.S. national parks indicates that terrestrial PAs could efficiently serve as a core network of freshwater PAs to help mitigate the decline of aquatic biodiversity. Although there are opportunities to implement more proactive management practices to increase freshwater fish diversity and

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

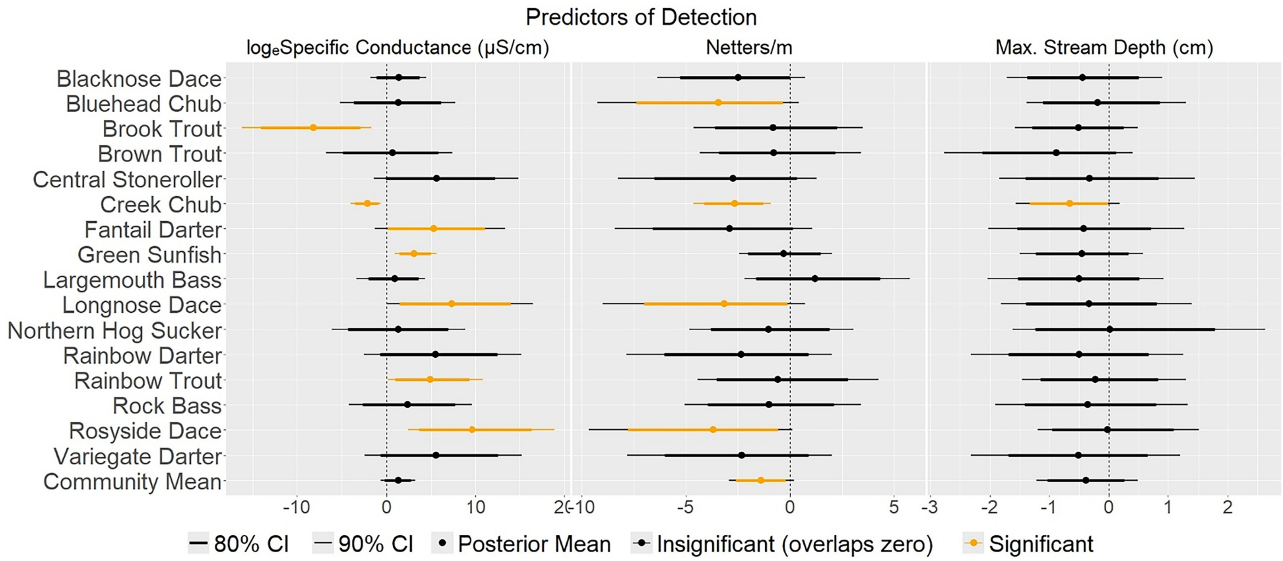

Figure 7. Estimated posterior mean effects with credible intervals (CIs) of habitat and effort variables on species detection probabilities at New River Gorge National Park and Preserve in 2023. See Table 2 for species scientific name.

improve the resilience of aquatic habitats, such as targeted removal of nonnative species and impoundments, strategic additions of LWD, and riverbank stabilization along nearby trails, it is important to note that NPS management policies prioritize the preservation of natural resources with minimal intervention (NPS, 2006). Therefore, as long as the stream fish communities in DEWA and NERI continue to remain relatively intact and unchanged, these PAs can be considered effective at meeting their established conservation goal—that is, to maintain the "anti-degradation" of wadeable stream fish and their surrounding ecosystems (Marshall et al., 2016; Tzilkowski et al., 2016). Our results are also consistent with recent ERMN reports that indicate stable or increasing riparian bird abundance for most species in DEWA and NERI from 2007 to 2019, and that both parks maintained high proportions of benthic macroinvertebrate diversity, which exceeded regional benchmarks for quality streams from 2014 to 2019 (Marshall, 2021a, 2021b; Tzilkowski, 2021). Similarly, other studies have concluded that PAs were effective methods for conserving fish species in lakes, rivers, and streams (Acreman et al., 2020; Suski & Cooke, 2007). Finally, this study serves as a temporal benchmark for the continued monitoring of stream fish in ERMN parks to detect early warning signs of environmental decline so that appropriate management strategies can be developed and adapted if necessary. This long-term monitoring will help ensure that wadeable streams in the ERMN maintain their ecological integrity. In turn, these stream ecosystems can serve as references for those in unprotected areas in the Appalachian region of the United States that are likely to experience increased degradation as stressors and demands on freshwater resources continue to rise.

Limitations and improvements

Because the scope of this project was limited to streams within the parks due to the budgetary, safety, and legal challenges that additional sampling on private lands would have imposed and because of the fact that NPS I&M guidelines do not call for monitoring conditions beyond park boundaries, we did not directly compare DEWA and NERI fish communities to those in nearby unprotected areas. Thus, we could not determine if overall freshwater fish biodiversity was significantly greater in wadeable streams inside the parks than in the surrounding area, although future studies may be able to make that comparison. However, our results contradict the trend of rapid declines and extinctions of freshwater fishes in North America (Burkhead, 2012; Walsh et al., 2011) and elsewhere (Darwall & Freyhof, 2016; Su et al., 2021). As stream fish monitoring in the ERMN parks continues, incorporating species count data from repeat surveys into a Bayesian analysis framework through the use of *N*-mixture models or even implementing other more conventional survey methodologies such as mark–recapture could provide local estimates of abundance and detect population declines before a substantial reduction in estimated occupancy might emerge (Ficetola et al., 2018; Lamothe et al., 2023). However, given our inability to confidently standardized fish counts and factors influencing detection between sampling periods due to incomplete EF effort records and habitat data from 2013, which violates multiple assumptions of *N*-mixture models, occupancy was adopted as the primary variable of interest for the current study and sampling design. Additionally, we did not attempt to estimate transitional states of colonization and extinction using dynamic occupancy models (Royle & Kéry, 2007) due to lack of sufficient replicates of the primary sampling season (annual surveys), sites differing between years, and substantial temporal gaps (8–10 years) in the two primary surveys, although this analysis could be possible with continued long-term monitoring. Lastly, the lack of significant decadal changes in mean occupancy probabilities specifically at NERI is possibly due to the comparatively low number of sample sites where fish were detected (n sites with fish detected in 2023 = 21) in each sampling period, with several sites being sampled only once in 2023 due to timing constraints. At similar average rates of occupancy and detection ($\psi = 0.2$; $P = 0.8$), other studies have shown that a significantly

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

larger number of sites or repeat visits may be necessary to detect even moderate levels of change (e.g., a 50% proportional reduction in occupancy; Guillera-Arroita & Lahoz-Monfort, 2012; Lamothe et al., 2023). While greatly increasing the number of sites or visits would be logistically and monetarily unfeasible for the ERMN monitoring program, they might consider replacing some of the randomly selected sites repeatedly found to be "fishless" at NERI due to natural barriers and hydrologic regimes with other new sites so that the total number of sites with persistent stream fish communities equals that of DEWA (n sites with fish detected in 2023 = 29), where significant differences in estimates of occupancy were detected between sampling periods for some species. As ERMN wadeable stream fish monitoring is still relatively new compared to the other "vital signs" being monitored (e.g., riparian birds and benthic macroinvertebrates), study design and sampling protocols may continue to adapt with increasing knowledge and research capacity.

SUPPLEMENTARY MATERIAL

Supplementary material (see online Supplementary Material) is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

Model code is available at https://doi.org/10.5066/P1KGDEWL. Raw data are available at https://doi.org/10.57830/2302037. Photo vouchers and other supporting information are available at https://irma.nps.gov/DataStore/Reference/Profile/2304804.

ETHICS STATEMENT

All fish sampling was conducted under state and federal permits and in accordance with the Pennsylvania State University Institutional Animal Care and Use Committee Protocol #202001614.

FUNDING

This work was supported by the National Park Service under Cooperative Agreement P17AC01033 and Task Agreement P20AC01018. F. E. Buderman was also supported by the U.S. Department of Agriculture National Institute of Food and Agriculture and Hatch Appropriations under Hatch Project PEN04758 and accession number 1024904.

CONFLICTS OF INTEREST

The authors declare that there is no conflict of interest.

ACKNOWLEDGMENTS

We thank Penn State field technicians Jacob Haglund, Isaac Nulton, Valerie Kuppek, and Alanna Lowther for their work in collecting fish and habitat data used in this study. We also thank NPS Natural Resources staff Jennifer Flippin, Doug Manning, Andy Weber, and Jonathan Malzone and numerous seasonal technicians and interns for their additional field support. Additional thanks to ERMN data manager Kristina Callahan for sourcing GIS data and creating the database used to house data from this study. Additionally, we appreciate the efforts of ERMN seasonal technicians Scott Stollery and Nikki Flood in installing and retrieving temperature loggers during this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Acreman, M., Hughes, K. A., Arthington, A. H., Tickner, D., & Dueñas, M.-A. (2020). Protected areas and freshwater biodiversity: A novel systematic review distils eight lessons for effective conservation. *Conservation Letters*, **13**, Article e12684. https://doi.org/10.1111/conl.12684

Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J. (2016). Fish conservation in freshwater and marine realms: Status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **26**, 838–857. https://doi.org/10.1002/aqc.2712

Boizard, J., Magnan, P., & Angers, B. (2009). Effects of dynamic landscape elements on fish dispersal: The example of Creek Chub (*Semotilus atromaculatus*). *Molecular Ecology*, **18**, 430–441. https://doi.org/10.1111/j.1365-294X.2008.04044.x

Bulbul Ali, A., & Mishra, A. (2022). Effects of dissolved oxygen concentration on freshwater fish: A review. *International Journal of Fisheries and Aquatic Studies*, **10**, 113–127. https://doi.org/10.22271/fish.2022.v10.i4b.2693

Burkhead, N. M. (2012). Extinction rates in North American freshwater fishes, 1900–2010. *BioScience*, **62**, 798–808. https://doi.org/10.1525/bio.2012.62.9.5

Carline, R. F., & Machung, J. F. (2001). Critical thermal maxima of wild and domestic strains of trout. *Transactions of the American Fisheries Society*, **130**, 1211–1216. https://doi.org/10.1577/1548-8659(2001)130<1211:CTMOWA>2.0.CO;2

Cincotta, D. A., Chambers, D. B., & Messinger, T. (1999). Recent changes in the distribution of fish species in the New River basin in West Virginia and Virginia. In *Proceedings of the New River symposium, Boone, North Carolina* (pp. 98–106). National Park Service.

Darwall, W. R. T., & Freyhof, J. (2016). Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 1–36). Cambridge University Press. https://doi.org/10.1017/CBO9781139627085.002

Dewitz, J., & U.S. Geological Survey. (2021). *National Land Cover Database (NLCD) 2019 products* (Version 3.0, February 2024) U.S. Geological Survey. https://doi.org/10.5066/P9KZCM54

Dittman, D. E., Machut, L. S., & Johnson, J. H. (2009). *American Eel history, status, and management options: Delaware River drainage*. New York State Department of Environmental Conservation.

Faulk, E. (2015). *Patterns in distribution of stream fishes in the eastern rivers and mountains network: A multi-species occupancy approach* [Master's thesis, The Pennsylvania State University]. PennState University Libraries. https://etda.libraries.psu.edu/files/final_submissions/10526

Faulk, E., & Weber, A. (2017). *Eastern Rivers and Mountains Network stream fish monitoring program: Summary of 2013–2014 pilot sampling* (Natural Resource Data Series NPS/ERMN/NRDS—2017/1084). National Park Service.

Fenske, K. H., Wilberg, M. J., Secor, D. H., & Fabrizio, M. C. (2011). An age- and sex-structured assessment model for American Eels (*Anguilla rostrata*) in the Potomac River, Maryland. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1024–1037. https://doi.org/10.1139/f2011-038

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

Ficetola, G. F., Barzaghi, B., Melotto, A., Muraro, M., Lunghi, E., Canedoli, C., Lo Parrino, E., Nanni, V., Silva-Rocha, I., Urso, A., Carretero, M. A., Salvi, D., Scali, S., Scarì, G., Pennati, R., Andreone, F., & Manenti, R. (2018). *N*-mixture models reliably estimate the abundance of small vertebrates. *Scientific Reports*, **8**, Article 10357. https://doi.org/10.1038/s41598-018-28432-8

Fitzgerald, D., Lanno, R., & Dixon, D. (1999). A comparison of a sentinel species evaluation using Creek Chub (*Semotilus atromaculatus mitchill*) to a fish community evaluation for the initial identification of environmental stressors in small streams. *Ecotoxicology*, **8**, 33–48. https://doi.org/10.1023/A:1008853413528

Geldmann, J., Coad, L., Barnes, M., Craigie, I. D., Hockings, M., Knights, K., Leverington, F., Cuadros, I. C., Zamora, C., Woodley, S., & Burgess, N. D. (2015). Changes in protected area management effectiveness over time: A global analysis. *Biological Conservation*, **191**, 692–699. https://doi.org/10.1016/j.biocon.2015.08.029

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis* (3rd ed.). CRC Press/Taylor Francis Group.

Grabarkiewicz, J., & Davis, W. (2008). *An introduction to freshwater fishes as biological indicators* (EPA-260-R-08-016). U.S. Environmental Protection Agency.

Grossman, G. D., Ratajczak, R. E., Jr., Crawford, M., & Freeman, M. C. (1998). Assemblage organization in stream fishes: Effects of environmental variation and interspecific interactions. *Ecological Monographs*, **68**, 395–420. https://doi.org/10.1890/0012-9615(1998)068[0395:AOISFE]2.0.CO;2

Grossman, G. D., & Sabo, J. L. (2010). Incorporating environmental variation into models of community stability: Examples from stream fish. In K. B. Geido, & D. A. Jackson (Eds.), *Community ecology of stream fishes: Concepts, approaches, and techniques* (**Symposium 73**, pp. 407–426). American Fisheries Society. https://doi.org/10.47886/9781934874141.ch20

Guillera-Arroita, G., & Lahoz-Monfort, J. J. (2012). Designing studies to detect differences in species occupancy: Power analysis under imperfect detection. *Methods in Ecology and Evolution*, **3**, 860–869. https://doi.org/10.1111/j.2041-210X.2012.00225.x

Halliwell, D. B., Langdon, R. W., Daniels, R. A., Kurtenbach, J. P., & Jacobson, R. A. (1999). Classification of freshwater fish species of the northeastern United States for use in development of indices of biological integrity, with regional applications. In T. P. Simon (Ed.), *Assessing the sustainability and biological integrity of water resources using fish communities* (pp. 301–338). CRC Press.

Heck, M. P., Shultz, L. D., Hockman-Wert, D., Dinger, E. C., & Dunham, J. B. (2018). *Monitoring stream temperatures—A guide for non-specialists* (Techniques and Methods 3-A25). U.S. Geological Survey. https://doi.org/10.3133/tm3A25.

Hermoso, V., Abell, R., Linke, S., & Boon, P. (2016). The role of protected areas for freshwater biodiversity conservation: Challenges and opportunities in a rapidly changing world. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **26**, 3–11. https://doi.org/10.1002/aqc.2681

Horwitz, R., Overbeck, P., Keller, D., & Moser, S. (2014). *Fish inventories of Delaware Water Gap National Recreation Area and Upper Delaware Scenic and Recreational River* (Natural Resource Report NPS/ERMN/NRR—2014/864). National Park Service.

Hudy, M., Thieling, T. M., Gillespie, N., & Smith, E. P. (2008). Distribution, status, and land use characteristics of subwatersheds within the native range of Brook Trout in the eastern United States. *North American Journal of Fisheries Management*, **28**, 1069–1085. https://doi.org/10.1577/M07-017.1

Hughes, K. (2021). *The world's forgotten fishes*. World Wide Fund for Nature.

Infante, D. M., & Allan, J. D. (2010). Response of stream fish assemblages to local-scale habitat as influenced by landscape: A mechanistic investigation of stream fish assemblages. In K. B. Gido, & D. A. Jackson (Eds.), *Community ecology of stream fishes: Concepts, approaches, and techniques* (**Symposium 73**, pp. 371–397). American Fisheries Society. https://doi.org/10.47886/9781934874141.ch18

Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities—The roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 157–170. https://doi.org/10.1139/f00-239

Jenkins, R. E., & Burkhead, N. M. (1994). *The freshwater fishes of Virginia*. American Fisheries Society.

Kanno, Y., Letcher, B. H., Rosner, A. L., O'Neil, K. P., & Nislow, K. H. (2015). Environmental factors affecting Brook Trout occurrence in headwater stream segments. *Transactions of the American Fisheries Society*, **144**, 373–382. https://doi.org/10.1080/00028487.2014.991446

Kaufmann, P. R., Levine, P., Robison, E. G., Seeliger, C., & Peck, D. V. (1999). *Quantifying physical habitat in wadeable streams* (EPA/620/R-99/003). U.S. Environmental Protection Agency.

Kellner, K. (2021). *jagsUI: A wrapper around "rjags" to streamline "jags" analyses*. R package version 1.5.2. https://CRAN.R-project.org/package=jagsUI

Kéry, M., & Royle, J. A. (2016). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS*. Academic Press.

Kirk, M. A., Hazlett, M. A., Shaffer, C. L., & Wissinger, S. A. (2022). Forested watersheds mitigate the thermal degradation of headwater fish assemblages under future climate change. *Ecology of Freshwater Fish*, **31**, 559–570. https://doi.org/10.1111/eff.12650

Lamothe, K. A., Reid, S. M., & Drake, D. A. R. (2023). *Considerations around effort and power for an occupancy-based Redside Dace (*Clinostomus elongatus*) monitoring program across spatial and temporal scales (*Research Document 2023/034*)*. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat.

Lawrence, D. J., Larson, E. R., Liermann, C. A. R., Mims, M. C., Pool, T. K., & Olden, J. D. (2011). National parks as protected areas for U.S. freshwater fish diversity. *Conservation Letters*, **4**, 364–371. https://doi.org/10.1111/j.1755-263X.2011.00185.x

Lemmon, P. E. (1957). A new instrument for measuring forest overstory density. *Journal of Forestry*, **55**, 667–669. https://academic.oup.com/jof/article/55/9/664/4685661

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence* (2nd ed.). Academic Press.

MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, **42**, 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

Makowski, D., Ben-Shachar, M., & Lüdecke, D. (2019). Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology*, **10**, Article 2767. https://doi.org/10.3389/fpsyg.2019.02767

Marshall, M. R. (2021a). *Streamside bird monitoring in the Eastern Rivers and Mountains Network: Delaware Water Gap National Recreation Area 2007–2019* (Natural Resource Report NPS/ERMN/NRR—2021/2326). National Park Service.

Marshall, M. R. (2021b). *Streamside bird monitoring in the Eastern Rivers and Mountains Network: New River Gorge National Park and Preserve 2007–2019* (Natural Resource Report NPS/ERMN/NRR—2021/2329). National Park Service.

Marshall, M. R., & Piekielek, N. B. (2007). *Eastern Rivers and Mountains Network ecological monitoring plan* (Natural Resource Report NPS/ERMN/NRR—2007/017). National Park Service.

Marshall, M. R., Tzilkowski, C. J., & Callahan, K. K. (2016). *Streamside bird monitoring protocol for the Eastern Rivers and Mountains Network: Protocol narrative* (Version 3.0, Natural Resource Report NPS/ERMN/NRR—2016/1224). National Park Service.

Morrill, D. P., Keiler, D. H., & Rohrback, C. R. (2024). Patterns in fish-assemblage structure over a decade of monitoring in the Upper Delaware River watershed. *Northeastern Naturalist*, **31**, 188–201. https://doi.org/10.1656/045.031.0203

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafafs/vnae001/8081928 by guest on 19 March 2025

National Park Service. (2006). *Management policies*. U.S. Government Printing Office.

National Park Service. (2012). *Delaware River basin: Wild and scenic river values*. National Park Service.

National Park Service. (2023). *NPS Acreage 12-31-2023* (Quarterly acreage report). National Park Service, Land Resources Division.

Nielsen, L. A. (1982). The bait-fish industry in Ohio and West Virginia, with special reference to the Ohio River sport fishery. *North American Journal of Fisheries Management*, **2**, 323–238. https://doi.org/10.1577/1548-8659(1982)2<232:TBIIOA>2.0.CO;2

Northrup, J. M., & Gerber, B. D. (2018). A comment on priors for Bayesian occupancy models. *PLoS One*, **13**, Article e0192819. https://doi.org/10.1371/journal.pone.0192819

Pennsylvania Fish and Boat Commission. (2021). *2021 Pennsylvania fishing summary/boating handbook*. Pennsylvania Fish and Boat Commission.

Pennsylvania Fish and Boat Commission. (2022). *2022 Pennsylvania fishing summary/boating handbook*. Pennsylvania Fish and Boat Commission.

Pike, C., Casselman, J., Crook, J., DeLucia, M.-B., Jacoby, D., & Gollock, M. (2023). *Anguilla rostrata*. *IUCN Red List of Threatened Species,* 2023, Article e.T191108A129638652. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T191108A129638652.en

Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling* (Version 4.3.1). https://sourceforge.net/projects/mcmc-jags/files/

Pringle, R. M. (2017). Upgrading protected areas to conserve wild biodiversity. *Nature*, **546**, 91–99. https://doi.org/10.1038/nature22902

Rabeni, C. F., Lyons, J., Mercado-Silva, N., & Peterson, J. T. (2009). Warmwater fish in wadeable streams. In S. A. Bonar, W. A. Hubert, & D. W. Willis (Eds.), *Standard methods for sampling North American freshwater fishes* (pp. 119–138). American Fisheries Society. https://doi.org/10.47886/9781934874103

R Core Team. (2022). *A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, **94**, 849–873. https://doi.org/10.1111/brv.12480

Reynolds, J. B., & Kolz, A. L. (2013). Electrofishing. In A. V. Zale, D. L. Parrish, & T. M. Sutton (Eds.), *Fisheries techniques* (3rd ed., pp. 305–361). American Fisheries Society. https://doi.org/10.47886/9781934874295.ch8

Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, **88**, 1813–1823. https://doi.org/10.1890/06-0669.1

Schmidt, B. R., Cruickshank, S. S., Bühler, C., & Bergamini, A. (2023). Observers are a key source of detection heterogeneity and biased occupancy estimates in species monitoring. *Biological Conservation*, **283**, Article 110102. https://doi.org/10.1016/j.biocon.2023.110102

Schultz, A. A., Maughan, O. E., Bonar, S. A., & Matter, W. J. (2003). Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. *North American Journal of Fisheries Management*, **23**, 203–511. https://doi.org/10.1577/1548-8675(2003)023<0503:EOFOAO>2.0.CO;2

Stauffer, J. R., Boltz, J. M., & White, L. R. (1995). The fishes of West Virginia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **146**, 1–389. http://www.jstor.org/stable/4065019

Stum, M. (2024). *Decadal changes in stream fish communities and contemporary ecological drivers of species occupancy in two Appalachian U.S. national parks* [Master's thesis, The Pennsylvania State University]. PennState University Libraries. https://etda.libraries.psu.edu/catalog/34278mbs6798

Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., & Brosse, S. (2021). Human impacts on global freshwater fish biodiversity. *Science*, **371**, 835–838. https://doi.org/10.1126/science.abd3369

Suski, C. D., & Cooke, S. J. (2007). Conservation of aquatic resources through the use of freshwater protected areas: Opportunities and challenges. *Biodiversity & Conservation*, **16**, 2015–2029. https://doi.org/10.1007/s10531-006-9060-7

Tzilkowski, C. J. (2021). *Benthic macroinvertebrate monitoring in Eastern Rivers and Mountains Network wadeable streams: 2014–2019 summary report* (Natural Resource Report NPS/ERMN/NRR—2021/2329). National Park Service.

Tzilkowski, C. J. (2024). *Sub-hourly stream temperature measurements throughout Delaware Water Gap National Recreation Area and New River Gorge National Park and Preserve (2022–2023) data package*. National Park Service. https://doi.org/10.57830/2302125

Tzilkowski, C. J., Weber, A. S., Callahan, K. K., & Marshall, M. R. (2016). *Protocol implementation plan for benthic macroinvertebrate monitoring in the Eastern Rivers and Mountains Network* (Natural Resource Report NPS/ERMN/NRR—2016/1265). National Park Service.

United Nations Environment Programme World Conservation Monitoring Center and International Union for the Conservation of Nature. (2021). *Protected planet report 2020*. United Nations Environment Programme World Conservation Monitoring Center; International Union for the Conservation of Nature.

U.S. Environmental Protection Agency. (2004). *Wadeable stream assessment: Field operations manual* (EPA841-B04-004). U.S. Environmental Protection Agency, Office of Water and Office of Research and Development.

U.S. Geological Survey (2018a). *USGS National Hydrography Dataset Plus High Resolution (NHDPlus HR) for 4-digit Hydrologic Unit – 0204* [GeoPackage]. U.S. Geological Survey. https://apps.nationalmap.gov/downloader/#/

U.S. Geological Survey (2018b). *USGS National Hydrography Dataset Plus High Resolution (NHDPlus HR) for 4-digit Hydrologic Unit – 0505* [GeoPackage]. U.S. Geological Survey. https://apps.nationalmap.gov/downloader/#/

Visconti, P., Butchart, S. H. M., Brooks, T. M., Langhammer, P. F., Marnewick, D., Vergara, S., Yanosky, A., & Watson, J. E. M. (2019). Protected area targets post-2020. *Science*, **364**, 239–241. https://doi.org/10.1126/science.aav6886

Walker, R. H., & Adams, G. L. (2016). Ecological factors influencing movement of Creek Chub in an intermittent stream of the Ozark Mountains, Arkansas. *Ecology of Freshwater Fish*, **25**, 190–202. https://doi.org/10.1111/eff.12201

Walsh, S. J., Jelks, H. L., & Burkhead, N. M. (2011). The decline of North American freshwater fishes. *American Currents*, **36**, 10–17. https://www.nanfa.org/ac/freshwater-fishes-decline.pdf

Wang, L., Seelbach, P., & Hughes, R. (Eds.). (2006). *Landscape influences on stream habitats and biological assemblages* (Symposium 48). American Fisheries Society. https://doi.org/10.47886/9781888569766

Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, **515**, 67–73. https://doi.org/10.1038/nature13947

Wellman, D. I. (2004). *Post-flood recovery and distributions of fishes within the New River Gorge National River, West Virginia* [Master's thesis, West Virginia University]. The Research Repository @ WVU. https://researchrepository.wvu.edu/etd/2001

West Virginia Division of Natural Resources. (2022). *West Virginia DNR fishing regulations summary 2022*. West Virginia Division of Natural Resources.

White, S., Faulk, E., Tzilkowski, C., Weber, A., Marshall, M., & Wagner, T. (2020). Predicting fish species richness and habitat relationships using Bayesian hierarchical multispecies occupancy models. *Canadian Journal of Fisheries and Aquatic Sciences*, **77**, 602–610. https://doi.org/10.1139/cjfas-2019-0125

Wofford, J. E. B., & Demarest, E. D. (2018). *Shenandoah National Park fish monitoring protocol* (Version 5.0, Natural Resource Report NPS/SHEN/NRR—2018/1646). National Park Service.

Downloaded from https://academic.oup.com/tafs/advance-article/doi/10.1093/tafs/vnae001/8081928 by guest on 19 March 2025