STREAM FISH POPULATION TRENDS AND RESPONSE TO FLOW VARIABILITY AT REGIONAL AND NATIONAL SCALES

by

EDWARD SAGE STOWE

(Under the Direction of Seth J. Wenger and Mary C. Freeman)

ABSTRACT

Fishes of streams and rivers are a highly diverse group of animals that play important roles in freshwater ecosystems and sustain many human populations. However, stream fishes are globally imperiled by dams, water extraction, pollution, exploitation, and the spread of invasive species—stressors that will be exacerbated by climate change. Stream fish conservation is hampered by a poor understanding of the status of many species and an inability to predict how species will respond to changes in environmental variation like streamflow. In this dissertation, I used long-term datasets and hierarchical models to provide insight into stream fish population trends and response to streamflow variability to inform their conservation and management. First, I assessed population trends of an endangered stream fish, the Amber Darter *Percina antesella*, and demonstrated that both of its known populations are declining precipitously and in synchronous fashion, which compounds its overall extinction rate. I then compiled over twenty long-term fish time-series datasets from across the contiguous U.S. to perform two largescale analyses. First, I assessed characteristics of stream fish population trends in over 200 subwatersheds. I found that stream fishes at the subwatershed scale are declining by a median annual rate of 0.3% but that patterns in trends are spatially variable: systems in the arid

Southwest and Great Plains have declined, losing opportunistic and periodic fish taxa, while Eastern sites demonstrated more positive trends, driven by increases in cosmopolitan species. Using the same large dataset, I next explored whether fishes of two ubiquitous guilds—riffle dwellers and nest builders—responded to low- and high-flow events based on hypothesized mechanistic flow-ecology relationships. I found few consistent responses to flow among guild members and little overall support for the hypotheses that stable low flows benefit nest fishes, moderate flows benefit riffle fishes, and extreme high flows harm both guilds. Overall my results highlight important variability in both how stream fish populations are changing through time and how they respond to extreme flows, information that can be employed to better conserve and manage these important animals.

INDEX WORDS: Bayesian analysis, Extinction risk, Fish conservation, Flow ecology, Hierarchical models, Population trends, Status assessments, Stream fishes

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Freshwater ecosystems worldwide support a tremendous amount of biodiversity. Despite covering less than 1% of the Earth's surface, they are estimated to harbor over 100,000 species [1], including 18,000 different fishes, a quarter of all vertebrates [2]. The high biodiversity, abundance, and biomass of freshwater fishes make them important constituents of their ecosystems, with key roles in freshwater food webs and nutrient cycling [3]. Freshwater fish also serve as a key source of protein in many parts of the world [4].

Freshwater ecosystems have been characterized by a profound loss of biodiversity in historical and recent time periods, with rates of extinction five times higher than in terrestrial ecosystems [1]. Fishes have not been spared. Pronounced changes in fish biodiversity have occurred in half of the world's rivers [5], and numerous fish taxa have gone extinct worldwide, including 55 fishes in North America in the last century [6], with many other taxa severely imperiled [7]. Fishes in flowing waters may be particularly susceptible to extinction as rivers and streams become "lentified" by dams, water withdrawals, and climate change [8]. Still, our understanding of the extent to which fishes have declined is incomplete. While extinction risk analyses such as the IUCN Red List broadly indicate degrees of imperilment, there are relatively few quantitative assessments of fish trends available.

The principal factors that contribute to the loss of freshwater fishes are flow modification, overexploitation, water pollution, habitat degradation, and species invasion [1]. Many fish extirpations documented during historical times have unambiguous causes, especially those of large, migratory species [9]. For example, nearly all diadromous sturgeon species have declined or gone extinct throughout the world following overharvesting for caviar and extensive damming of spawning rivers [10], a fate shared by many Pacific salmon populations [11]. Alteration of flow regimes has also had a dire effect on many taxa of fish. Dams in the Great Plains, for example, have eliminated many of the flow pulses that pelagic-spawning minnows need to carry out their life cycle, resulting in numerous extirpations in this region [12].

The proximate causes of many contemporary fish declines, however, are poorly understood. Most fishes live in waterbodies subject to degradation by several pathways. Urban and agricultural land use can impact fishes through increased stream temperature and flashiness; introduced contaminants, pesticides and heavy metals; and altered physical habitat. Similarly, dams alter hydrology, in-stream habitat, temperature, and connectivity. Different stressors may interact and produce synergistic or antagonistic effects [13], and fish may respond to stressors decades after their occurrence [14]. Finally, the impact of emerging threats such as climate change and new classes of pollutants on fishes remain poorly understood [15]. Consequently, widespread declines of fish communities occur with little understanding of the proximate causes [16].

Functional traits of fishes—intrinsic characteristics of species that influence organismal performance [17]—are a possible explanatory factor for the variation in declines occurring across fish taxa. In addition to migratory fishes, other large-bodied taxa have also been disproportionately affected by extinction, often from overfishing [18]. Small fishes have also been more vulnerable to extinction because of smaller range sizes and limited dispersal capacity [19]. Traits that characterize different life-history strategies also distinguish fishes that are vulnerable to extinction from those that can persist in response to environmental change. Fishes with high parental care, low fecundity, and intermediate size—termed equilibrium species [20]—frequently persist in human-altered rivers, including those affected by dams [21]. Fishes representing other life-history strategies—periodic and opportunistic fishes—often fare poorly under altered environmental variability, and thus comprise many species that have been extirpated. Other ecological traits can also be predictive of extirpation risk. For example, fishes that spawn in gravel may be extirpated in rivers with high sediment loads, with the exception of nest-spawning taxa that engineer their own spawning environment [22]. Still, while there are statistical correlations among traits and risk of imperilment, for many species, the linkage between traits and extinction risk is poorly understood, and co-occurring taxa in decline may share few ecological or life-history traits [16].

Numerous measures have been proposed to stem the decline of stream fishes and promote their recovery, include improving water quality, protecting key habitats, reducing overfishing, controlling non-native taxa, and restoring connectivity [23]. Many such measures are carried out in response to species being granted protected status under statutes such as the Endangered Species Act. Among the most promoted measures to recover stream fishes is the restoration of natural flow regimes, accomplished by altering dam operations or water withdrawals so that discharge variation resembles attributes of the flow regime important for native biota [24, 25]. Successful implementation of environmental flows requires an understanding of how different species are likely to respond to flow changes, but this is not well studied for most taxa.

In this dissertation I used long-term datasets of fish counts to estimate trends in fish populations at two spatial scales, and explored how fishes respond interannually to changes in streamflow. By exploring how stream fish are changing through time and what drives these changes, I aim to provide data that can improve the management and conservation of fishes and inform recovery actions.

In Chapter 2, I analyzed population trends of the Amber Darter *Percina antesella*, an endangered fish found in two rivers of the Upper Coosa basin prized for biodiversity but experiencing substantial declines in their fish fauna [16]. Managing endangered species requires a comprehensive understanding of the status of different populations to assess their overall resilience and prioritize conservation actions. Separate populations of endangered taxa are frequently analyzed independently, but doing so can overlook synchronous dynamics among populations that may increase overall extinction risk [26]. I analyzed Amber Darter abundance data using a hierarchical method that estimates trends for its two populations, while simultaneously assessing empirical support for existence of non-independent dynamics among populations. My analysis provides managers with valuable information on the current status of the two Amber Darter populations, and also demonstrates a method for exploring non-independent dynamics in the vulnerability assessments of imperiled taxa.

In Chapter 3, I analyzed trends of fish populations from across the contiguous U.S. No previous continent-scale fish trend analysis has been conducted, which limits our understanding of the magnitude of population trends, how different stressors and species attributes contribute to trends, and whether trends vary among ecological regions. To do so, I compiled 22 datasets from across the U.S. with counts of 283 different fish species. I used a Bayesian hierarchical model to estimate species trends as a function of a subwatershed-level mean trend, and related subwatershed trends to potential stressor variables. I also assessed whether species-level trends are predicted by life-history and ecological traits.

In Chapter 4, I used the dataset compiled in Chapter 3 to examine how fish populations respond to different flow metrics. I used Bayesian hierarchical models to test mechanistic hypotheses linking low- and high-flow metrics to the response of riffle-dwelling and nest-building fishes, two widespread, important guilds of fishes predicted to respond differentially to flow events. I examined fish response to flow metrics as a function of different hydrologic and climatic contexts, and also assessed if population responses to hydrologic drivers are a function of life-history traits.

The ultimate goal of the dissertation is conservation-driven. The subsequent chapters provide information on the status of fish taxa at regional and continental scales, and how fish populations change in response to both long-term stressors and short-term variation in flow conditions. With stream fish populations facing a future with numerous stressors, scarce water resources, and a changing climate, research should focus on improving our understanding of the mechanisms that determine fish population changes so that management and conservation measures are as effective as possible.

CHAPTER 2

INCORPORATING SPATIAL SYNCHRONY IN THE STATUS ASSESSMENT OF A THREATENED SPECIES WITH MULTIVARIATE ANALYSIS[1]

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[1] Stowe ES, Wenger SJ, Freeman MC, Freeman BJ. Incorporating spatial synchrony in the status assessment of a threatened species with multivariate analysis. Biol. Conserv. 2020; 248:108612. Reprinted here with permission of the publisher.

ABSTRACT

Spatial synchrony—correlated abundance fluctuations among distinct populations—is associated with increased extinction risk but is not a component of widely-used extinction risk assessments (e.g., IUCN Red List, U.S. Fish and Wildlife Service's Species Status Assessment). Alongside traditional viability metrics (i.e., the number of populations, their spatial extent, the status of each population), consideration of spatial synchrony in these assessments may provide additional insight into extinction risk as well as the relative importance of intrinsic and extrinsic factors on population dynamics. We demonstrate a method for estimating abundance trends in populations of the endangered freshwater fish, the Amber Darter (*Percina antesella*), while simultaneously assessing empirical support for existence of spatial synchrony among its two populations in the Conasauga and Etowah rivers in Georgia, U.S.A. Our analysis was performed using multivariate autoregressive state-space (MARSS) models with annual sampling data from 1996-2018 at 16 sites distributed between the two rivers. Our results indicate that Amber Darter populations have declined substantially, with 9% annual losses in both the Conasauga and Etowah rivers, suggesting rangewide imperilment. Furthermore, model selection indicated little support for models with fully independent dynamics between rivers, which may compound overall extinction risk. This analysis demonstrates the utility of tools such as MARSS models for assessing spatial synchrony and long-term population trajectories of imperiled species, resulting in improved vulnerability assessments that do not assume independence among separate populations.

Keywords: extinction risk analysis, spatial synchrony, endangered species, Amber Darter, multivariate autoregressive state-space model

INTRODUCTION

Spatial synchrony, or correlated abundance fluctuations among populations in different locations, is a widespread phenomenon that occurs in diverse taxa, including mammals [27], birds [28, 29], and insects [30]. The degree of spatial synchrony among the populations of a species can have consequences for that organism and for the wider ecosystem. Asynchronous population dynamics have been associated with increased ecosystem stability and resource provisioning via the portfolio effect, most notably with Pacific salmon stocks [31, 32]. Conversely, organisms whose separate populations are synchronized face higher global extinction risk, because several populations simultaneously experiencing low population densities are more likely to be extirpated by catastrophic events than populations with uncorrelated dynamics [26]. Furthermore, with spatially synchronized populations, the ability of one population to "rescue" another during periods of vulnerability is compromised [33].

In spite of the recognized importance of spatial asynchrony for species persistence, common extinction risk evaluations, including those conducted for the International Union for the Conservation of Nature (IUCN) Red List and the species status assessments (SSAs) mandated under the United States Endangered Species Act (ESA), do not consider spatial synchrony. The five criteria used to evaluate if a species belongs in an IUCN Red List threatened category (i.e., Vulnerable, Endangered, or Critically Endangered) are a) population size reduction; b) geographic range size; c) small population size and decline; d) very small or restricted population; and e) a quantitative analysis that indicates the probability of extinction in the wild [34]. In similar fashion, SSAs primarily focus on the number and spatial extent of populations, the status of each separate population, and the genetic differentiation among populations, a proxy for the adaptive potential that each population confers to the species as a whole [35]. Depending on data availability, demographic or count-based population viability analysis (PVA) may be used to examine trends in separate populations as they relate to putative population drivers, enabling the forecasting of abundances based on different covariate scenarios [36]. While such an approach can provide valuable insight into the status of a species, additional information on the independence of dynamics among populations can enhance our understanding of overall species vulnerability.

In this study we utilize an analytical approach that can estimate population parameters of imperiled taxa consistent with the needs of IUCN Red List assessments and SSAs—in particular, estimates of the long-term abundance trends of multiple, separate populations—while concurrently assessing evidence for independent variation among populations. Beyond increasing our understanding of overall species vulnerability, evaluating spatial synchrony among populations can provide insight into the scale at which important population drivers operate. The presence of synchronous dynamics among geographically distinct populations may indicate the importance of regional processes or long-distance dispersal in shaping population trajectories, whereas asynchronous dynamics may indicate the primacy of local factors [37].

We conducted our analysis on the Amber Darter (*Percina antesella*), a small benthic fish designated as endangered under the U.S. ESA. This species was selected because its protected status requires periodic status assessments, and because its presence in two distinct populations provides an opportunity to assess whether the degree of independence between these populations compounds or mitigates global extinction risk. Using count data from long-term sampling and a time-series approach—multivariate, autoregressive state-space (MARSS) modelling—we address the following questions related to Amber Darter status:

1. What are the long-term population trends in counts of Amber Darters in its two locations?

2. Do population dynamics in the separate locations exhibit spatial synchrony?
3. What are expected counts of Amber Darters in the future, assuming contemporary trends continue?

Consistent with the tacit assumption of most status assessments, we expected that Amber Darter population dynamics would be independent between rivers given the geographic separation of the populations and a large impoundment restricting the exchange of individuals. Considering the protected status of the Amber Darter, our results should be of direct use to managers assessing the vulnerability of the species. This example may also provide an impetus for others to consider population independence when assessing extinction risk in various taxa.

METHODS

Species identity and study area

The Amber Darter (*Percina antesella*) is a small-bodied fish endemic to the upper Coosa River basin in north Georgia and southeastern Tennessee. It was designated as federally Endangered in 1985 because of its limited distribution [38]. The species is currently found within two disjunct circa 50-km reaches in the mainstems of the Conasauga and Etowah rivers (Figure 1.1), as well as in downstream portions of two large Etowah River tributaries. One individual was captured in the Coosawattee River—adjacent to the Consauga—in 2010. In both rivers, it is found over cobble and gravel substrate within riffles and feeds on benthic invertebrates, including snails and limpets [39]. Whereas occupancy of Amber Darter has declined by over 50% during the last two decades in the Conasauga River, no such declines in occupancy have been identified in the Etowah River [16].

The Conasauga and Etowah Rivers are part of the Coosa River Basin, a highly biodiverse but imperiled drainage. A mainstem dam and reservoir in the Etowah River fragments many aquatic populations within the basin, including Amber Darters, which may have previously existed as one continuous population [40]. Significant contemporary threats to biodiversity in the upper Coosa watershed include excess nutrients and pesticides from agricultural runoff in the Conasauga [41–43], and urbanization in the Etowah [44, 45] although the limited distribution of the Amber Darter makes it difficult to infer sensitivity to land use from occurrence patterns [46].

Fish surveys

Data for this analysis come from 22 years of fish sampling from the Conasauga and Etowah rivers. Fish surveys were conducted by three to four people using a seine (2.4 m x 1.8 m; 3-mm mesh) in shoals—shallow areas with swift currents and predominantly rocky substrate—during low-flow conditions. Each survey consisted of many seine-sets (median: 79.5, range: 20 - 189), in which two people held the seine in flowing water while others moved downstream toward the net, disturbing the stream bed to displace fish into the net. In areas with low water velocity, we hauled the seine through the water column to collect fishes. Crews attempted to sample the full range of wadeable habitats in each survey. We typically identified, recorded, and released fishes after each seine-set.

Data from the Conasauga River comprised 103 surveys collected at six sites within a 21-km reach (median distance between sites = 3.4 km, range = 1.8 - 7.1 km) in 18 years from 1996 through 2018. No sites were surveyed in 2004, 2009, 2011, 2012, or 2015. We surveyed at least five of the six sites in all the years that included sampling, with the exception of 2018, in which two sites were sampled. All surveys took place in September or October.

Data from the Etowah River comprised 176 surveys conducted at 10 sites within a 41-km reach (median distance between sites = 2.4 km, range = 0.3 - 13.0 km) in 20 years from 1997 through 2018. We sampled at least nine of 10 sites in 16 years. We did not conduct any surveys in 2010 or 2011 and sampled only two sites in 2013. We conducted annual sampling in late summer and autumn (August–November).

Multivariate Autoregressive State-Space Analyses

We used multivariate autoregressive state-space models (MARSS, [47, 48]) to analyze long-term trends and independence of populations of Amber Darters in both rivers. We chose MARSS models because they can estimate population parameters of interest such as long-term annual growth rate from multiple time series (e.g., time series of Amber Darters counts at each site) while simultaneously testing whether abundance trajectories or annual fluctuations in the Conasauga and Etowah rivers co-vary through time.

MARSS models have separate observation and process components. Multiple observation time series (e.g., counts at discrete locations) are used to estimate one or more underlying process time series (e.g., overall population abundance trajectory). Such state-space models partition variance into process error—true fluctuations in underlying population abundance related to environmental stochasticity—and observation error, which can come in multiple forms, including sampling error and measurement error arising from the detection process (sensu [49]). Accounting for observation error can be important for limiting bias in the identification of abundance trends or drivers on population dynamics [50].

Model Framework

In MARSS models, *n* represents the number of discrete sampling locations, while *m* represents the number of unknown, underlying abundance trajectories on a log-scale (sometimes thought of as subpopulation abundances). The process model is:

$$\begin{bmatrix} x_{1,t} \\ \vdots \\ x_{m,t} \end{bmatrix} = \begin{bmatrix} x_{1,t-1} \\ \vdots \\ x_{m,t-1} \end{bmatrix} + \begin{bmatrix} u_1 \\ \vdots \\ u_m \end{bmatrix} + \begin{bmatrix} w_{1,t} \\ \vdots \\ w_{m,t} \end{bmatrix}, \text{where } \begin{bmatrix} w_{1,t} \\ \vdots \\ w_{m,t} \end{bmatrix} \sim MVN\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \boldsymbol{Q}\right) \qquad (1)$$

where $x_{i,t}$ is the state in year *t* and abundance trajectory *i* out of of *m* underlying trajectories where *m* may vary from 1 (all *n* sites share the same fate) to *n* (all sampling sites have separate trajectories). $x_{i,t}$ depends on the value of x_i in the previous time step, the annual growth rate *u*, and the process error w_i. We assume the process errors are drawn from a multivariate normal (MVN) distribution with mean 0, and variance-covariance matrix $\boldsymbol{Q}$. Different specifications of $\boldsymbol{Q}$ will either permit covariance between separate underlying states (e.g., x_1 and x_2) or constrain separate underlying states to have temporally-independent process error. Covariance parameter estimates indicate the degree of correlation in the annual error term, thus providing a measure of spatial synchrony.

The observation model is:

$$\begin{bmatrix} y_{1,t} \\ \vdots \\ y_{n,t} \end{bmatrix} = \mathbf{Z} \begin{bmatrix} x_{1,t} \\ \vdots \\ x_{m,t} \end{bmatrix} + \begin{bmatrix} a_1 \\ \vdots \\ a_n \end{bmatrix} + d \begin{bmatrix} D_{1,t} \\ \vdots \\ D_{n,t} \end{bmatrix} + \begin{bmatrix} v_{1,t} \\ \vdots \\ v_{n,t} \end{bmatrix}, \text{where } \begin{bmatrix} v_{1,t} \\ \vdots \\ v_{n,t} \end{bmatrix} \sim MVN\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \boldsymbol{R}\right) \qquad (2)$$

in which y_{jt} represents the observed count from location *j* at time *t*. Each y_j is related to a corresponding, underlying abundance trajectory x_i in Equation 1, via **Z**, an *n* x *m* matrix of ones and zeroes, with a single "one" per row. Given that Z defines how observations relate to underlying states, different specifications of **Z** among separate models can be used to indicate a different total number of underlying states *m* and/or a change in which observation time series relates to which underlying state. The *a* variables represent scaling terms for each observation time series (which can be thought of as a fixed “site effect”), thus allowing separate observation time series to be scaled to the same corresponding underlying state. For example, two observation time series may have temporally-similar fluctuations in abundance through time (i.e., shared good and bad years), but might be measured at different scales or with different methods, and the *a* parameter will allow these two time series to estimate the same underlying abundance trajectory. The *d* parameter estimates the effect of time-varying covariates *D* that might alter the observation process. Finally, *v* is the observation error, drawn from a MVN distribution with mean of 0 and variance-covariance matrix $\boldsymbol{R}$.

Model specifications

We used 27 MARSS model specifications to test different hypotheses about long-term trends and independence of Conasauga and Etowah Amber Darter populations (Table 1.1). We included one model with a single underlying state ($m = 1$) to represent the possibility that regional factors, particularly yearly temperature and precipitation—rather than local factors—are the principal drivers of population dynamics at sites in both rivers. Next, we included eight models with two underlying states ($m = 2$), representing separate abundance trajectories in the Conasauga and Etowah rivers, a scenario that might arise with local dispersal among sites within rivers and river-specific landscape factors driving year-to-year dynamics. Of the models with two underlying states, models varied to allow different degrees of independence between rivers. We included models in which the growth rate parameter (*u*) was allowed to differ between the Conasauga and Etowah population, which would allow for different long-term trends, or constrained the growth rate to be the same. We also allowed the level of process variance to be the same or different between the Conasauga and Etowah, and finally permitted covariance in the process error in some models, to incorporate the possibility that good and bad years are correlated between rivers, while not permitting this covariance in other models. Finally, we included 18 models with separate trajectories at each of the 16 sites (m = 16), reflecting the possibility that dynamics at each site are largely independent, governed by local factors, with low dispersal among sites. Again, these models differed in their growth rate and variance-covariance parameters (Table 1.1) to allow for different degrees of independence or synchrony throughout the time period of the study. More specifically, growth, process variance, and process covariance were allowed to be equal across all sites, equal within river (meaning one parameter was estimated for all sites within the same river despite different underlying states), and unequal (meaning different parameters were estimated for each of the 16 sites).

In all models, we assumed that observation errors were uncorrelated (i.e., the off-diagonals of the **R** matrix are zero) and of equal magnitude between sites (i.e., the diagonal elements of the **R** matrix are all equal). Using a single parameter assumes no difference in mean capture efficiency of Amber Darters among the 16 sites. Higher river discharges during sampling are expected to lead to lower capture efficiency, and therefore daily discharge on the day of sampling was included as a covariate in the observation process ($D_{n,t}$ in Equation 2). We used discharge data from two U.S. Geological Survey stream gages in the vicinity of the sampling reaches (02384500 in the Conasauga River near Eton, Georgia, and 02392000 in the Etowah River at Canton, Georgia).

Model fitting and selection

We performed all analyses in R 3.5.1 [51] using the MARSS package v.3.10.8 [48]. Data entered the MARSS models as a matrix of catch-per-unit-effort (CPUE) time series of Amber Darters at each of the 16 sites. CPUE was calculated as the number of Amber Darters caught per

100 seine-sets, a typical number of seine-sets per survey. It is standard practice in MARSS analyses to log-transform abundance values, as the underlying modeling framework is log-linear [52]. To account for the presence of some zero counts, we increased all count values by one before calculating CPUEs and then log-transforming the data. The MARSS package fits models using maximum likelihood via a constrained expectation-maximization algorithm. The maximum number of iterations allowed for model convergence was 1000; models that did not converge by this point were excluded from further consideration. For models that converged, Akaike's Information Criterion corrected for small sample size (AICc) and ΔAICc were used to rank models. For best-fit models, we calculated confidence intervals using parametric bootstrapping implemented within the MARSS package, which provides unbiased bootstrap parameter estimates [48, 53].

Spatial synchrony of model residuals

To further examine variation in counts not explained by the best-fit model that could arise from spatial processes, we assessed Spearman's Rank Correlation on the residuals from the top model for each pair of sites. MARSS models capture patterns of synchrony in time-series analysis via covariance and/or shared underlying states, but assessing model residuals between pairs of sites provides an opportunity to examine heterogeneity in synchrony on a site-to-site basis, and may highlight locations with stronger- or weaker-than-average synchrony. Negative correlations identified using this approach might indicate that dynamics at two sites are asynchronous, but because the MARSS model may have already captured any shared synchronous dynamics, such sites may merely have lower synchrony compare to sites with positive correlations.

Forecasting

Best-fit model parameters were used to simulate 10,000 expected CPUE time series at each site from 1996 to 2068 (i.e., the duration of the study, and 50 years into the future) to provide an estimate of future CPUEs if current trends persist. Simulations were accomplished via random draws of the process and observation error at each time step, using the MARSSsimulate function in the MARSS package. Using the MARSS model structure for forecasting means that the error structure is incorporated into each round of simulation, and consequently, counts at each site in a given year can result from synchronous processes (i.e., shared process error or covariance) depending on the model structure. For each site, we calculated the mean expected CPUE at each time-step, as well as 2.5% and 97.5% quantiles. Given that projections are based on fitted values of parameters without taking into account uncertainty in these estimates, the precision of these forecasts could be overstated.

RESULTS

From 1996 to 2018, raw counts of Amber Darters declined in the Conasauga and Etowah rivers (Figure 1.2). In both rivers, an increasing number of surveys failed to detect Amber Darters over the time period of the study. Count declines and non-detections were not limited to particular sites or segments of river within the sampled areas (Figure 1.2).

Model selection

Nine MARSS models converged; nearly all models that did not converge had covariance constrained to zero or unequal process variance. The model that best fit the data featured one underlying state for the two rivers, thus constraining all sites to the same long-term growth rate and process error parameter (Table 1.2; Figure 1.3). Other top models also showed little support for independent dynamics between rivers: all models with ΔAIC < 4 included positive covariance among underlying abundance trajectories, suggesting temporally-correlated process error for the Conasauga and Etowah Amber Darter populations. There was also not substantial support for differences in growth rate between rivers: of the top six models, only the fourth and fifth best models included a different population growth rate parameter (*u*) between rivers.

Parameter estimates

Annual population growth rate estimates (*u*) were strongly negative in all models (Table A1). In the top model, this parameter was estimated at -0.09 ± 0.03, indicating an average per-year decline rate of 9%, which amounts to an approximate 86% decline in the rivers over the 23-year study period. The growth rate parameter estimates did not vary substantially between the different models, but in models with separate growth rate parameters between rivers, Conasauga declines were steeper than those in the Etowah (Table A1). In the top model, most of the variance was partitioned into observation variance (0.37) as opposed to process variance (0.01). This large observation variance implies that, while overall trends between sites were similar, large site-to-site variation in counts still existed that could not be explained by fluctuations in the underlying abundance trajectory.

Spatial synchrony of model residuals

Synchrony between pairs of sites—beyond what was captured by the top MARSS model—varied considerably based on Spearman’s rank correlation of model residuals (Figure 1.4). Seven of the nine largest correlation values were between pairs of sites within the same river. Adjacent areas with the highest degree of synchrony included three sites in the Conasauga (con214, con251, and con148).

Forecasted populations

CPUEs are projected to approach very low numbers at all sites by 2050 if the population trends from the top model persist (Figure 1.5). Conasauga sites are generally forecasted to reach low CPUEs (i.e., one individual in 200 seine-sets) sooner than Etowah sites, with all but one Conasauga site projected to reach this level within the next 13 years. Most Etowah sites are not projected to reach these CPUE values until later, with expected CPUEs declining below this level between 2033 to 2042 for eight of 10 sites.

DISCUSSION

Our analysis demonstrated the utility of simultaneously evaluating long-term trends and independence of the two populations of the endangered Amber Darter. Doing so uncovered declines in both populations, including the Etowah River population that previously had been considered stable. We also found scant evidence of strongly independent dynamics between populations that might have otherwise conferred an extra measure of protection from extinction. We argue that assessments of the status of imperiled species in multiple locations should evaluate spatial synchrony whenever the data allow. An implicit assumption of analyses that do not assess synchrony is that populations in separate locations are independent, which may lead to overly optimistic viability estimates.

Amber Darter count trends and future projections

The substantial decreases in counts of Amber Darters in each of two rivers during the last two decades suggest rangewide population declines. While count trends in the Conasauga were not surprising given declines detected there using occupancy modeling, the Etowah declines had not been evident based on occupancy data [16]. Thus, analyses of count data may reveal population trends not apparent from occupancy modeling, potentially serving as an early warning signal, as other studies have demonstrated [54]. Forecasting indicates that if the trends of the past two decades continue into the future, Amber Darters will become increasingly scarce, if not extirpated, from both rivers by mid-century. Indeed, no Amber Darters were captured in the Conasauga River during 2019 sampling (authors' unpublished data) for the second year in a row, suggesting they have already reached perilously low abundances in that river. Given that these rivers are thought to constitute the entirety of the species' range, these results imply that the Amber Darter is on a trajectory towards extinction. While the forecasting approach presented here is simplistic, it is sufficient to illustrate the grave prospects for Amber Darters in these systems if conditions do not change.

Population independence and spatial synchrony

MARSS modeling did not provide support for strongly independent dynamics between the Etowah and Conasauga populations, which would confer additional resilience to the species as a whole. The top model indicated that all observation time series, regardless of river, corresponded to a single underlying abundance trajectory, reflecting the overall degree of similarity in count trends across the region and the presence of shared fluctuations from the long-term trend. Models with less support based on AICc did possess multiple underlying states—either between rivers (m=2) or between all individual sites (m=16)—but still indicated a lack of independent dynamics between rivers, both through shared growth rate parameters in some cases, and through positive covariance in the process error, which reflects correlated year-to-year abundance fluctuations between underlying states.

Some caveats should be considered before concluding that dynamics of the Conasauga and Etowah populations are highly correlated, however. First, all well-supported models had high observation error compared to process error. This means that while estimates of process error in a given year show high correlations between sites or rivers, the magnitude of this term (i.e., the upward or downward deviations in the abundance trajectory in any given year) is small. It is difficult to separate the high observation error into its constituent components, but it may in part reflect low capture efficiency for these fish. Per-individual detection probabilities for other darter species in the Etowah basin have been estimated at between 9% and 22% [55], which could obscure patterns of spatial synchrony or asynchrony. If habitat suitability for the species changed differentially among sites over time, this could potentially cause high observation error, but such a circumstance might be reasonably accommodated by models featuring a separate underlying state for each site (i.e., $m = 16$). The assessment of correlation in model residuals showed high spatial variability in population dynamics and suggested the possibility that the greatest spatial synchrony may exist between adjacent sites within the same river, consistent with the idea that local factors here may also be important drivers of population dynamics. Finally, the failure of some models to converge means that some potential variance-covariance structures could not be fully assessed (e.g., those with zero covariance). However, models featuring each $\mathbf{Z}$ structure did converge, enabling a comparison among models that represent each latent state configuration of interest (i.e., $m = 1$, 2, or 16).

Given these sources of uncertainty, it is possible that synchrony among the two Amber Darter populations is only weak. Nonetheless, even weak synchrony would represent an unexpected and important finding. Populations in the two rivers are isolated and unable to exchange individuals, and exist in different physiographic regions. Thus, one by default might expect these populations to show clear asynchrony. That such independence is not apparent in this analysis is cause for concern.

Local and Regional Drivers of Declines

Identifying the cause or causes of fish declines in the upper Coosa Basin has proved difficult. Freeman et al. [16] remarked extensively on the possibility that agricultural practices are harming aquatic organisms in the Conasauga River; this has seemed a parsimonious explanation because the Conasauga watershed has greater agriculture extent and intensity, and appeared to have more severe fish declines, than the Etowah watershed [16]. However, rangewide Amber Darter declines warrant the examination of potential stressors occurring in both rivers, including ones that operate at regional scales. The geographic proximity (i.e., ~70 km overland distance) of the two populations suggests that shared climatic factors might play a role in driving shared population responses. Indeed, fish populations separated by greater distances have demonstrated spatial synchrony, with correlated hydrological variability suspected as the proximate mechanism for non-independence [56]. Accordingly, climate-change induced hydrological extremes occurring synchronously in the Conasauga and Etowah rivers could cause similar population fluctuations or trends through time; both rivers have experienced anomalous low- and high-flows during the sample period, including several severe recent droughts. However, flow metrics have previously shown little power to explain changes in persistence and colonization of fishes in either river [16].

Might other regional factors beyond hydrological variation explain shared declines between Amber Darter populations? Altered thermal regimes as a result of climate change can cause fish declines [57] and would likely have similar impacts in both rivers. However, there are currently few examples of warming stream temperatures causing severe population declines in warm-water, fluvial fish taxa; most research has focused on distributional changes in cold-water taxa [58]. We cannot rule out stressors operating at local scales but occurring across the region, such as sediment pollution, which is often implicated in the declines of aquatic taxa, as it interferes with feeding and spawning [59]. Various forms of land use change can lead to sediment pollution, including both the agricultural intensification taking place in the Conasauga basin and increased suburban development in the Etowah Basin. However, sediment pollution is less likely to occur synchronously through time across both watersheds, compared to factors related to climate. It is possible that different drivers might be responsible for similar abundance trends between rivers, or that the fish fauna in each river is responding to broad degradation from diverse anthropogenic activities.

Management implications

Irrespective of mechanism, evidence of Amber Darter declines in both rivers and the potential synchrony in declines may call for new management and conservation efforts, which are largely local in scope at present. In the Conasauga, notable conservation measures include land protection/acquisition along the mainstem river and key tributaries, government technical and financial assistance to farmers to promote runoff-reducing agricultural practices, prioritization of parcels for application of Farm Bill and other conservation funds, and development of numeric nutrient criteria for the mainstem river by the state environmental protection agency (Robin Goodloe, U.S. Fish and Wildlife Service, personal communication). Etowah conservation measures similarly include land protection and conservation prioritization efforts, as well as coordination among Federal and State agencies to reduce the impacts of urban development on aquatic and forested habitats. Such local efforts—if successful in improving water quality, quantity, and connectivity throughout the basin—could mitigate climate threats such as shifting hydrologic or thermal regimes. However, the regional nature of the declines could encourage additional conservation measures at this same scale, such as the expansion of partnerships that work on conservation across the entire upper Coosa Basin, and additional research investigating the scale at which other biotic changes across the basin are occurring. For example, our result in this study has encouraged us to now look for evidence that other fish taxa are varying asynchronously between these rivers. Efforts focused specifically on the Amber Darter could include the development of methods to enhance detection of Amber Darters (e.g., use of eDNA), comprehensive assessments of Amber Darters in other portions of the species' potential range (e.g., Coosawattee River), and the possible creation of an ark population.

MARSS modeling for extinction risk analyses

Our analysis highlights some benefits of incorporating MARSS modeling into extinction risk analyses including species status assessments (SSA). SSAs gauge overall extinction risk largely on the number of populations and the status of each population [35]. Our analysis estimated trends in separate populations of Amber Darters consistent with the needs of an SSA, and yet the integrated nature of the analysis provided additional insights that a typical count-based PVA might overlook, including an understanding of whether dynamics among separate populations are correlated, with implications for the overall extinction risk of the species. While the population demarcations of Amber Darters are relatively unambiguous given their non-overlapping ranges in the Conasauga and Etowah rivers, in such cases where population boundaries in SSAs are arbitrary or not well resolved, MARSS can provide a tool for estimating the number and configuration of populations. For example, Ward et al. [60] used MARSS analysis to demonstrate that Gulf of California sea lions appear to be structured in four subpopulations based on abundance time series at 13 breeding sites. Given that the number of populations is of crucial importance within SSAs for determining relative extinction risk, any tool that strengthens our ability to quantitatively evaluate the appropriate number of populations should enhance risk assessments. MARSS models can also incorporate covariates to assess the effect of abiotic and biotic drivers on abundance trajectories. For example, Ruhí et al. [61] used MARSS models to show that anomalous droughts and floods drove changes in fish abundances. Likewise, Greenville et al. [62] incorporated annual rainfall data in MARSS models to assess the extent to which regional climate synchronizes desert mammal species. Finally, using the MARSS model structure to forecast future population dynamics enables the incorporation of spatial synchrony into future simulations in the form of shared process error and/or covariance. Process variance or covariance parameters, as well as the **Z** structure (i.e., hypothesized number of underlying states and which observations correspond to which state), can be adjusted to simulate how different population structures or degrees of synchrony might affect extinction risk.

A limitation of MARSS models is the extensive data requirements (typically several time series with durations of at least one to two decades for annually-sampled populations), making this approach unavailable for many species. The performance of these models declines with missing values, although this is still superior to time-series approaches that do not accommodate missing values at all. A feature of MARSS that helps to overcome the data requirements is the potential to include multiple survey types in a single analysis, which can be accomodated via the scaling term a and through the specification of different observation variance parameters for time series collected using different methods. For example, Tolimieri et al. [63] were able to estimate rockfish population trajectories in Puget Sound from surveys that used multiple gear types. In the case of rare, difficult-to-detect fishes such as the Amber Darter, incorporating data from additional observation methods (e.g., eDNA, trawl surveys in non-shoal habitat, etc.) might improve the precision of parameter and trend estimates.

Alternative analytical approaches

In addition to MARSS models, other techniques may prove useful in incorporating synchrony into extinction risk analyses. Dynamic factor analysis (DFA) [64] identifies latent trends common to sets of time series and has been used to examine synchrony and its climatic drivers in populations of salmon [65, 66] and caribou [67] and also to identify large-scale common trends among populations of insectivorous birds [29]. Whereas MARSS models link each observation time series to one underlying process time series, in DFA each observation time series receives a factor loading (i.e., an affinity score) for each latent process. The latent processes identified by DFA are random walks that lack growth rate terms, however, which are generally of little value for forecasting. Another approach to evaluating synchrony is to use models with random effects that partition temporal variation among populations or species into synchronous and asynchronous components. Examples using this method include assessment of non-independence in survival rates among seabird populations and species [68, 69], as well as estimation of trends and synchrony in observations of alpine rock ptarmigans [70]. Numerous other approaches have examined spatial synchrony without explicitly considering long-term trends, with cross-correlation coefficients perhaps the most commonly-used index of synchrony [28, 71, 72]. Further increases in model realism can be achieved with fully explicit spatiotemporal techniques (e.g., empirical variograms), which can estimate changes in covariance between locations as a function of the intervening distance. Such techniques are most frequently performed with regularly-spaced (e.g., gridded) data and have been used most widely in geostatistics [73].

When data are too sparse for complex modeling routines, more ad hoc approaches may still enable some consideration of spatial synchrony in the context of extinction risk analyses.

For example, Höckendorff et al. [74] characterized various aspects of fish population time series (e.g., “did counts of population *i* increase in years 1-3?”) and used a clustering technique to group time series based on similarities in responses through time. Similar approaches could be adapted to a range of data amounts or types and might be most useful when specific attributes of the time series in question are of greater interest than overall levels of synchrony. However, incorporating long-term trend analysis directly in such approaches might be less straightforward than the estimation of long-term population growth rates in MARSS models.

CONCLUSIONS

Irrespective of analytical technique, the extent to which ecologists can jointly analyze separate populations when assessing extinction risk should have substantial benefits, including: the ability to borrow information from data-rich populations to estimate parameters from less-studied populations [75]; the capacity to assess the scale of influence of regional factors on population variation; and the ability to infer population structure and metapopulation dynamics when movement or genetic data are not available [60]. Such integrative approaches that assess population changes across space and time are crucial to best predict when and where species will experience the greatest threats under the non-stationary conditions of the Anthropocene [76].

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Table 1.1. Multivariate autoregressive state-space models tested using count data from the Conasauga and Etowah rivers. For each **Z** structure (i.e., number of underlying states), we tested all combinations of the listed growth and variance-covariance structures **Q**. The number in parentheses refers to the total number of models corresponding to that **Z** structure. Unconstrained **Q** indicates that all variance-covariance terms are estimated separately.

States	Growth	Variance-covariance (**Q**)
One (1)	One value	One value for variance (covariance not applicable)
Two (8)	Equal Unequal	Equal variance – no covariance Equal variance – equal covariance Unequal variance – no covariance Unequal variance – equal covariance
Sixteen (18)	Equal Unequal Equal within river	Equal variance – no covariance Equal variance – equal covariance Unequal variance – no covariance Unconstrained Equal within river – no covariance Equal within river – covariance within river

Table 1.2. Model specifications and model selection results for the converged MARSS models.

Model specifications			Model selection		
States	Growth	Variance-covariance	AICc	ΔAIC	Weight
1	One value	One value	559.64	0.00	0.51
2	Equal	Equal var. – Equal covar.	562.26	2.61	0.14
16	Equal	Equal var. – Equal covar.	562.73	3.09	0.11
2	Unequal	Equal var. – Equal covar.	563.04	3.40	0.09
16	Equal within river	Equal var. – Equal covar.	563.56	3.92	0.07
2	Equal	Unequal var. – Equal covar.	564.21	4.56	0.05
2	Unequal	Unequal var. – Equal covar.	565.35	5.71	0.03
16	Unequal	Equal var. – Equal covar.	575.91	16.27	0.00
16	Unequal	Unconstrained	1288.06	728.41	0.00

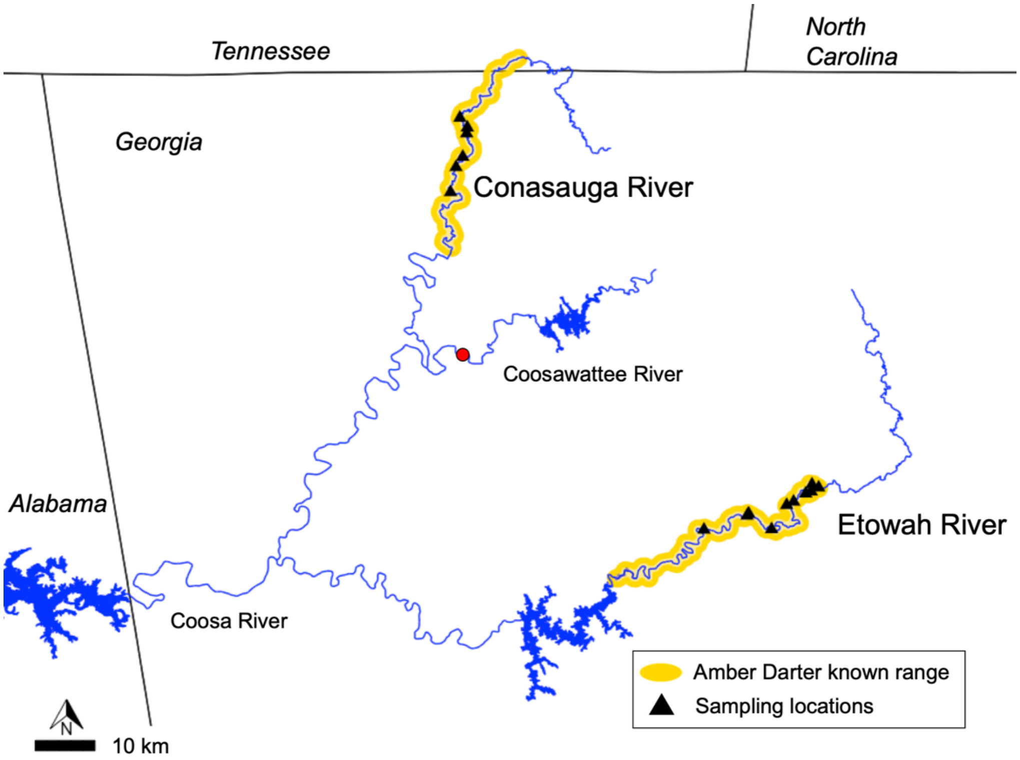

Figure 1.1. Approximate known historic range of Amber Darter in the Conasauga and Etowah river mainstems, northwest Georgia, U.S.A. State boundaries are shown for reference. Capture of a single Amber Darter in 2010 in the Coosawattee River is indicated by the red point. Black triangles indicate long-term sampling locations from which the data used in this study originated.

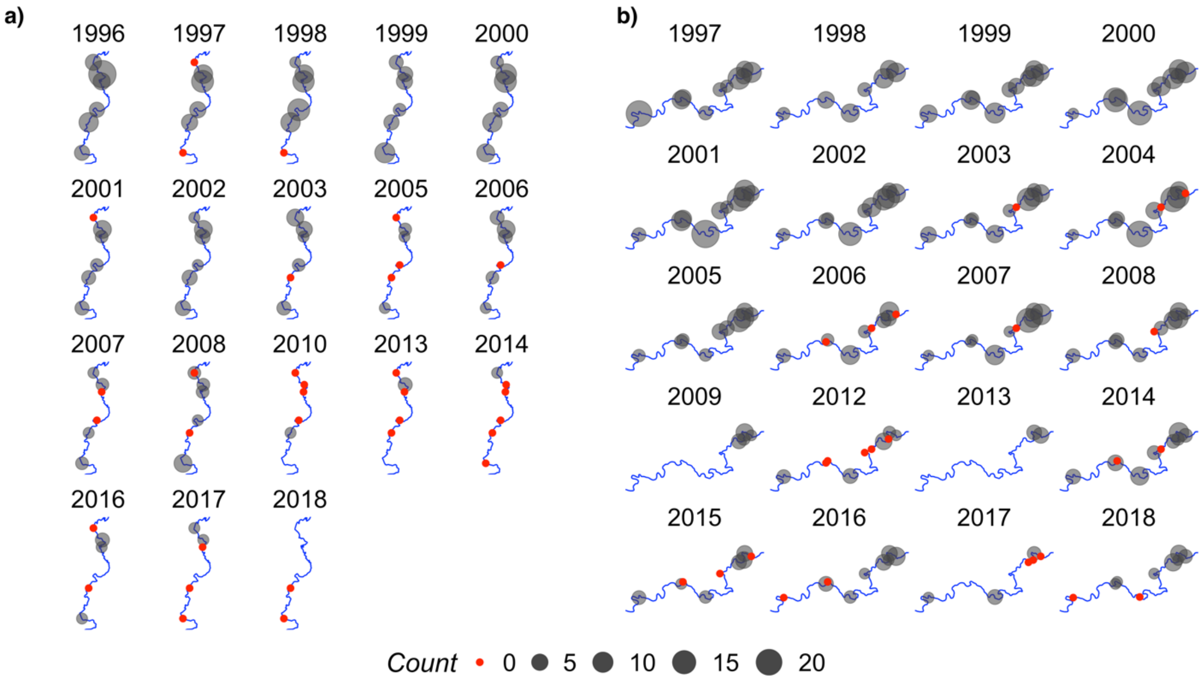

Figure 1.2. Counts of Amber Darters at 16 long-term sampling locations in the Conasauga (a) and Etowah (b) river sampling reaches from 1996 to 2018. Sites are not depicted in years when they were not sampled. Absent years indicate that no sampling was conducted during that time period.

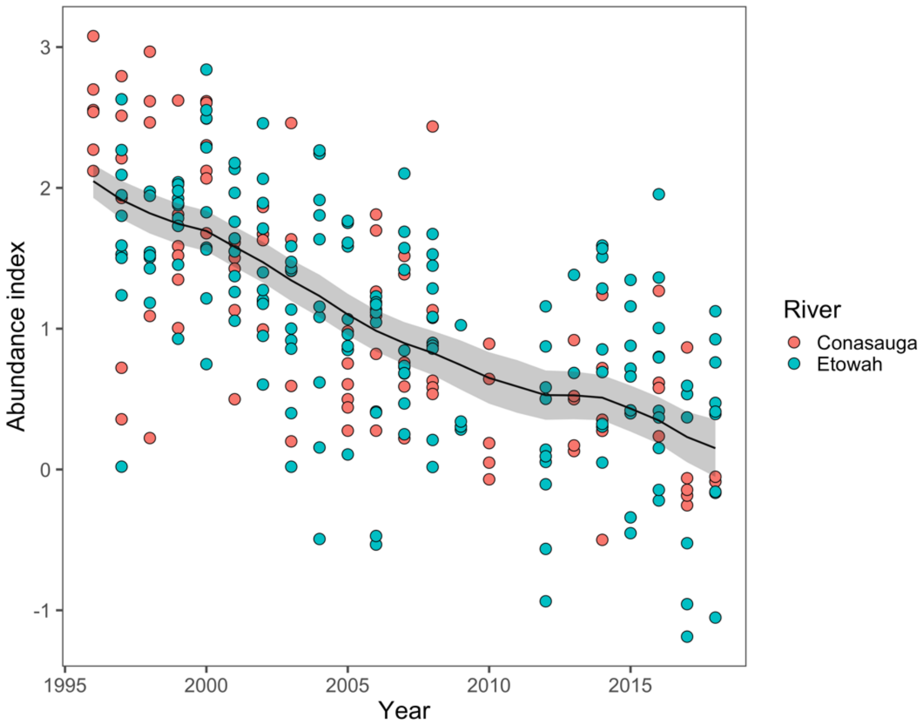

Figure 1.3. Estimated abundance trajectory from the top MARSS model. Points represent log-transformed CPUEs scaled to the underlying trajectory using each site's *a* parameter. Shaded area represents 95% confidence intervals on the underlying state trajectory.

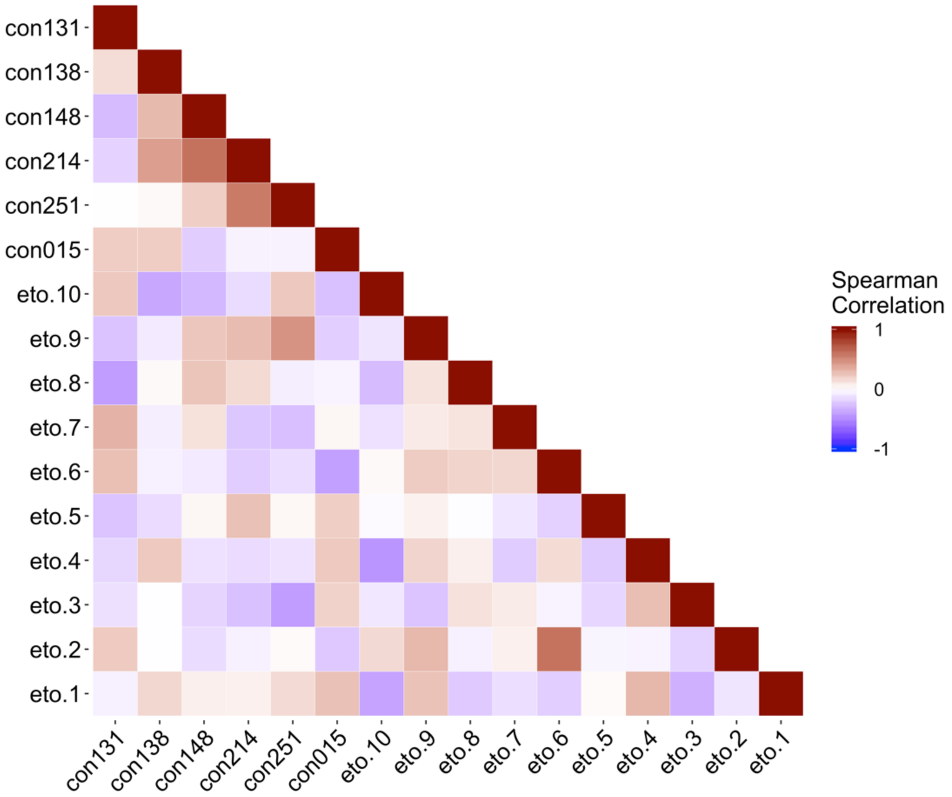

Figure 1.4. Spearman’s rank correlations on model residuals from the best-fit MARSS model among different sites in the Conasauga and Etowah rivers. Sites are arranged according to proximity. Spearman’s rank correlations range from +1 (perfect positive correlation) to -1 (perfect negative correlation), with zero-values indicating no correlation.

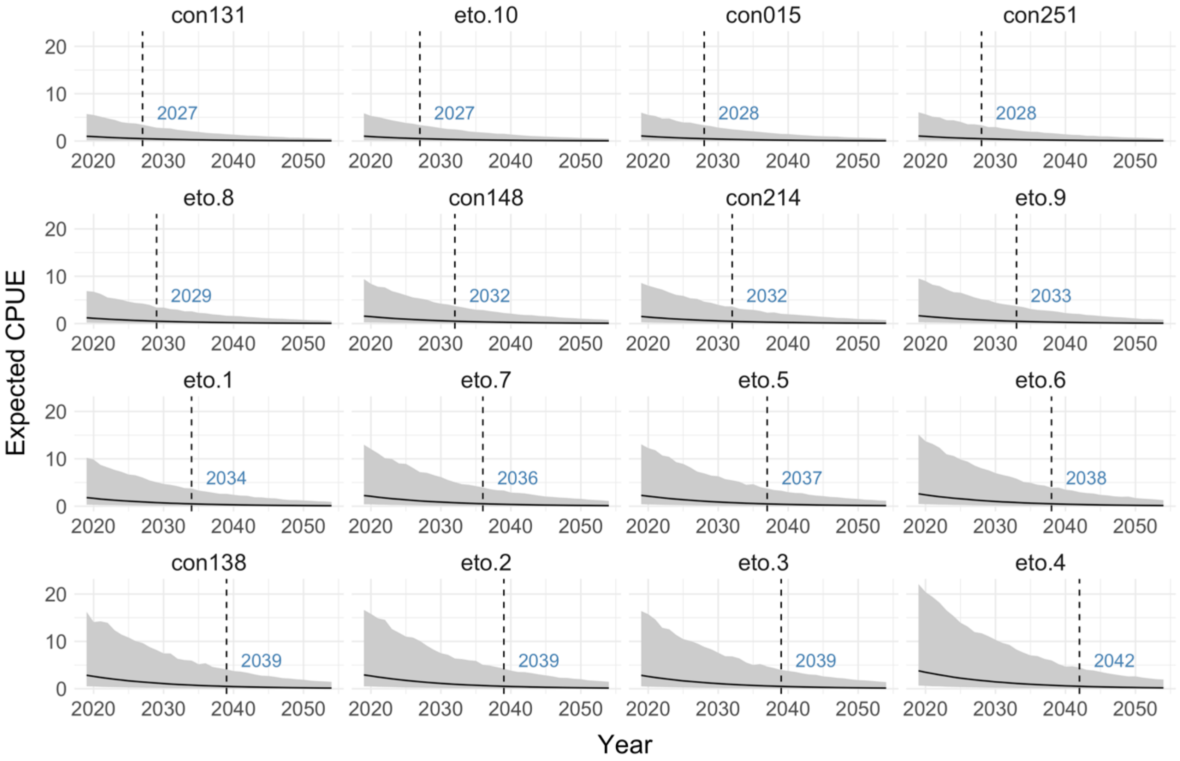

Figure 1.5. Mean expected CPUE (i.e., number of fish caught in 100 kicksets) at each site from 2019-2068 from 10,000 simulations using parameters from the best-fit model. Gray shaded areas represent values between the 2.5% and 97.5% quantiles of the simulated data at each time-step. Years in blue correspond to the year in which expected CPUE declines below 0.5 (i.e., one fish in 200 kicksets).

CHAPTER 3

INVESTIGATING DECLINES IN STREAM FISH POPULATIONS ACROSS THE CONTIGUOUS UNITED STATES [2]

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[2] To be submitted to *Global Change Biology* with MC Freeman, KR Bestgen, D Carlisle, EA Frimpong, NR Franssen, KB Gido, Y Kanno, C Luce, SK McKay, MC Mims, JD Olden, NL Poff, DL Propst, AH Roy, A Walters, SJ Wenger as co-authors

ABSTRACT

Stream fishes are globally imperiled, a result of widespread damming, water extraction, pollution, exploitation and spread of invasive species. However, current trends in stream fish populations have not been widely assessed. The roles that different stressors and species attributes play in fish population trends—and whether these vary among ecological regions—are also poorly understood. We estimated mean trends in stream fish populations within 218 subwatersheds across the contiguous U.S. using 22 datasets entailing annual counts of a total of 283 species. We also assessed if variation in trends among subwatersheds and species were related to stressors and life-history traits. Subwatersheds had a median annual decline of 0.3%, but substantial variability in trends, including both large declines and increases. Positive trends were mostly confined to the East, especially at a set of sites in the North Carolina Piedmont, while negative trends occurred throughout the U.S., particularly in the arid Southwest. Measures of contemporary stressors (e.g., land use change, non-native species abundance, etc.) showed little ability to predict trends. However, positive trends in the East may be related to increases in cosmopolitan taxa in response to warmer, drier conditions, while declines in fishes in the Great Plains and West were largely among opportunistic and periodic fishes. There results document stream fish declines across the continental U.S. that appear unrelated to identified stressors.

INTRODUCTION

Recent analyses across disparate groups of organisms have suggested that the earth is undergoing a biodiversity crisis [77]. Studies have estimated that the world’s wild mammal biomass has declined by 83% [78]; that three billion North American birds have been lost since 1970 [79], along with 70% of the world’s seabirds [80]; and that the current extinction rate of amphibian species may be 200 times greater than historical extinction rates [81]. Some of the most alarming losses have occurred in non-vertebrates: studies have documented precipitous declines in broad groups of insects in both temperate, urbanized [82] and tropical, undeveloped locations [83]. Across taxonomic groups, declines are found in not just rare species, but increasingly in common taxa [84–86].

Freshwater fishes are considered to be among the most imperiled group of organisms, with 31% of assessed taxa considered threatened with extinction, a rate higher than mammals and birds [87]. A status assessment of North American fishes suggested that 39% are imperiled [7], with fishes of streams and rivers especially vulnerable. Stream fish populations are primarily threatened by water pollution, flow modification, habitat destruction, non-native species invasions, and in some regions, overexploitation [1]. In recent years, scientists have identified emerging threats that pose additional challenges for stream fishes and other freshwater organisms and exacerbate other stressors [15]. Foremost among these novel stressors is climate change, potentially threatening 50% of freshwater fish species around the globe [87]. Declines in fish taxa in some regions have been linked to specific causes: for example, reductions in streamflow and the expansion of non-native fishes have been implicated in the declines of native fishes in the southwestern U.S. [61, 88], while the declines and extirpations of some anadromous fishes have been unambiguously caused by dams blocking access to spawning habitat. However, attributing declines to specific stressors is frequently difficult: considerable delays can exist between the onset of a threat and fish population response, particularly for longer-lived taxa [14, 89], and stressors typically co-occur and often interact [13]. Consequently, the relative importance of different stressors on fish populations both at local and broad scales and among ecological regions is not well understood, and in some cases the cause of widespread declines within a fish community is enigmatic [16].

The intrinsic characteristics of some fishes predispose them to declines and extinctions in the face of environmental upheaval [90]. Both the smallest and largest fish appear to face increased risks of extinction. Small fishes often have limited dispersal capacity and small ranges [18, 19], and higher susceptibility to adverse interactions with non-native taxa [91]. Large fishes are subject to greater fishing pressure, have had their habitat fragmented by dams in the case of migratory taxa, and frequently have “slower” life histories that often fare poorly under novel environmental circumstances [18, 19]. Species requiring stable conditions with pronounced seasonality are often considered to be more susceptible to stressors that reduce the predictability of the environment [92]. However, the extent to which fish traits are predictive of declines is not resolved; while some studies have demonstrated correlations between traits and declining taxa [93], others found no clear relationships [16]. A greater understanding of how fish traits relate to extinction risk is crucial to predict species that may require proactive management and conservation.

Here, we used 22 long-term fish count datasets from rivers and streams across the contiguous United States to estimate mean trends in fish species abundance at the subwatershed scale (Hydrologic Unit Code 12) and identify locations and ecological regions that have experienced declines of their fish fauna in recent decades. We also modeled variation in trends among subwatersheds as a function of potential threats to examine the relative importance of different contemporaneous stressors among ecological regions. Finally, we assessed whether declining species were more likely to possess certain life-history or ecological traits. Our analysis is the first continental-scale examination of empirical fish population trends, and the first to evaluate whether fishes are experiencing declines at rates comparable to those of birds, insects, or mammals.

METHODS

Datasets and survey data

Candidate datasets for our analysis were either generated by co-authors, collected from agency partners, or gleaned from two public sources: the National Water Quality Assessment (NAWQA) dataset [94], a U.S. Geological Survey dataset collected to examine the Nation's water quality, and RivFishTIME [95], a global database of fish time-series data. We screened available datasets using the following criteria: a) fish surveys occurred in lotic habitat (e.g., streams and rivers); b) surveys consisted of known, consistent sampling methods; c) surveys occurred at consistent locations with known coordinates; d) survey methodology targeted the community of fish species within the sampled habitat and resulted in abundance data for each species encountered; e) surveys occurred at an annual or near-annual time-step during consistent seasons; and f) sampling at each site spanned ten or more years between the first and last sampling events, and occurred in at least five separate years. We used the rfishbase package v 3.1.10 [96] in R to ensure all fish taxa names were consistent and current. We removed fish taxa from our analysis if they were not identified to the species level. At the subwatershed scale (HUC12), we removed all taxa that occurred in fewer than a fifth of the surveys or had total counts below 20. If fewer than 3 taxa remained after removing rare fishes, we removed that subwatershed from the analysis.

Site and watershed data

We standardized all sampling site coordinates to latitude-longitude format using the World Geodetic System 1984 (WGS84) reference system, re-projecting any sites that were received in alternative projections. We used the sf package v 0.9-8 [97] in R to determine the HUC8 of each site and to associate each sampling site to a stream segment from the National Hydrography Plus dataset (NHD Plus, [98]) in order to determine segment-specific attributes for each site. To do this, we first calculated the distance from each sample location to all adjacent stream segments within 1000 meters (Euclidean distance). For sites that sampled waterbodies with known names, we selected the closest stream segment containing the same name as the corresponding site. For sites that lacked a waterbody name attribute, we selected the nearest stream segment. We used ArcMap v. 10.7.1 [99] to confirm that final stream segment selection was reasonable based on proximity to the sampling location and stream size.

Predictor data

We assessed whether subwatershed-level trends were a function of six predictors, chosen to represent known contributors to freshwater fish declines: change in urban land cover [100], change in agricultural land cover [101], change in mean air temperature [102], change in the relative abundance of non-native species [91], proportion of drought years [61], and degree of hydrologic alteration at a site [103]. For all predictors, we calculated one value of each predictor per subwatershed (HUC12), as this was the scale at which we estimated trends. All predictors were scaled by subtracting the mean and dividing by the standard deviation to improve model fitting and interpretation. Twenty-two subwatersheds with outlier predictor variables, defined as values > 3 or < -3, were removed from the analysis.

We calculated the percent land cover class for all subwatersheds (HUC12) with fish sampling data for each year during the fish sampling period. For a majority of sites (n = 356) we used the USGS Land Change Monitoring, Assessment, and Projection v 1.1 (LCMAP) dataset, which includes land cover data comprising eight land cover classes at a 30 m resolution for the contiguous U.S. on an annual timestep [104]. For 51 sites where fish sampling pre-dated 1985, we used land cover data generated by the USGS FOREcasting SCEnarios of Land-use Change (FOR-SCE) model, which also exists at an annual timestep but comprises additional land cover categories and has a resolution of 250 m [105, 106]. For both data sources, we calculated the percent land cover at the HUC12 scale for urban and agricultural land cover for all years overlapping the fish sampling record. For the LCMAP data these categories are among the 8 land cover categories (termed "developed," and "cropland," respectively). For the FOR-SCE data, we used the land cover class termed "developed" to represent urban land cover and for agricultural land cover we summed the "cultivated cropland" category and the "hay/pasture" category. For all sites, we calculated the annual rate of urban and agricultural land cover change during the fish sampling period by regressing proportional land cover against year for each cover class of interest using linear models in program R. The β term on year from these models represents the rate of land cover change through time. We expected that the effect of land use change on fishes might depend on the starting land use condition, so we also examined models that included initial agricultural and urban land cover, but these variables were not explanatory, so were not included in the final analysis.

To calculate the change in mean air temperature during the period of fish sampling, we used temperature data from the PRISM climate project [107], which developed estimates of air temperature data at 4km resolution for the contiguous U.S from 1891 to present. We used the *prism* R package [108] to download annual temperature data from the PRISM climate project [107], and calculated mean annual temperature at each site for each year during the fish sampling period. We estimated change in temperature in each HUC12 by regressing annual temperature against year; for HUC12s that had multiple sites, we included a random intercept for site.

To calculate the normalized change in abundance of non-native taxa in each HUC12, we used the USGS Nonindigenous Aquatic Species Database [109], as well as reports and the scientific literature to identify each taxon in each HUC12 as native or non-native. We calculated the change in non-native abundance at each site by regressing non-native abundance against year, and then divided this rate of change by a modeled estimate of the initial total abundance of all fishes at the site so that the change index would represent increases or decreases relative to the starting fish abundance. For HUC12s that had multiple sites, we calculated the mean value of this change index.

To represent the effect of drought during the fish sampling period, we used the Palmer Hydrological Drought Index (PHDI) from the U.S. Climate Divisional dataset, which is calculated monthly for each U.S. climate division from 1895 to present. PHDI is a long-term drought index developed to quantify the effect of drought on streams and other waterbodies, with values primarily ranging between -6 and +6. We calculated the mean July - September PHDI value within each climate division for each year during the fish sampling period. For HUC12s overlapping multiple climate divisions, we calculated a weighted average of the PHDI based on the proportion of the HUC12 in each climate division. We calculated the median value of the PHDI across the fish sampling period to represent the magnitude of drought that occurred during the fish sampling years.

To estimate the degree of hydrologic alteration in a HUC12, we used a dataset that modeled hydrological alteration for millions of stream segments within the contiguous U.S. using streamflow data from over 7,000 USGS gages and 51 predictor variables [110]. We extracted values representing the degree of hydrologic alteration in mean annual flow for each of the NHD stream segments associated with our sampling locations. Hydrologic alteration estimates are scaled from 0 to 1 to indicate a likelihood of hydrologic alteration. For HUC12s with multiple fish sampling locations, we calculated the mean value of hydrologic alteration of the sites.

Because drivers of trends are expected to vary by biome, we categorized each watershed into one of three ecological regions. Our categorizations are based on the EPA's Level I Ecoregions, which divides the continental U.S. into 12 different zones based on geology, vegetation, climate, and other factors [111]. We grouped watersheds within the North American Deserts (n = 26), Temperate Sierras (n = 12), and Mediterranean California (n = 1) ecoregions as the Dry West ecoregion. We classified watersheds in the Eastern Temperate Forests (n = 103) and Northern Forests (n = 32) ecoregions as Eastern Forest. We retained the original Great Plains category (n = 47). There were few subwatersheds with comparable data in the Marine West Coast Forest and Northwestern Forested Mountains, so we omitted those watersheds.

Modeling

We used hierarchical Bayesian models to estimate trends of fish species abundances as a function of HUC12-level mean trends, which were then modeled as a function of stressor covariates, in order to determine which if any stressors were associated with fish declines in a HUC12. At the core of these models is the relationship between counts and year:

$$1.\ N_{h,sp,si,t} \sim Poisson\left(\mu_{h,sp,si,t}\right);$$

$$\log(\mu_{h,sp,si,t}) = N0_{h,sp,si} + SpTrend_{h,sp}Year_t + \log(Effort_{h,si,t}) + \varepsilon_{h,sp,si,t};$$

$$\varepsilon_{h,sp,si,t} \sim Normal(0, \sigma_1^2)$$

where $N_{h,sp,si,t}$ is the count of species *sp* at site *si* within HUC12 watershed *h* in year *t*. Errors were assumed to be Poisson distributed with an extra error term ($\varepsilon_{h,sp,si,t}$) to account for overdispersion [112]. Counts were modeled as a function of a species-site-specific intercept ($N0_{h,sp,si}$), and a species-subwatershed-specific trend parameter ($SpTrend_{h,sp}$). We included an offset term $log(Effort_{h,si,t})$ to account for interannual variability in sampling effort that occurred within some of the datasets [113].

Because we were interested in determining the extent to which subwatershed characteristics contributed to species declines, we modeled species trends ($SpTrend_{h,sp}$) as draws from a normal distribution with mean ($HUC12Trend_h$) and a variance (σ_h^2). The HUC12 trends were then modeled as a function of covariates, as follows:

$$SpTrend_{h,sp} \sim Normal(HUC12Trend_h, \sigma_h^2);$$

$$HUC12Trend_{h,e} = \beta0e + \beta1eUrbanChange_h + \beta2eAgChange_h + \beta3eTempChange_h + \beta4eNonnativeChange_h + \beta5eDrought_h + \beta6eHydroAlt_h + HUC4Eff + HUC8Eff + HUCErr_h$$

Here, the β terms represent the relationship between each type of stressor and the mean HUC12-level trends. We allowed each β term to be estimated differently based on ecological region *e*. Because the HUC12s in the analysis are not randomly or uniformly distributed across the U.S., we also included random intercepts for subregion (HUC4) and subbasin (HUC8) and a normally-distributed error term to account for unexplained variation in trends ($HUCErr_h$).

We fit models using the software JAGS [114] implemented with the runjags package [115] in R. We used uninformative priors for model parameters. For each model, we ran six chains for a 25,000-iteration burn-in period (including a 5,000-iteration adaptation) followed by a 50,000-iteration sampling period (retaining every 5th sample), for a total of 10,000 samples included in the posterior parameter estimates. We assessed model convergence using the Brooks-Gelman-Rubin statistic and by visually inspecting parameter traceplots, and evaluated the significance of parameters using 90% Bayesian credible intervals.

Life history and ecological trait data

To assess the extent to which species-level trends were a function of life history and ecological traits, we used a dataset of traits synthesized from various reports, agencies, literature sources, and expert opinion (Julian Olden, unpublished; and [92]). We partitioned species using three life-history traits: ln(fecundity), or the number of eggs or offspring per female per spawning season; ln(length at maturation), or the mean female length at maturation (mm); and parental investment, defined as ln(egg size + 1) + ln(parental care + 1), or the mean diameter of oocytes (mm) and an index of parental care [116]. These traits have been used to delineate three fish life-history strategies thought to have divergent responses to anthropogenic influences [117]: opportunistic fishes characterized by low fecundity, minimal parental care and small size at maturation; periodic fishes characterized by high fecundity, low parental care, and large size at maturation; and equilibrium fishes characterized by average fecundity, high parental care, and large size at maturation. For species that did not have trait values for each life-history trait (10.1% of trait values) we used the average trait value for that genus.

We examined linkages among traits and trends by first calculating a dissimilarity matrix of traits using Gower’s distance, and performing a principle coordinates analysis (PCOA) on this matrix using the *ade4* package [118], in order to display in two dimensions the relative similarity of different species based on life-history traits. We mapped ecological traits onto the PCOA by calculating average PCOA axis values for species possessing each level of the ecological trait categories. We included the following ecological traits from the same database as the life-history traits: trophic guild, temperature preference, substrate preference, reproductive guild, and vertical position. We plotted density surfaces to visualize areas in trait space with greater numbers of declining and increasing fish species. In cases where multiple trends for the same species occur within some subbasins (i.e., Hydrologic Unit Code 8), we used the trend category (increasing, decreasing, or no change) that occurred most frequently in the subbasin.

RESULTS

Data Summary

We used data from 22 different fish count datasets, consisting of 3,818 separate surveys from 310 different sampling sites in 218 different HUC12 subwatersheds (Table B1). Sampling occurred a mean of 12.3 times at each site over a mean of 18.4 years. We retained a total of 283 different fish species, with trends estimated for a mean of 12.1 native species per subwatershed. Survey years ranged from 1969 to 2019, with an average subwatershed midpoint year of 2002. Only three subwatersheds contained surveys from before 1978. (Figure B1).

There was substantial overlap among ecological regions in most of the variables representing aquatic stressors (Figure 3.1). The Eastern Forest ecoregion was characterized by a broader range of urban and agricultural land use change values compared to the other ecological regions. Subwatersheds in the Dry West generally had lower drought index values representing more severe drought compared to the other ecoregions, while the majority of drought index values for the Great Plains suggested wetter conditions in this ecoregion.

Subwatershed trends

Estimates for the subwatershed-level mean trend ($HUC12Trend_h$) varied considerably, with a median estimate equivalent to an annual decline of 0.3%, equivalent to a 5.0% decline in counts of the average taxa over 18 years, the mean period of time over which sampling occurred at each site. Out of 218 subwatersheds, 37 had significantly negative mean trend estimates based on 90% Bayesian credible intervals, and 35 had significantly positive mean trend estimates, leaving 199 trend estimates that overlapped zero (Figure 3.2). Subwatersheds with significantly negative trends were distributed throughout the U.S. and found in sixteen states, with the greatest concentrations in the southwest and Oklahoma (Figure 3.3). Several negative trends occurred in each ecoregion: 17 in the Dry West, 13 in the Eastern Forest, and 3 in the Great Plains. Subwatersheds with positive trends were less evenly distributed. Over 24 positive trends were from North Carolina, 21 of which came from the North Carolina Department of Environmental Quality data source. Only 5 positive trends occurred outside of the Eastern Forest ecoregion. Subwatershed trends were negatively correlated with the number of years of fish sampling that occurred within a subwatershed (Figure 3.4). The majority of cases in which trend estimates were significantly positive were at sites featuring sampling in 10 or fewer years. The majority of subwatersheds with 20 or more years of sampling had significantly declining trends.

Covariate effects

Effects of subwatershed-level predictors on HUC trends varied by ecological region, although estimates of all covariates but one were non-significant based on 90% Bayesian credible intervals overlapping zero (Figure 3.5). In the Dry West, much of the variation in trends was explained by the negative intercept. Non-native species in this ecoregion had a highly variable effect on trends. In the Eastern Forest ecoregion, there was a significantly-negative effect of the drought index, indicating a negative relationship to wetter conditions. Both temperature change and change in non-native taxa had a positive but non-significant relationship with trends. In the Great Plains, no parameter deviated substantially from zero, but both the change in agriculture and degree of hydrologic alteration had slight negative correlations with trend.

Species traits

The first two axes of the PCOA represented over 94% of the variation in life-history traits. PCOA axis 1 was positively correlated with length at maturity and fecundity, while PCOA axis 2 was negatively correlated with parental investment (Figure 3.6). The highest number of declining taxa were found in the trait space characterized by small length at maturity, low fecundity, and low parental investment. This area of trait space was also correlated with species that occupy sand habitats and spawn in open substrate. Declining species from all ecological regions, but especially those from the Great Plains, were represented in this location. Some increasing taxa from the Dry West and Eastern Forest were also found in this region of trait space. The region of the PCOA associated with high fecundity—typically periodic fishes—was associated with the decline of some taxa, most prominently from the Dry West. The greatest number of taxa with positive trends were found in a region of trait space associated with higher parental investment, including brood hiding and nest spawning, as well as a benthic vertical position, although this area of trait space also featured declining taxa in the Eastern Forest.

DISCUSSION

Across subwatersheds of the contiguous U.S., the median watershed-level population trend of native fishes was -0.3% annually, which represents a non-trivial level of decline. This is comparable to the 11% declines in biomass observed in North American stream macroinvertebrates over a 27 year period [119], an annual rate of -0.4%. Subwatershed trends displayed substantial variability, including both large positive and negative trends, although a majority of trend estimates overlapped zero.

There was notable spatial variation among subwatershed trends. Subwatersheds with negative trends were found across ecoregions, but many of the most pronounced declines were found in the Southwest. Declines in the native fish fauna of southwestern rivers have been documented extensively, including the loss of native taxa in the Gila and San Francisco River [120], the Verde River [121], and the Virgin River [122]. Our analysis found that the strongest negative decline (~18.6% annually) in the U.S. was from a Verde River subwatershed. Declines of nearly this magnitude were observed in the Virgin and San Juan Rivers as well. While these declines had been noted previously, this analysis places these trends in a continental context and suggests that species declines experienced by the native fish communities of many Southwestern rivers are unparalleled in the United States. Several declines were apparent in fish communities of the Great Plains as well.

Putative positive trends should be treated with caution for two reasons: they were primarily found in datasets with fewer sampling years, and were primarily found in a small subset of locations and datasets, especially North Carolina. Some research from the state has demonstrated that during midpoints in the process of habitat homogenization, native species from downstream can invade and increase in abundance, and such processes could result in the appearance of positive subwatershed trends [123].

The relatively large intercept for the Dry West watersheds suggests that the observed declines cannot be explained by the covariates we tested, in contrast to previous analyses that implicated non-native species, hydrologic alteration, and low streamflow in Southwestern fish declines [88, 124]. For example, the influence of non-native species was highly variable: watersheds with pronounced declines experienced both the greatest increases in non-native taxa (e.g., some Virgin River subwatersheds), and the greatest declines (e.g., all San Juan subwatersheds). Similarly, we expected drought and hydrologic alteration to be predictors of fish trends in the Great Plains. The rivers of this ecoregion have been extensively dammed and dewatered, resulting in extirpations of some fluvial-dependent taxa [125], yet we did not see an effect of these predictors.

In the Eastern Forest ecoregion, there was a positive effect of changes in temperature and non-native abundance, and a negative effect of wetter conditions, although only the last of these predictors was significant. In aggregate, these results suggest that common, cosmopolitan taxa may be increasing in abundance as some parts of the East become drier and warmer, conditions favorable to many cosmopolitan species like *Lepomis* sunfish, which comprise several of the increasing taxa in North Carolina. The positive effect of non-native change may reflect co-occurring increases in the non-native and native cosmopolitan species as opposed to any direct benefit of increased non-native fishes. Drier conditions may also promote increases in the aggregation of fishes, which can create the impression of increasing abundance [126].

It is notable yet not entirely unexpected that changes in agriculture or urban land cover during the time period of fish sampling had little measurable impact on subwatershed trends. Urban and agricultural land cover have been strongly linked to changes in fish communities, and even low-levels of urban and agricultural land cover in a watershed (e.g., 1-12% urban land cover) have been linked to marked changes in fish communities [127, 128]. Our datasets included many subwatersheds with low levels of land cover and consequently fish communities that might be susceptible to land use change; for example, half of the subwatersheds in the Eastern Forest ecoregion had initial urban land use of < 2.4%. However, fish communities have been shown to respond to legacy as opposed to contemporary land use change [14], and also may experience an increase in tolerant taxa occurring before sensitive species are lost [129]. Legacy effects and biotic homogenization processes might not be detected in this analysis. Assessing land use and fish trends at the subwatershed scale may also partially obscure land cover effects, with a potential mismatch between areas of land conversion and those with fish sampling. Finally, fishes in different regions—even those of the same species—have variable susceptibility to land use change, and our broad ecological regions encompass areas with taxa known to have differing susceptibility to land conversion (e.g., Piedmont versus Coastal Plain locations in the Eastern Forests, [128]).

The analysis of species traits indicates that declining and increasing taxa are found throughout life-history trait space, but certain trait syndromes appear more susceptible to declines or increases. While a number of taxa with small lengths at maturity and low parental investment—termed opportunistic species—had significantly positive trends, declining species were even more prevalent in this group. This is consistent with findings from global and European analyses: while some opportunistic taxa are capable of exploiting disturbances and anthropogenic changes, studies have suggested that small fishes are generally more susceptible to habitat loss and the introduction of non-native taxa [18, 19]. Small, pelagic-spawning fishes in this region of trait space have been very prone to declines and extirpation, particularly in the Great Plains: their reliance on eggs that float downstream in the water column renders them very susceptible to reduced flows resulting from drought and hydrologic alteration [130]. Our analysis demonstrated some declines in periodic fish characterized by high fecundity and large size, particularly in the Dry West, where species with “slow” life history traits have faced high rates of extirpation [124]. This guild also includes some of the most threatened freshwater fish, such as sturgeon. In many locations, particularly the East, the most susceptible periodic fishes may have already been extirpated [11], suggesting a potential underestimate in our analysis of the risk of declines for taxa in this guild. The greatest concentration of increasing taxa was found in the region of trait space associated with higher parental investment, including nest-guarding taxa. This trend occurred in the Great Plains, but was most prominent in the East, in line with the evidence linking positive watershed trends to warmer, drier conditions. Many species with high parental investment—for example, *Lepomis* sunfishes, and mosquitofishes—are known to fare well in warm, lentic, human-altered landscapes and are sometimes considered “native invaders” [131]. Increasing taxa were also found in the adjacent region of trait space featuring invertivore-piscivores. Many such species are also associated with anthropogenic disturbance, such as catfishes in the genera *Ictalurus* and *Ameiurus*.

Our analysis assessed subwatershed-level trends in response to predictor variables from the time period contemporary to fish sampling, but there are some reasons why the true effects of a stressor in a subwatershed may not have been observed. First, some covariates do not reflect the most proximate relationship between a stressor and fish populations. For example, our drought predictor—primarily intended to capture the effects of low flows—was not correlated to trends in ecoregions where we may have expected it to, namely the Dry West and Great Plains. This metric may be a poor proxy in locations with intense water abstraction, the influence of dams, or conversely, groundwater inputs. Air temperature may also be misaligned with changes in water temperature given groundwater inputs. Still, without the availability of long-term, accurate modeled streamflow and water temperature data, such proxies may be the best available options. Agricultural and urban land cover are also not metrics that directly impact fish populations, but are instead meant to capture alterations to flow, water chemistry, or other in-stream factors brought about by conversion of land cover. While the effects of agriculture and urban land cover on freshwater fishes are widely established, an analysis looking at trends in fish populations as a function of contemporary changes in land cover may miss an effect of these stressors because of delays between land cover change and impacts to biology. For example, the best predictor for present-day fish and macroinvertebrate diversity in North Carolina streams was shown to be watershed land use four decades prior [14].

Many studies of broad-scale species trends have used total abundance or total richness, whereas we examined trends in individual species. This choice was deliberate. Trends in overall abundance may be driven by the trajectory of a few common species, and can mask widespread declines in rarer species. Conversely, species richness may remain constant even when abundances decline precipitously, as long as abundances remain non-zero. Our interest was in understanding trends at the species level, as this is the main unit of management. Nevertheless, we acknowledge limitations to this approach. Because it is difficult to accurately estimate trends of very rare taxa (e.g., [132]), we removed taxa from the analysis that were encountered too infrequently, and consequently, the decline or loss of such species would not be detected with this analysis. Taxa extirpated or reduced to low numbers before the onset of monitoring are also not included. This may account for the western bias in observed declines: many of the most sensitive taxa in the East may not be present in our dataset given historic range contractions or extirpations following development in decades preceding our fish sampling datasets.

Long-term fish monitoring data in the contiguous U.S., while becoming more common, are still not as spatially or temporally comprehensive as datasets for taxa like birds [79] and macroinvertebrates [119], meaning that assessments of fish population trends at broad spatial scales are not yet capable of providing a complete view of the status of the region's ichthyofauna. Still, this analysis of counts in fish trends within 218 different subwatersheds provides insight into the relative magnitude of fish trends in locations throughout the contiguous U.S., the extent to which different stressors are associated with trends across ecoregions, and attributes of the fish species that are declining or increasing. This work suggests that declines of native fishes are widespread throughout the contiguous U.S. and in many cases severe. When coupled with the declines of other stream taxa like macroinvertebrates occurring across the U.S. [119], it suggests that concerns for the status of the fishes of the contiguous U.S. are warranted.

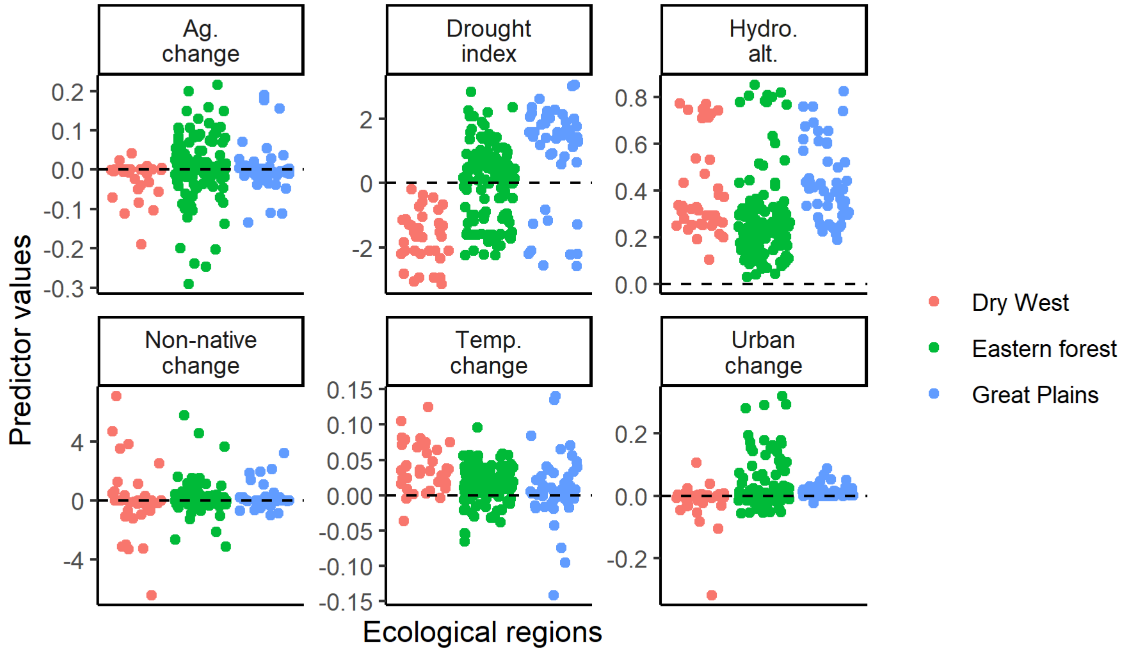

Figure 3.1. Values of predictor variables within different ecological regions. The Urban and Ag. Change categories represent modeled annual percent changes in these land cover categories. Temp. change is modeled annual change in degrees C. Nonnative change is modeled change in abundance of nonnative species relative to initial community-wide abundance. Drought index refers to the Palmer Hydrologic Drought Index, with positive values representing wetter conditions. Hydrologic Alteration is a scaled value from 0-1, with 1 representing maximum hydrologic alteration [110].

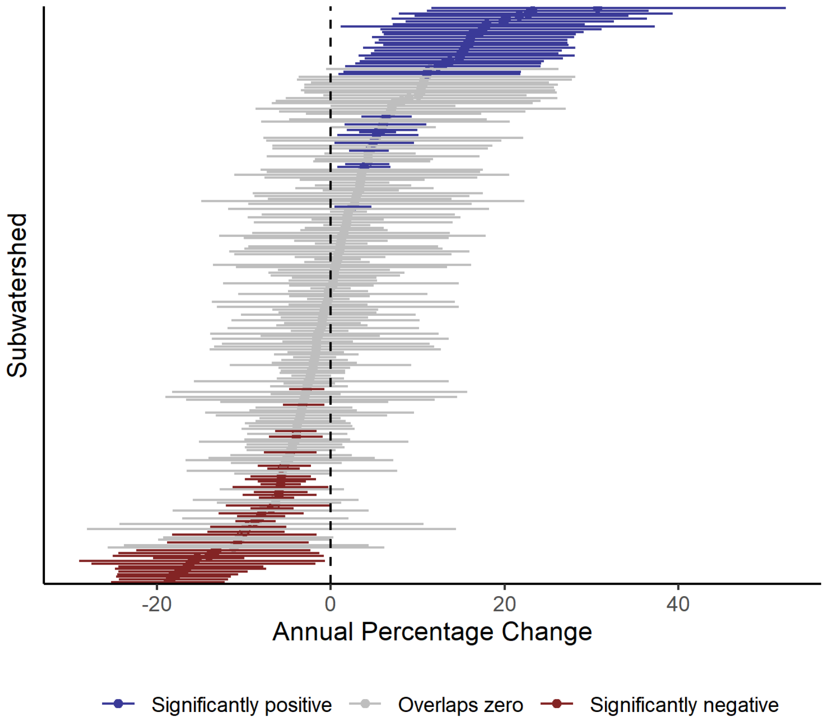

Figure 3.2. Mean trend in abundance of species (i.e., the $HUC12Trend_h$ term) for each HUC12 subwatershed. Points represent estimates of the mean, and lines indicate 90% Bayesian confidence intervals, with points and lines in blue and red representing significantly positive and negative trends respectively.

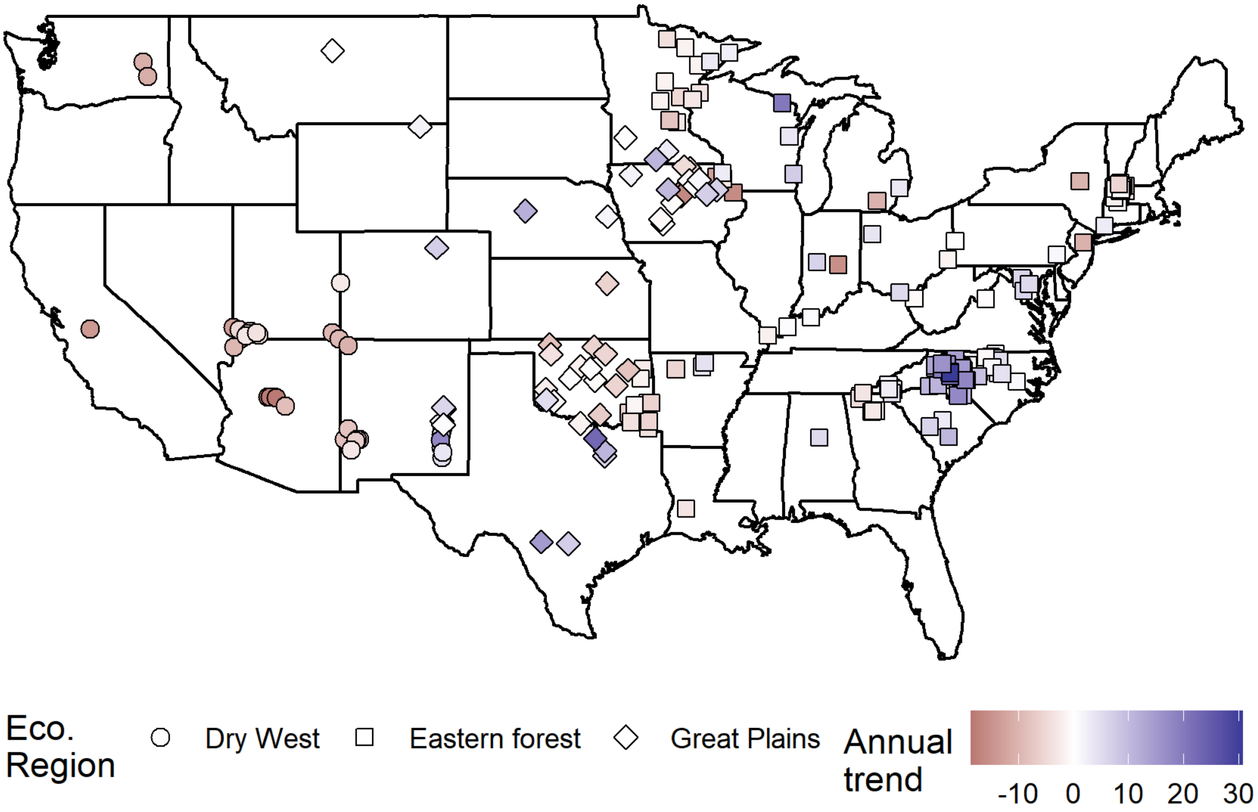

Figure 3.3. Location of HUC12 subwatersheds with mean trend in abundance of species (i.e., the $HUC12Trend_h$ term), identified into three ecoregions. Blue and red points represent positive and negative trends respectively, with darker colors indicating stronger trends.

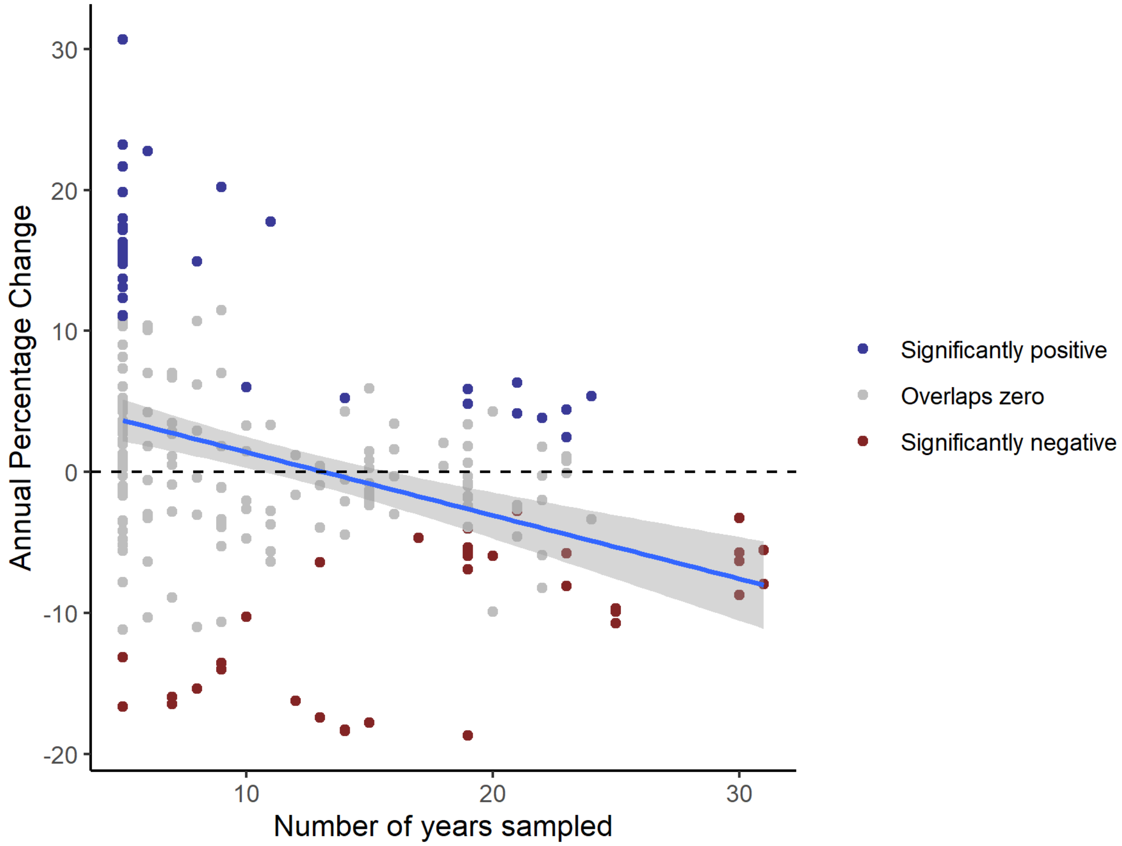

Figure 3.4. Mean subwatershed trends in abundance as a function of the number of years in which sampling occurred. The line represents a linear regression along with 95% confidence intervals.

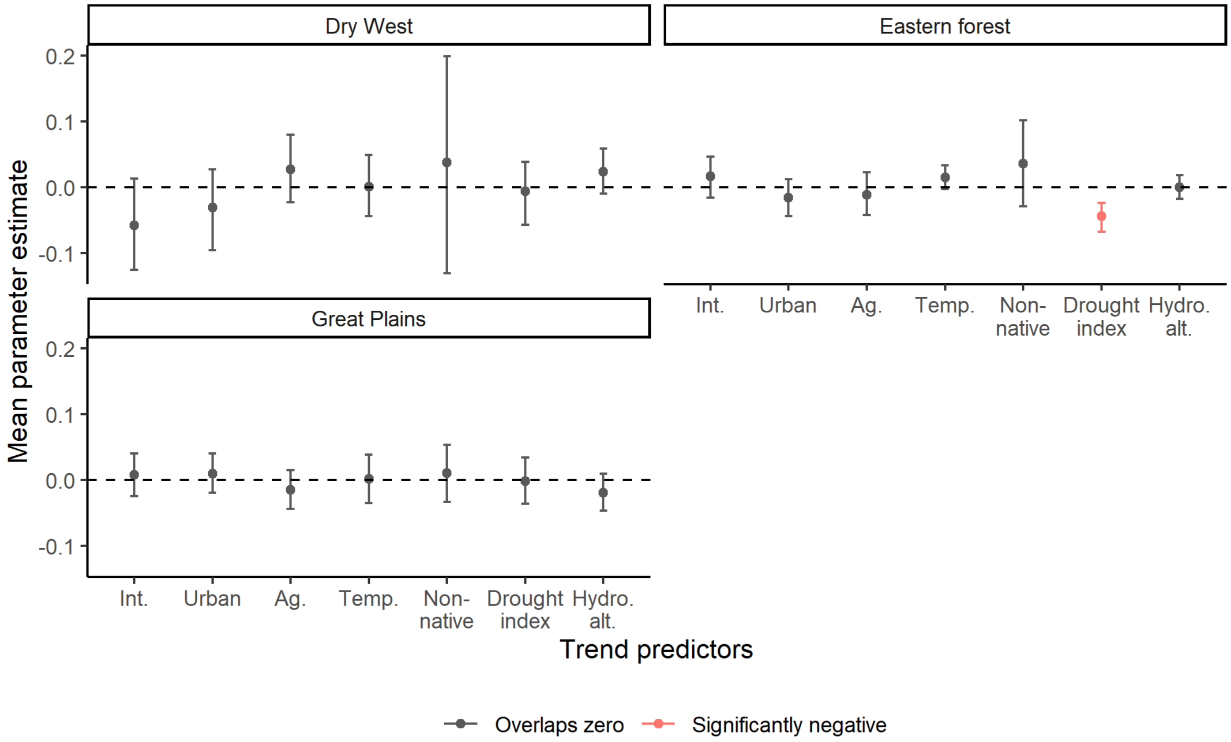

Figure 3.5. Parameter estimates of subwatershed trend predictors for three ecological regions on the scale of the link function. Points are mean estimates, and bars represent confidence intervals. Int. refers to the region-specific intercept. The Urban, Ag., Temp., and Non-native categories refer to modeled changes in these attributes at the subwatershed scale. Drought index refers to the Palmer Hydrologic Drought Index, with positive values representing wetter conditions. Hydrologic Alteration is a scaled value from 0-1, with 1 representing maximum hydrologic alteration from [110].

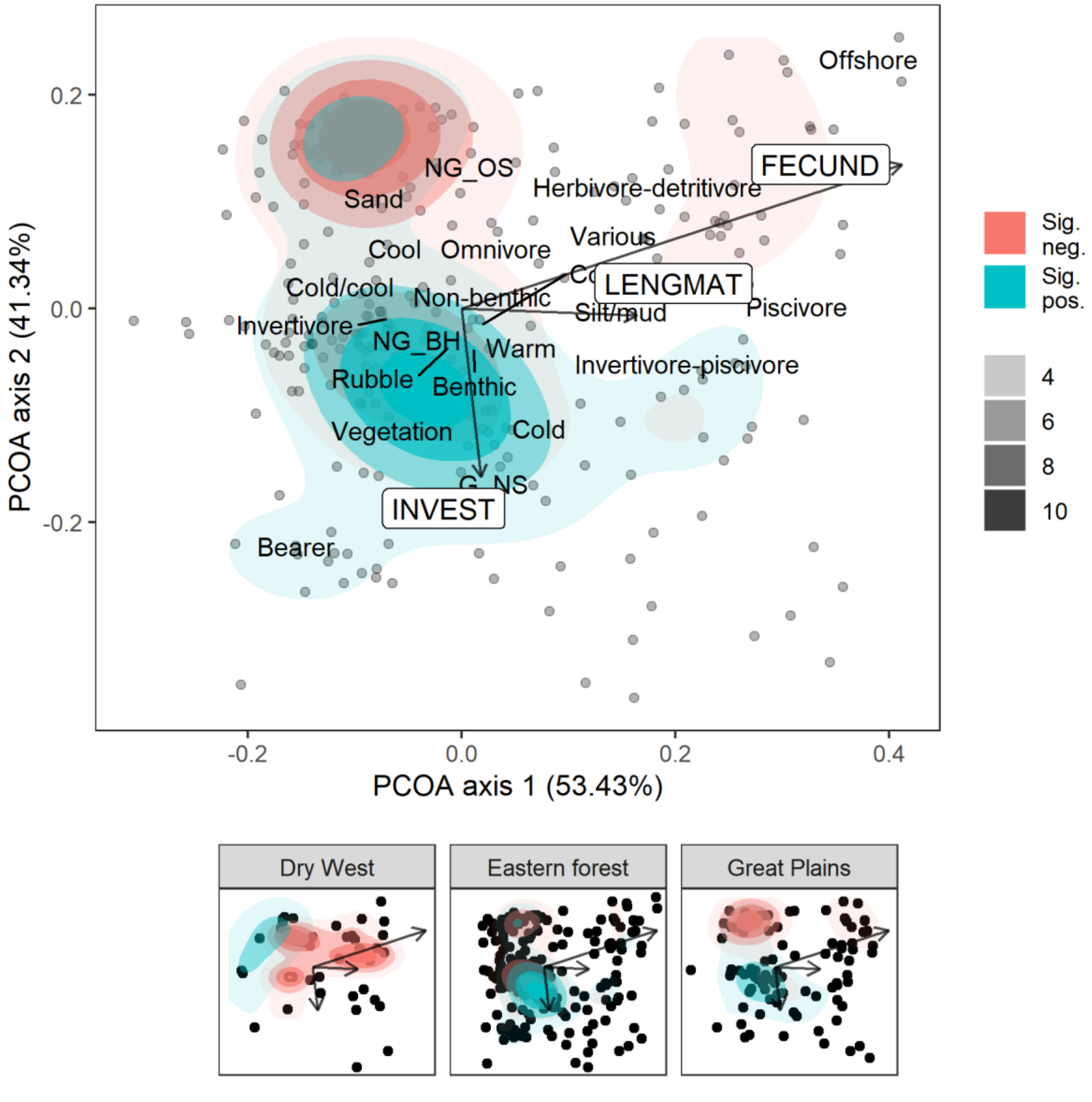

Figure 3.6. Principle coordinate analysis (PCOA) showing associations among three fish life-history traits: length at maturity, fecundity, and parental investment. Points represent locations of each species in trait space. Vectors indicate correlation, with the length and direction reflecting the relationship between each trait and the PCOA axes. Supplemental ecological traits indicate the average location in trait space of each trait. Shading indicates density of species with significantly positive and significantly negative traits based on 90% confidence interval. Abbreviations refer to spawning traits, in order of least to most parental care: NG_OS is non-

guarding open substrate; NG_BH is non-guarding brood hider; and G_NS is guarding, nest spawning.

CHAPTER 4

TESTING HYPOTHESIZED FLOW-ECOLOGY RELATIONSHIPS OF NORTH AMERICAN STREAM FISH GUILDS ACROSS HYDROLOGIC AND CLIMATIC REGIMES[3]

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[3] To be submitted to *Freshwater Biology* with MC Freeman, KR Bestgen, D Carlisle, EA Frimpong, NR Franssen, KB Gido, Y Kanno, C Luce, SK McKay, MC Mims, JD Olden, NL Poff, DL Propst, AH Roy, A Walters, SJ Wenger as co-authors

ABSTRACT

Ecologists identify extreme events as potential drivers of population variability. In the case of stream fishes, extreme flow events and elevated flow variability are widely hypothesized to influence population dynamics. However, generalizable flow effects have proven elusive, potentially obscured by context- and species-specific characteristics. In this analysis we aggregated data from 23 fish count datasets composed of 162 sampling sites from across the contiguous U.S. We used hierarchical Bayesian models to test mechanistic hypotheses linking high- and low-flow drivers to the response of riffle-dwelling and nest-building fishes among different hydrologic and climatic regimes. We found shared guild-level flow responses in only a minority of hydrologic and climate regimes; these occurred more frequently with nest-building than riffle-dwelling taxa. Our predictions that low- and moderate-flow events would favor nest and riffle fishes respectively also received only partial support; nest fishes in particular responded positively to high flow metrics in several regimes in contrast to expectations. Life-history traits also predicted response to flow conditions for only a subset of metrics and regimes. These results suggest that extreme flow events are not uniformly significant to stream fishes, and it is important to understand the contexts in which the effects of flow extremes and variability matter most.

INTRODUCTION

Alteration of the natural flow regime has been implicated in the declines of numerous stream fishes [130, 133]. Flow-related impacts to stream fishes are projected to increase globally with the expansion of dams, hydropower generation, water withdrawals, and land use change [134, 135]. These effects will be exacerbated in coming decades by climate change, with extreme flow events like droughts and floods expected to increase in severity [15]. There is growing recognition among water managers that long-term sustainability requires balancing human water demands with ecosystem flow needs [136]. However, in order to maximize benefits to stream animals while minimizing human costs, water managers will need accurate predictions from ecologists concerning how changes in discharge will impact stream organisms so that scarce water is used efficiently and effectively.

Predicting how populations or communities of fish will respond to specific management actions that alter discharge is difficult given the state of flow ecology [137, 138]. Much of our current knowledge of fish-flow relationships is based on correlative studies linking organism responses to specific flow metrics. Such statistical approaches have generated important insights concerning long-term fish community shifts expected to occur under altered flow regimes [21] or flow conditions correlated with increased local survival or recruitment (e.g., [139]). However, the flow-ecology relationships identified in many studies do not lend themselves to management-relevant predictions. Relationships are often weak, inconsistent or noisy. The extent to which relationships can be transferred varies by species, and has been shown to decline when relationships are transferred to different basins or hydrologic regimes (e.g., free-flowing to regulated systems) [140]. Still, it is infeasible to develop specific flow-ecology relationships at each location where flow alteration will occur [140], and thus more general relationships between biota and flow must be uncovered.

Effective prediction of fish response to flow requires a mechanistic understanding of the links between flow events (or components of the flow regime) and fish population responses [138, 141]. Mechanistic hypotheses will likely need to incorporate both species characteristics and spatial context, as these factors modulate organismal response to flow events [141]. For example, whether a species persists in a location following hydrologic alteration may depend on its life-history strategy [21]; its affinity for fast-flowing riffle habitat [142]; or its spawning mode [24, 130]. Biological responses to flow events also depend on a stream's hydrologic class and its climatic regime [117, 143–145]. Linking flow-ecology relationships to traits and stream context may be the key to transferring flow ecology relationships to understudied regions and species [140]. Recognizing the need for mechanistic hypotheses, Freeman et al. [138] proposed a set of predictions of specific hydrologic events that are expected to affect fishes, conditional on species' traits, stream context and other factors. They proposed that hypotheses could be tested using long-term time series of fish abundances, which are increasingly common [95].

The hypotheses in Freeman et al. [138] are based on frequently-cited ideas about how flows, especially flow extremes, affect fishes. Among these ideas are that anomalous low flows, flow variability, and high flows tend to be harmful for fish populations, especially during the spawning and growing season [146–148]. Low flows reduce habitat and prey availability, impair water quality, and increase predation pressure [149]. An exception to the "low flows are bad" paradigm is for nest-building fishes whose young-of-year are believed to benefit from stable, low flows after spawning [150]. Anomalous high flows can disrupt spawning, destroy nests, and displace eggs and larval fish [147, 151]; however, when such flows occur before spawning, they flush fine sediment from rocky substrates and improve reproduction, especially in riffle-spawning fishes [152]. Implicit in all of these hypotheses is the idea that flows are among the most important determinants of fish population and community dynamics.

Here, we used Bayesian hierarchical models to test mechanistic fish-flow hypotheses on 23 long-term datasets from across the continental United States. To maximize the ease of transferability and the breadth of sites and species that we could include in our analysis, our hypotheses focused on riffle-dependent fishes and nest-building fishes. Riffle-dependent fishes and nest-building fishes are widespread and important components of fish assemblages. Riffle taxa include numerous imperiled species, while nest-building fishes include many sport fishes as well as numerous troublesome invasive fishes. We expected that response to flow events might depend on site context, and therefore assessed how flow-ecology relationships varied across different hydrologic and climatic regimes. We also evaluated whether response to hydrologic metrics was a function of life-history traits. Our analysis provides a first continent-wide examination of the temporal response of fish abundances to flow events, and indicates varying levels of support for oft-cited ideas about effects of stream flow on fish population dynamics.

METHODS

Datasets and survey data

Candidate datasets for our analysis were either generated by co-authors, collected from agency partners, or gleaned from two public sources: the National Water Quality Assessment (NAWQA) dataset [94], a U.S. Geological Survey dataset collected to examine the nation’s water quality, and RivFishTIME [95], a global database of fish time-series data. We screened available datasets using the following criteria: a) fish surveys occurred in lotic habitat (e.g., streams and rivers) not directly downstream of dams; b) surveys consisted of known, consistent sampling methods; c) surveys occurred at consistent locations with known coordinates; d) survey methodology targeted the community of fish species within the sampled habitat and resulted in abundance data for each species encountered; e) surveys occurred at an annual or near annual time-step during consistent seasons; and f) sampling at each site spanned ten or more years between the first and last sampling events, and occurred in at least five separate years. We removed sites that lacked adequate flow data (see *Gage and flow data* section). Some datasets contained multiple samples within some years. We retained only one survey per year, by selecting only surveys in the summer or fall. In the few cases where there were multiple summer/fall samples, we selected the survey that included the greatest number of species. We used the rfishbase package v 3.1.10 [96] in R to ensure all fish taxa names were consistent and current. We removed fish taxa from our analysis if they were not identified to the species level, if they occurred in fewer than half of the surveys within a Hydrologic Unit Code 8 watershed (HUC8).

Site and watershed data

We standardized all sampling site coordinates to latitude-longitude format using the World Geodetic System 1984 (WGS84) reference system, re-projecting any sites that were received in alternative projections. We used the sf package v 0.9-8 [97] in R to determine the HUC8 of each site and to associate each sampling site to a stream segment from the National Hydrography Plus dataset (NHD Plus) [98]. To do this, we first calculated the distance from each sample location to all adjacent stream segments within 1000 meters (Euclidean distance). For sites that sampled waterbodies with known names, we selected the closest stream segment containing the same name as the corresponding site. For sites that lacked a waterbody name attribute, we selected the nearest stream segment. We used ArcMap v. 10.7.1 to assess whether each stream segment selection was reasonable based on proximity to the sampling location and stream size.

To determine whether site context affected flow effects, we assigned each site to a hydrological regime and a climatic regime. The hydrological regime data were drawn from McManamay and DeRolph [153], who empirically classified each stream segment in NHD Plus based on its size, gradient, hydrology, temperature, network bifurcation, and valley confinement. Their approach generated nested hierarchies of hydrologic classes for each stream segment; for our analysis we used the hierarchy with four different hydrologic classes listed from lowest to highest baseflow: intermittent, perennial, snowmelt, and stable. We assigned each site to the hydrologic class of the NHD stream segment associated with that site. We then assigned each site to one of three climate classes (arid, temperate or cold) using the Köppen-Geiger climate classification calculated at 1-km resolution for the time period of 1980-2016 [154]. Because we estimated flow effects for each species at the HUC8 scale (see *Modeling* section below), all sites within a watershed were given the same regime classifications. Of 162 sites, the hydrologic regime was only changed for three sites within two HUC8s, to match the majority hydrologic regime within that HUC8. No site's climate classification was altered by this rule.

Trait Data

We defined nest-building fishes as species within Balon's [155] guarder-nest spawner guild (B.2). We defined riffle-dwelling fish as those that predominantly reside in riffle habitat; this category therefore includes many taxa that might also be considered lithophiles, rheophiles, and/or fluvial specialists. We used taxonomic reference material, expert opinion, and information on habitat preference and spawning mode from two databases of fish traits [92, 156] to assign fish to riffle-dwelling and nest-building guilds. Given that membership in these guilds is phylogenetically-linked, and that limited natural history data exist for some of these taxa, we decided to designate guild membership at the genus level. Within-genus variability for both guild classifications was low, but in the few instances where it existed we classified genera based on the guild of the majority of species within that genus.

For models containing continuous life-history traits, we used a dataset synthesized from various reports, agencies, literature sources, and expert opinion (Julian Olden, unpublished; and [92]). We used three life-history traits: ln(fecundity), or the number of eggs or offspring per female per spawning season; ln(length at maturation), or the mean female length at maturation (mm); and parental investment, defined as ln(egg size + 1) + ln(parental care + 1), or the mean diameter of oocytes (mm) and an index of parental care [116]. These traits were used to delineate three fish life-history strategies thought to have divergent responses to flow variability [117]: opportunistic fishes characterized by low fecundity, minimal parental care and small size at maturation; periodic fishes characterized by high fecundity, low parental care, and large size at maturation; and equilibrium fishes characterized by average fecundity, high parental care, and large size at maturation. To improve model fitting and interpretation, we standardized our continuous traits by subtracting the mean from each trait value and dividing by the trait's standard deviation.

To control for the effect of phylogeny on continuous traits, we estimated relatedness among taxa with a method used by Tedesco et al. [157] and Olden and Kennard [158]. We created a phylogenetic similarity matrix, in which species of the same genus were assigned a value of 1, species within the same family a value of 0.5, species within the same order a value of 0.33, and all other species a value of 0.25. We converted this matrix to a dissimilarity matrix by subtracting it from 1, and then ran a principle coordinate analysis (PCoA) on this dissimilarity matrix. We used the first two axes of the PCoA to represent relatedness among taxa.

Gage and flow data

We calculated flow metrics representing our hydrologic drivers using discharge data from USGS stream gages. To find potential gages for each fish sampling site, we used the sf package in R to identify all gages within 50 km of each site. Gage locations were determined using the “gages” GIS layer in the NHD Plus dataset [98]. For each site, nearby gages were retained if their flow record was missing 10 or fewer days over the time period of fish sampling (all but seven selected gages were missing zero days of the flow record; these seven gages were each missing only 1 or 2 days of flow data). We then used screening notes from USGS’s Gages-II dataset [159] to remove gages with dams, locks, or other diversions in the immediate vicinity of the gage that might cause discharge patterns at the gage to diverge from those at the site. We subsequently calculated two additional screening criteria for each potential site-gage pair. The first was an index representing the distance between sites and potential gages, calculated as the Euclidean distance in km between the site and a potential gage, divided by 50 km, with small values representing close proximity of site and gage. The second was an index representing the relative watershed areas at sites and potential gages, calculated by subtracting from 1 the ratio of the watershed area between site and gage (with the smaller of the watershed areas always in the numerator). Thus, small values of this index indicate sites and gages with similar watershed areas. We weighted the distance index as being twice as important as the watershed ratio index, and then selected the gage for each site that minimized the sum of the two indices. We mapped each possible gage-site match as well as other matches with similar index scores to ensure that no major hydrologic discontinuities (e.g., dams) existed between the gage and site; this caused us to reject several potential gage-site matches. In a small number of cases, we changed the selected gage to an alternative gage if the alternative existed in the same waterbody as the fish sampling site but was slightly further away from the selected gage.

We calculated flow metrics intended to represent the specific hydrologic drivers of interest identified in each hypothesis (Table 4.1). In addition to the flow metrics that represent our hypotheses, we also calculated mean annual flow to indicate whether a year was wetter or drier than average, in order to compare our results to this and similar metrics that have been used in prior fish-flow analyses (e.g., [103]). To calculate metrics pertaining to early spring, spring, and summer at each gage, we used each gage's hydrograph to determine which dates should comprise each season, using the following procedure. We first generated an annual flow signal by calculating the mean flow on each day of the year over the gage's period of record and then calculating the 25-day rolling mean of these mean daily flows to smooth the signal. Next, we calculated mean annual discharge over the period of record, and determined the date at which our flow signal fell below mean annual discharge. We considered this date to represent the transition from higher spring flows to lower summer flows, and thus defined spring as the 60 days preceding this date and summer as the 60 days following this date. We considered early spring flows to be the 60 days preceding the spring season (See Figure C1 for an example hydrograph depicting seasons). All flow metrics at a gage were standardized based on the flow record at that gage in one of two ways: (1) metrics representing discharge were divided by the average value of that flow metric at that gage across all of the years in our dataset; (2) metrics indicating number of high-flow or low-flow days were standardized by calculating gage-specific discharge percentiles over the duration of the fish sampling period, the exceedance of which represented an extreme flow.

Modeling

We used two-level hierarchical Bayesian models to estimate effects of flow metrics on fish abundances and relate these flow effects to species guilds and site context. Each model included only a single flow metric, a single fish guild variable, and a variable for either climatic or hydrologic regime. At the core of these models is the relationship between counts and flows:

1. $N_{h,sp,si,t} \sim Poisson\left(\mu_{h,sp,si,t}\right);$

$$\log\left(\mu_{h,sp,si,t}\right) = N0_{h,sp,si} + \beta1_{h,sp}Qmet_{h,si,t-1} + \beta2_{h,sp}Qsamp_{h,si,t} + \beta3_{h,si,sp}Year_{t} + \log\left(Effort_{h,si,t}\right) + \varepsilon_{h,sp,si,t};$$

$$\varepsilon_{h,sp,si,t} \sim Normal(0, \sigma_1^2)$$

where $N_{h,sp,si,t}$ is the count of species *sp* at site *si* within HUC8 watershed *h* in year *t*. Errors were assumed to be Poisson distributed with an extra error term ($\varepsilon_{h,sp,si,t}$) to allow for overdispersion. Counts were modeled as a function of a species-site-specific intercept ($N0_{h,sp,si}$), and a species-watershed-specific effect ($\beta1_{h,sp}$) of one of the flow metrics $Qmet_{h,si,t-1}$ specified in our table of hypotheses (Table 4.1). We included flow metrics from the prior year *t-1* because our hypotheses pertain to effects on eggs, larval fish, and young-of-year, and thus effects on these fish will not be apparent in our adult-focused fisheries datasets until the subsequent year. Our count sub-model also included an effect of the average flow during the sampling season $Qsamp_{h,si,t}$, as higher flows during sampling are expected to reduce capture efficiency [160]. Given that the presence of underlying populations trends can confound estimates of flow effects, we included a term $\beta3_{h,si,t}$ representing the linear effect of sampling year *t*. Finally, we included an offset term $log(Effort_{h,si,t})$ to account for interannual variability in sampling effort that occurred within some of the datasets [113]. The "count" level of the model (Equation 1) was identical for all of our hierarchical models.

We evaluated evidence that flow effects are conserved among guilds by modeling our species-watershed-specific flow metric ($\beta1_{h,sp}$) as draws from a normal distribution with mean $\mu_{g,r}$ and variance $\sigma_{g,r}^2$, as follows:

2. $\beta1_{h,sp} \sim Normal\left(\mu_{g,r}, \sigma_{g,r}^2\right);$

Thus, $\mu_{g,r}$ indicates the mean response of guild members to specific flow metrics and variance $\sigma_{g,r}^2$ indicates the variability in response among guild members. We ran models in which guild was either riffle-dwelling or nest-building fish, while regime was either Koppen-Geiger climate regime or hydrologic regime from McManamay and DeRolph [153].

The models relating flow effects to continuous traits were identical to the guild-regime models except as follows:

$$3.\ \beta 1_{h,sp} \sim Normal(\mu_{2,h,sp}, \sigma_2^2)$$

$$\mu_{2,h,sp} = \alpha 0_r + \alpha 1_r SizeMat_{h,sp} + \alpha 2_r Fecund_{h,sp} + \alpha 3_r Invest_{h,sp} + \alpha 4_r Phylog1_{h,sp} + \alpha 5_r Phylog2_{h,sp}$$

Here, flow effects $\beta 1_{h,sp}$ for each species within each watershed are modeled as a function of continuous life-history traits (size at maturity, fecundity, and investment), as well as the first two axes of the phylogeny PCOA. αX_r terms are again estimated separately for each regime. Continuous functional traits, including those representing phylogeny, have been used in similar Bayesian hierarchical models to represent how traits control plant growth rates in response to light availability and initial diameter [161].

We fit models using the software JAGS [114] implemented with the runjags package [115] in R. We used uninformative priors for model parameters. For each model, we ran six chains for a 35,000-iteration burn-in period (including a 5,000-iteration adaptation) followed by a 90,000-iteration sampling period (retaining every 5th sample), for a total of 75,000 samples included in the posterior parameter estimates. We assessed model convergence using the Brooks-Gelman-Rubin statistic and by visually inspecting parameter traceplots, and evaluated the significance of parameters using 90% Bayesian credible intervals.

To assess the extent to which our guild-flow specific parameters were predictive across different sites, species, and watersheds, we extended each JAGS model by 20,000 iterations and calculated an expected count in each time-step as follows:

$$4.\ \log\left(\widehat{N}_{h,sp,si,t}\right) = N0_{h,sp,si} + \mu_{g,r} Qmet_{h,si,t-1} + \beta 2_{h,sp} Qsamp_{h,si,t} + \beta 3_{h,si,sp} Year_t + \log\left(Effort_{h,si,t}\right)$$

Here, instead of using the species-watershed-specific flow effect ($\beta 1_{h,sp}$ term) from the original model to generate predictions, we used the guild-regime-specific mean ($\mu 1_{g,r}$), estimated from all members of that guild within that regime. Given that observed counts are also a function of average abundance of a species at a site, flow during sampling, trend through time, and sampling effort, we also calculated $\widehat{N}_{h,sp,si,t}$ values from a null model that contained these parameters but lacked the flow metric term ($Qmet_{h,si,t-1}$). To assess the extent to which including our guild-regime-specific flow effects alter the accuracy with which we predict counts, we calculated the squared correlation between predictions ($\widehat{N}_{h,sp,si,t}$) and observed counts, often called a pseudo-R^2, for both the flow models and the null model for each species at each site. We subtracted the pseudo-R^2 of the null model from the flow models for each species at each site, and then calculated the median change in pseudo-R^2 for each regime.

RESULTS

Data summary

We used data from 23 different fish count datasets, consisting of 2,254 separate surveys from 162 different sampling sites in 86 different HUC8 watersheds (Figure 4.1, Table C1). Sampling occurred a mean of 13.9 times at each site over a mean of 16.7 years. After removing rarer taxa, we retained 238 different fish species, including 92 riffle-dwelling and 62 nest-building fishes (Table C2). Flow metrics were calculated using 100 different USGS gages. The average Euclidean distance between gages and sites was 7.3 km, and the average ratio of watershed area at the sampling location to watershed area at the gage was 0.89 (Table C3). All regimes encompassed sites with a large range of watershed areas (Figure C1). Among climatic regimes, arid sites featured the largest median watershed areas (median = 6,259 km^2, interquartile range = 3,175 – 25,021 km^2), followed by sites in temperate (median = 718 km^2, IQR = 267 – 3,477 km^2) and cold regimes (median = 365 km^2, IQR = 88 – 850 km^2). Among hydrologic regimes, snowmelt sites had the largest median watersheds (median = 11,258 km^2, IQR = 1,933 – 26,101 km^2), followed by intermittent (median = 5,791 km^2, IQR = 732 – 33,237 km^2), stable baseflow (median = 758 km^2, IQR = 204 – 3,347 km^2), and perennial (median = 418 km^2, IQR = 132 – 813 km^2) sites.

Are fish-flow hypotheses supported across different climatic and hydrologic regimes?

Responses to flow metrics varied among guilds and regimes, and there was limited support for hypotheses. We observed a greater number of flow effects that were consistent within regimes for nest-building fishes (Figure 4.2) compared to riffle taxa (Figure 4.3), and also for models featuring climatic regimes as opposed to hydrologic regimes, based on the presence of parameter estimates with 90% Bayesian credible intervals that did not cross zero.

Support for hypothesized effects of low flows on fish abundances was limited to a few regimes. Riffle taxa were only negatively affected by extreme low flows as hypothesized in arid locations (Figure 4.3, H9). Relatedly, there was little support for the hypothesis that higher mean flows in spring and summer—the opposite of low-flows—would have a positive effect on riffle fishes (Figure 4.3, H6a,b); while spring mean flows had a positive effect in temperate locations, spring and summer mean flows had a negative effect on counts of riffle taxa in arid streams.

Stable low flows did not benefit nest fishes as hypothesized: they responded positively to higher low flows in arid and intermittent systems (Figure 4.2, H4). However, they did respond negatively to spring mean flows in arid and intermittent systems, which reflects some support for the hypothesis that lower flows benefit nest-building taxa.

Support for negative effects of variable and anomalous high flows on fish abundances was mixed. Nest species responded negatively to variable summer flows in arid, temperate and intermittent systems, as expected, but this effect was positive in cold and perennial systems, as was the effect of variable spring flows in arid and intermittent systems (Figure 4.2, H1). Likewise, there was mixed support for the prediction that extreme high flows during spawning and growing are detrimental to fish. For riffle fishes, spring floods had a negative effect on riffle taxa in arid systems but frequent summer high flows had no consistent effect on riffle taxa. For nest taxa, frequent summer high flows had the expected negative effect in cold climates, but summer floods had a positive effect in arid and intermittent streams contrary to expectations. Support for the hypothesis that early spring flows improve spawning substrates and lead to increased reproduction was not supported in any climatic or hydrologic regimes.

Riffle and nest taxa in some regimes responded consistently to flow metrics representing general patterns of wet and dry years (shaded region of Figures 4.2 and 4.3). For nest taxa, spring mean flow was negatively associated with abundances in both arid and intermittent streams, whereas summer mean flow was positively related to abundances in snowmelt systems. For riffle taxa, mean annual flow had positive effect in temperate and intermittent regions.

On average, including guild-regime-specific mean flow parameters ($\mu_{g,r}$) in models only led to very modest improvements in count predictions for the majority of non-snowmelt models, compared to predictions from a null model that featured an intercept, and effects of long-term trend, sampling effort, and flow during the sampling period (Figure 4.4). The greatest improvement to model performance on average, based on median changes in pseudo-R^2, were found for riffle fish models that featuring summer extreme high and low flows, as well as summer mean and flood flows for nest fishes in arid regions. Using guild-regime specific flow parameters in snowmelt locations, however, led to poorer predictions than the null model on average for riffle and nest fishes, as did using mean annual flow for nest fishes in arid regimes.

Are flow effects a function of life-history traits?

Of the 236 species used in the ‘guild’ analysis, life-history trait data were available for 202 taxa. Response to flow metrics was correlated with life-history traits in several instances, although more commonly when flow responses were stratified by hydrologic compared to climate regimes (Figure 4.5). Size at maturity was positively correlated with effects of mean annual flow and variable summer flows in arid regions, as well as mean annual flow, early spring flows, and variable summer flows in intermittent regions. Fecundity was positively related to effect of summer floods in temperate locations, while there was an opposite response in cold systems to frequent summer high flows. In intermittent systems, fishes with higher fecundity generally responded positively to various metrics representing higher mean flows (e.g., annual, early spring, spring, and summer mean flows). In perennial systems, the opposite effect was observed for mean annual flows and early spring flows, and fecundity was also negatively related to variable summer flows. Fish with greater parental investment scores generally responded positively to metrics representing both mean and extreme higher flows in arid, intermittent and stable systems; an exception to this was the response to frequent summer highs in intermittent systems. While variable summer flows caused negative responses in fishes with higher parental scores in arid and intermittent systems, variable spring flows had the opposite effect in temperate and intermittent locations.

DISCUSSION

We used 23 long-term datasets from 86 watersheds to test mechanistic flow-ecology relationships, representing a first effort to examine temporal responses by fishes to hydrologic drivers throughout the contiguous U.S. Across flow metrics, fish guilds, and hydrologic or climate regimes, we did not see broad support for most of our hypotheses, or many consistent responses to high, low, and variable flows. Similarly, guild-regime level parameters did not uniformly improve our ability to predict fish counts compared to null models, especially in snowmelt systems. Other authors have suggested that compared to regional studies, approaches that include data from large spatial scales with many species and substantial environmental gradients may demonstrate stronger relationships between fish traits and hydrological drivers [162], but this was not supported by our study.

We expected low flows to be detrimental to riffle fishes, but saw little evidence of this outside of arid regimes, suggesting that riffle taxa may be resilient to drought in many scenarios. Ours is not the first study to report neutral or even positive effects of drought on fish; for example, Katz and Freeman [163] found high young-of-year abundances of a riffle fish in severe drought years in a perennial system, and experimental droughts produced minimal responses among diverse species [164]. However, drought effects on fishes may be most pronounced following multiple years of drought [165], or in locations where fragmentation limits recolonization [130, 166], both scenarios that might be difficult to detect using our analytical approach and datasets. In some cases, higher abundances of riffle fishes during low-flow conditions have been ascribed, at least in part, to an aggregation effect, as reductions in water volume can cause local crowding of fishes without necessarily increasing overall abundances [126]. Our analysis, however, should be less susceptible to this bias, as we are inferring changes in recruitment as a response to flows using counts of adult fishes from the subsequent year where the effects of aggregation versus low flows are less likely to be conflated.

There was relatively little support for our hypothesis that stable low-flow conditions—along with an absence of variable and high summer flows—would benefit nest-building fishes. The only evidence in favor of this was the negative effect of variable summer flows in arid, temperate and intermittent systems. However, variable spring and summer flows had a positive effect in other regimes. Nest species responded positively to increasing 7-day minimum discharges in arid and intermittent systems, and showed no response to this low-flow metric in other regimes. Some intra-guild variability in flow-affinity for nest-building fishes may explain the lack of a stronger low-flow response. For example, Bonvechio and Allen [167] demonstrated that while black basses (*Micropterus* spp.) in four rivers in Florida were associated with low-flow conditions, sunfish taxa (*Lepomis* spp.)—also nest-builders—were associated with higher flow conditions.

The expectation of negative effects of high flows on nest-building fishes was not supported, with the exception of frequent high summer flows being detrimental in cold systems. Instead, spring floods had a positive effect on nest fishes in temperate and intermittent systems, and summer floods had a positive effect on nest fishes in arid and intermittent locations, corroborated by results from the life-history analysis demonstrating generally positive effects of higher flows on species with higher parental investment scores, many of which are nest builders. High flows are known to destroy nests [151, 168], or displace eggs and larval fish from nests

[169], and the restoration of higher flows in a dryland California stream led to reduced relative abundances of nest-building non-native fishes like largemouth bass [24]. However, many nest builders can spawn multiple times per year, and successful spawning may occur following even anomalous high flows [168], particularly in places where water temperatures may be above thresholds for spawning for long durations, which may be true in some of these intermittent and arid systems.

The absence of many strong guild-level flow effects in our study may be the result of observational effects, process effects, or both. It is also possible that fish-flow relationships are strong and important, but methodological or analytical issues obscure these relationships. Discharge data at selected gages might not adequately match flow conditions at each site; and seasonal windows might not adequately match the timing of spawning events. Of particular importance, flow metrics meant to indicate floods, droughts, or flows that alter bed structure and sediment may fail to accurately capture such events, a challenge when performing analyses at broad spatial scales. This could be especially true if flows at a site are already artificially high or low, and consequently low- and high-flow events may represent a reversion to historical conditions as opposed to extreme flows. Other observational challenges may relate to fish count data. While we included a covariate intended to account for discharge-induced variability in capture efficiency, fish count data never perfectly reflect true abundances of fishes. Further, grouping taxa and sites into two guilds and either four hydrologic or three climate regimes respectively might dilute strong flow effects observed within a subset of guild members. For example, it is possible that an alternating subset of guild members responds as we expect each year to flow effects depending on small differences in timing and antecedent conditions, but that these effects are obscured when aggregating these occurrences alongside guild members that do not respond.

On the other hand, the lack of evidence for hypothesized flow effects may indicate that flow is not as important in some systems as current theory dictates, and that many fish may exhibit substantial flexibility with respect to flow regime. Many stream fishes persist in environments following flow alteration—even extreme forms of it—via rapid evolution and phenotypic plasticity [170, 171]. Research suggests that in some contexts, the temperature or sediment regime or other factors can be more limiting to fishes than hydrologic variability [172]. For example, flood flows have been linked to spawning behavior and growth of fish only when temperatures exceed specific thresholds [173, 174]. Biotic factors can also modulate the overall effect of flow conditions on fishes. For example, Gido and Propst [150] suggested that low-flow years in the San Juan River may only be detrimental to native fishes when nonnative predators are abundant. In our study, biotic factors may obscure some flow effects because of the one-year lag between predicted effects on young-of-year (YOY) fish and observed counts of fishes. Large year classes of YOY fish during low flows may grow more slowly because of competition or other factors [163]; conversely, small YOY year classes may survive at higher rates if predation or competition is low. If mechanistic flow effects have the greatest impact on eggs and larval fish—the age classes with the lowest intrinsic rates of survival—such compensatory dynamics may dampen the effect of flow variability on fishes when such effects are assessed at the population level. Similarly, hydrologic drivers that have contrasting effects on YOY and adult segments of populations (e.g. [163]), or negative effects in the current year but positive effects in subsequent years [160], may also limit the extent to which flows generate meaningful population-level changes in abundance.

Several studies have assessed flow responses of fishes as a function of life-history traits to assess the extent to which natural or altered flow regimes act as filters of different life history strategies [21, 139, 162]. There is strong evidence that different flow regime types and alteration of flow regimes determine the proportion of fish assemblages composed of different life-history guilds [21, 117, 175], but weaker evidence that different guilds within a system respond predictably to interannual variation in flows [139]. Our analysis does not overturn this notion that temporal response to flow may be difficult to predict based on life-history traits, as we found a lack of a significant effect of life-history traits on flow response for the majority of our flow metrics and hydrologic/climate regimes (the non-visualized elements in Figure 4.5); and also documented flow metrics with contrasting trait-flow relationships among regimes. Additionally, while many of the relationships that we observed conform to life-history theory, a similar number oppose expectations. For example, opportunistic fish, characterized in part by the smallest lengths at maturity and lowest levels of parental investment, are expected to exploit variable flow conditions [117, 158]: while we observed a negative relationship between parental investment and variable summer flows in arid systems as expected, a positive relationship between length at maturity and variable flows in perennial systems suggests the opposite effect on opportunistic fish. Similar mixed support exists for hypothesized relationships between flow metrics and traits associated with equilibrium and periodic fishes. Non-zero relationships between traits and flow effects were most common among intermittent streams compared to other regime types, with fecundity and parental investment in intermittent streams being mostly positively correlated with metrics reflecting higher flows, excluding frequent high summer flows. High fecundity and high parental investment are associated with periodic and equilibrium life-history strategies respectively, guilds that are not favored in flashy intermittent systems

[175]. This result, therefore, indicates that higher flows that render intermittent systems more like perennial ones might benefit periodic and equilibrium fishes.

Results from our study have some important implication for managers. Our analysis underscores the extent to which higher discharges can benefit fishes in arid systems, but differs from other studies from dry climates (e.g., [24, 61]) in demonstrating that high-flow benefits can also extend to nest-building fishes. This is important because environmental flows simulating floods or flow spikes are among the most promising measures proposed to control nest-building non-native fishes that have devastated native fishes. Such approaches often depend on tight calibration to site-specific geomorphology, flow, and temperature regimes [169]. Our study suggests that more generalized high flows may have the unintended consequence of increasing the abundance of non-native nest-building fishes, so environmental flow interventions must be implemented with care.

Our analysis highlights both promising directions but also hurdles that must be overcome in order to better predict how fishes will respond to changes in flow conditions. The use of Bayesian hierarchical models enabled us to bring disparate datasets together and estimate guild-level flow response parameters from flow effects calculated at the species-watershed level. Without hierarchical models, propagating uncertainty from species-level estimates through to estimates of shared parameters is difficult. Our analysis also would not have been possible without the availability of long-term fish datasets from multiple sources across a wide spatial extent. Still, data from a substantial number of fish sampling locations could not be used because of the lack of adequate flow data. If more fish data and better modeled streamflow data become available, analyses could be stratified by a greater number of regimes and species guilds, which might reveal trends not evident in our groupings. For example, an analysis might include closer to the full 30 hydrologic classes available in the stream classification system by McManamay and DeRolph [153] or the >17 climate categories that comprise the contiguous U.S. [154], and also separate regimes by stream size. The acquisition of finer-grained trait data may also be critical for generating transferrable fish-flow relationships. While current trait databases are a valuable resource for fish ecologists, they do not capture regional variation in traits; furthermore, traits relating to spawning behavior, timing, and frequency—likely among the most important for predicting fish-flow relationships— are still poorly resolved for many taxa. Finally, using a diversity of analytical approaches may be required to find transferrable fish-flow relationships. Our approach flowed from our desire to test specific hypotheses, but doing so limited the number of metrics, guilds, and contexts that we examined. Dredging approaches using machine-learning techniques may generate additional insights [176].

Ecologists have been examining the relationship between flow and fish for decades, yet complex dynamics, antecedent conditions, and context dependence still make it difficult to determine exactly which flows matter to which fish. Our research demonstrates that a broad scale analysis has potential to improve our understanding of fish-flow relationships, but also shows that accurately explaining and predicting interannual variation in fish abundances is elusive. Nevertheless, with fishes under increasing pressure from a diverse array of stressors and water resources strained under novel demands and climate change, research must continue to focus on improving our mechanistic understanding of what effect flow has on fish populations. Otherwise, well-intentioned changes to flow management may be ineffective.

Table 4.1. Hypothesized mechanistic effects of flow conditions on riffle-dwelling and nest-building young-of-year (YOY) fish abundances, along with associated flow metrics, motivated by Freeman et al. [138]. Each flow metric is normalized to gage-specific flow metrics or discharge (Q). CV indicates coefficient of variation.

Hyp. Num.	Guild	Hydrologic driver	Mechanism	Season	Response	Flow metric
1 a,b	Nest-builder	Variable flow during spawning/growing	Disrupts nest-building and rearing of YOY	Spring Summer	Decreased YOY	Seasonal CV
2 a,b		Floods during spawning/growing	Destroy nests and dislodge eggs, displace larvae	Spring Summer	Decreased YOY	Seasonal peak Q
3		Frequent high flows after spawning	Nest abandonment; larval displacement	Summer	Decreased YOY	Num. days in top 95% of seasonal Q
4		Stable, low flows after spawning	Warm temperature; shallow-water refugia	Summer	Increased YOY	7-day avg. minimum summer Q
5	Riffle-dweller	High flows before spawning	Clean sediment from gravel	Early-spring	Increased YOY	Early-spring mean Q
6 a,b		Adequate flows during spawning/growing	Increased surface area of riffles for increased YOY growth, survival	Spring Summer	Increased YOY	Seasonal mean Q
7		Floods during spawning	Disrupted spawning; egg displacement	Spring	Decreased YOY	Spring peak Q
8		Frequent high flows after spawning	Mortality and displacement of larval fish	Summer	Decreased YOY	Num. days in top 95% of seasonal Q
9		Extreme low flows after spawning	Loss of juvenile habitat; thermal stress; increased predation and competition	Summer	Decreased YOY	Num. days in bottom 95% of summer Q

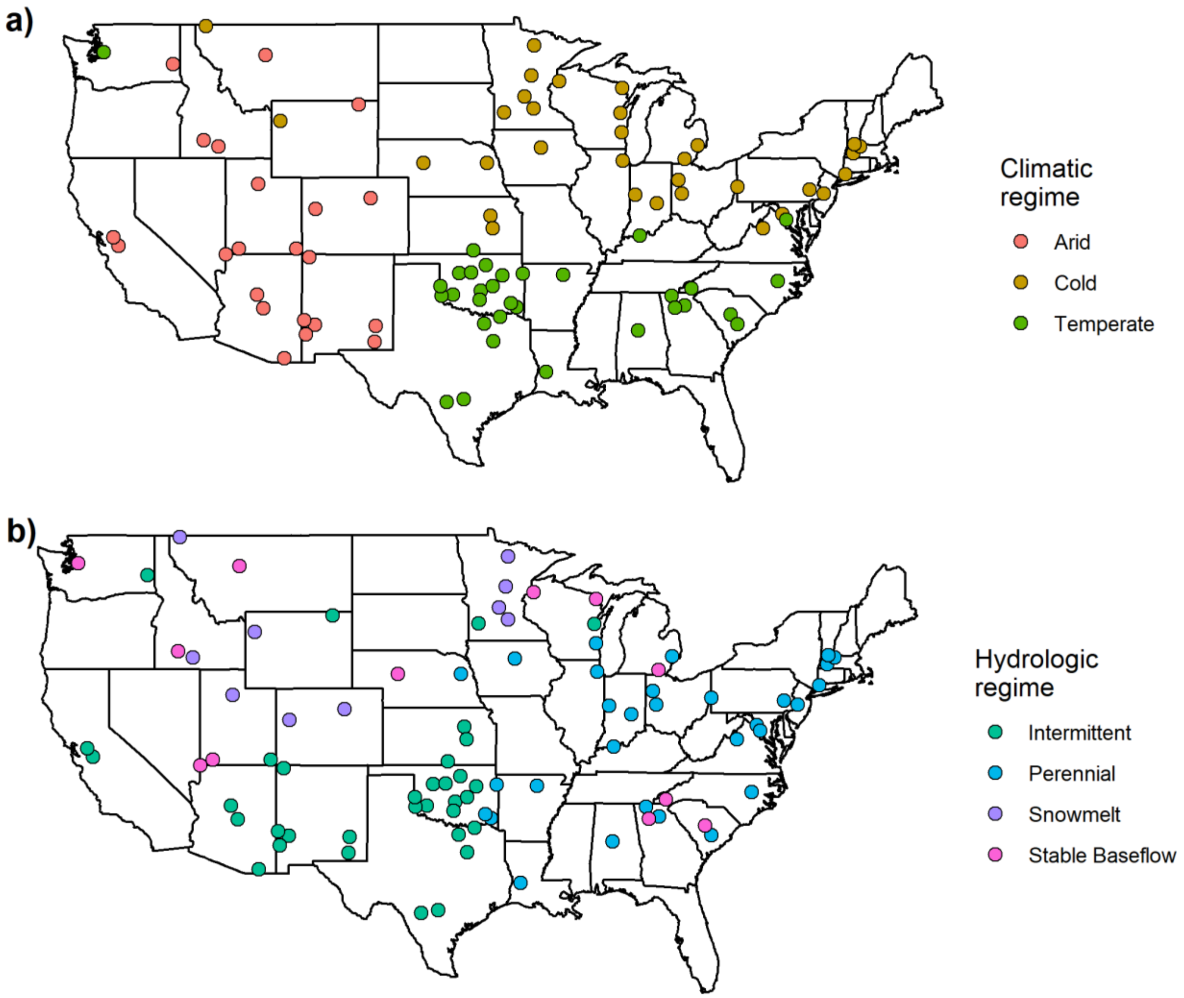

Figure 4.1. Locations of HUC8 watersheds with fish sampling data, along with associated a) climatic and b) hydrologic regimes from Beck et al. [154] and McManamay and DeRolph [153] respectively.

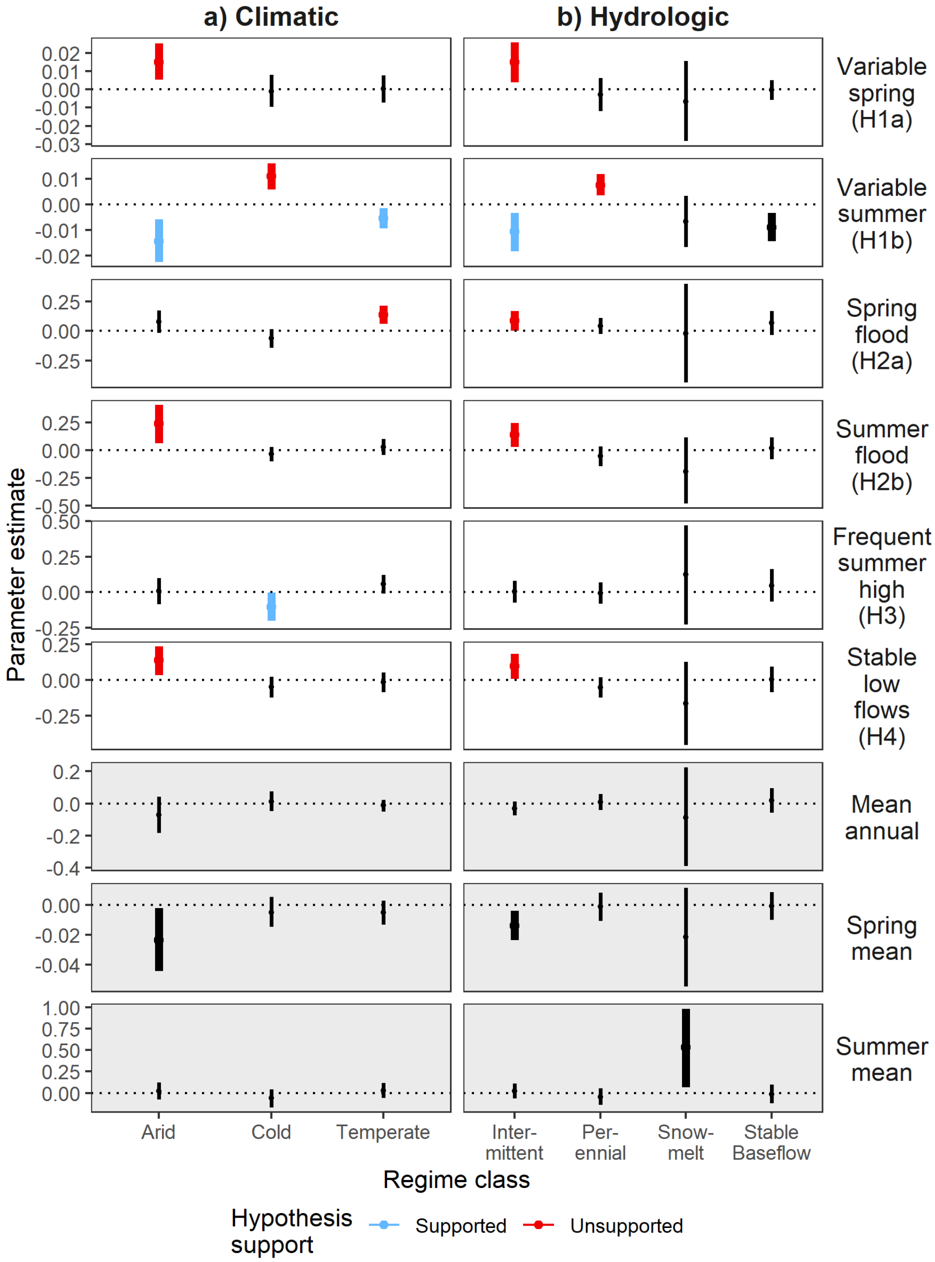

Figure 4.2. Parameter estimates relating abundance of nest-building fishes to different hydrologic drivers. Responses are stratified by a) climatic or b) hydrologic regime. The number in parentheses represents the hypothesis tested. Points are mean parameter estimates and lines are 90% Bayesian credible intervals. Bold points and lines indicate parameters that do not overlap zero, and colors indicate hypotheses that were supported or rejected. Shaded panels are metrics representing average flow conditions unconnected to specific flow hypotheses.

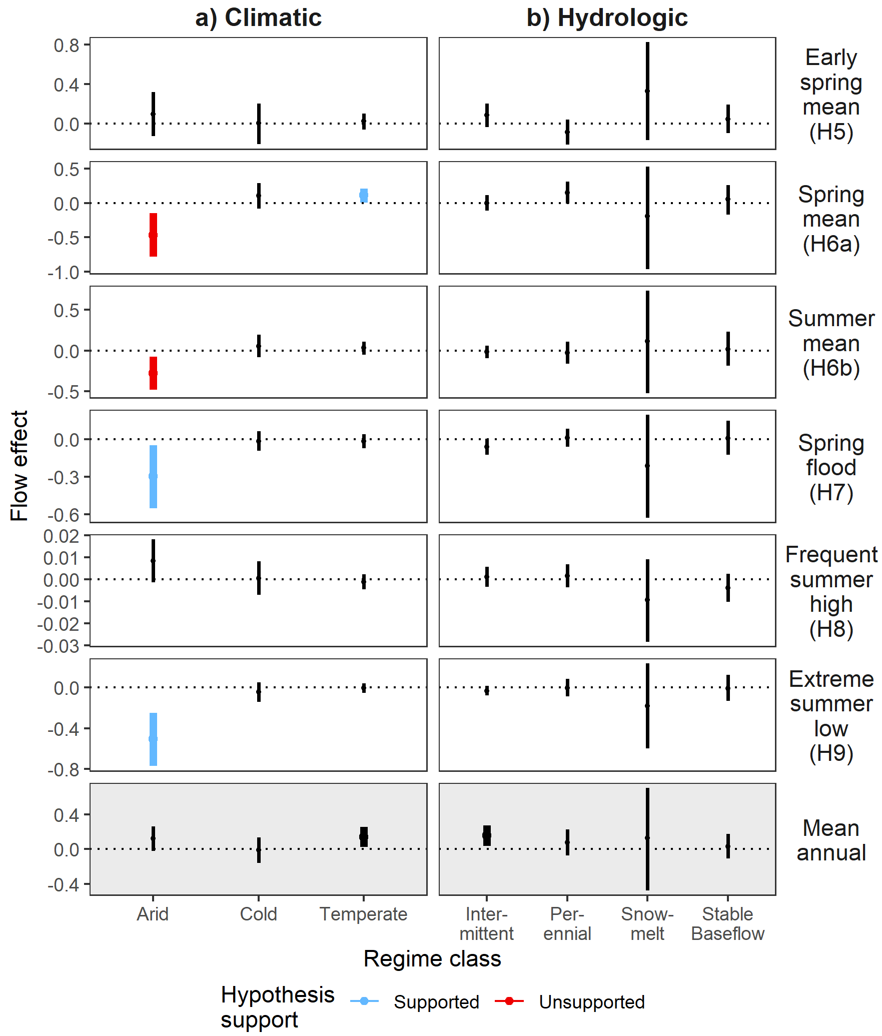

Figure 4.3. Parameter estimates relating abundance of riffle-dwelling fishes to different hydrologic drivers. Responses are stratified by a) climatic or b) hydrologic regime. The number in parentheses represents the hypothesis tested. Points are mean parameter estimates and lines are 90% Bayesian credible intervals. Bold points and lines indicate parameters that do not overlap zero, and colors indicate hypotheses that were supported or rejected. Shaded panels are metrics representing average flow conditions unconnected to specific flow hypotheses.

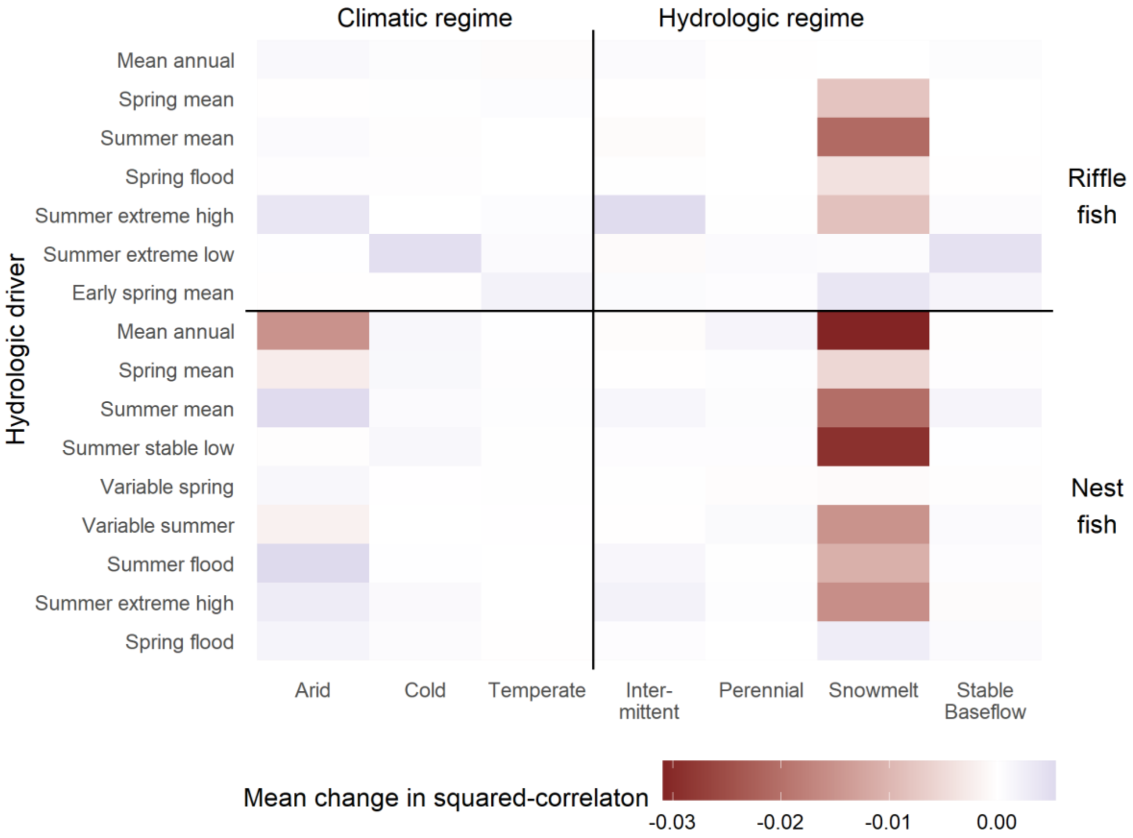

Figure 4.4. Median difference in pseudo-R^2 for models predicting counts with and without a mean guild-regime-specific flow metric.

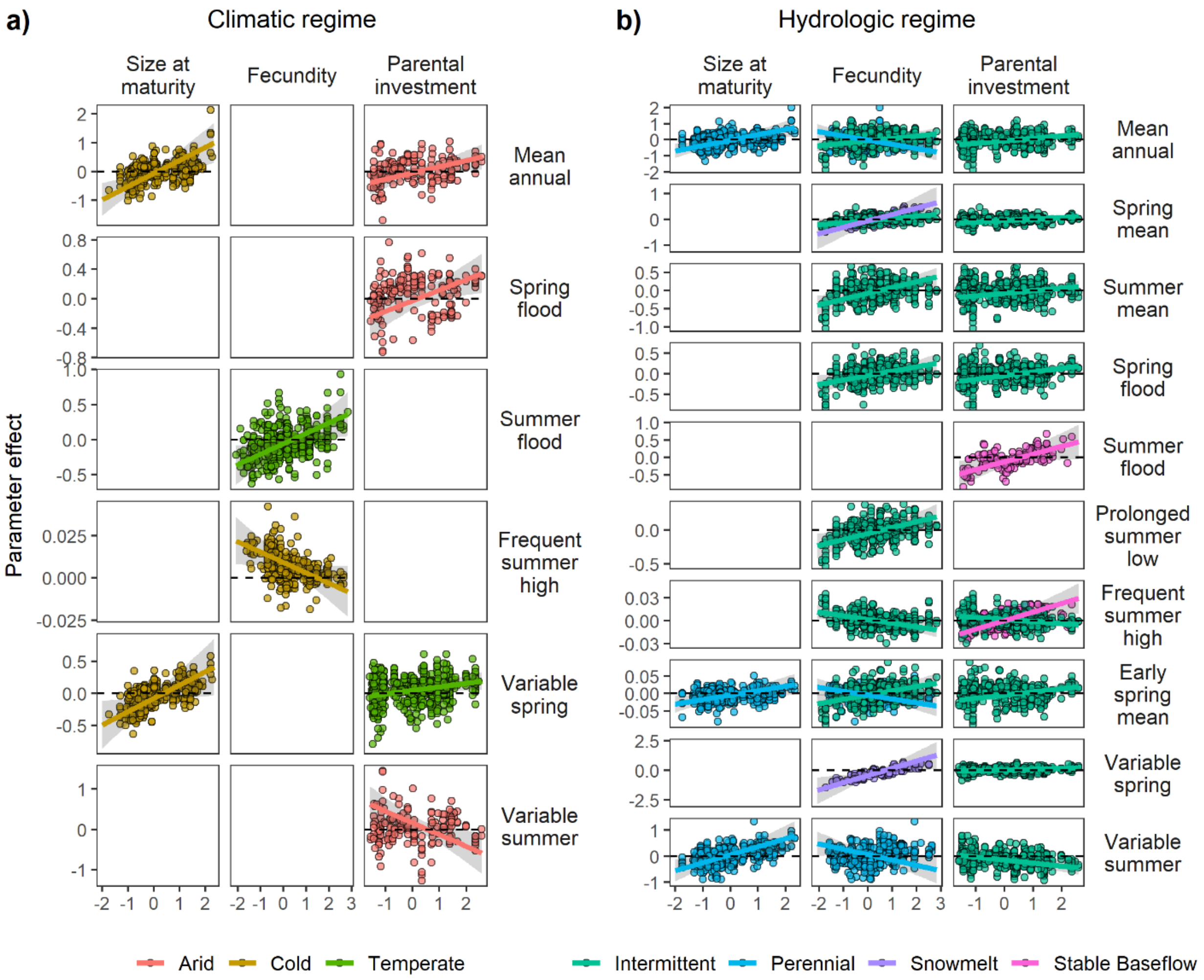

Figure 4.5. Responses to flow metrics as a function of continuous life history traits within either climatic or hydrologic regimes. Regression lines represent the predicted response to flow conditions at different values of the trait variable, and points are the modeled flow effects for species within each subbasin (HUC8). Cases in which trait variables had a non-significant effect on flow response are not shown. The shaded area represents 90% Bayesian credible intervals.

CHAPTER 5

CONCLUSIONS

The overarching goal of this dissertation was to understand changes in fish populations over short and long temporal scales to inform conservation. I characterized long-term trends of fishes at two spatial scales, and the inter-annual response of fish populations to extreme flow events across the contiguous U.S. I first estimated population trends of an endangered stream fish, the Amber Darter, in order to evaluate if its two populations were declining and whether the dynamics among its populations were independent (Chapter 2). For the subsequent two chapters, I compiled a large dataset of fish time series in order to examine fish population dynamics at the scale of the contiguous United States. In Chapter 3, I analyzed the magnitude and variability of fish population trends in subwatersheds across the U.S., and assessed whether trends were explicable based on stressors and species traits. Finally, in Chapter 4, I used the same dataset to explore whether two important guilds of fishes—nest-builders and riffle-dwellers—respond in predictable ways to high- and low-flow events. I also examined if life-history traits predicted how fishes responded to flow events.

In Chapter 2, I documented pronounced declines in both known populations of the endangered Amber Darter. The decline in the population from the Etowah River was unexpected, as a previous study using presence-absence data had not indicated that this taxon was declining [16]. My analysis suggested that the Amber Darter is at greater risk of extinction than previously thought; projections of current trends into the future indicate risk of the species' quasi-extinction by mid-century. The analysis approach I used—Multivariate Autoregressive State Space modeling—also did not indicate support for substantial independence among populations. Non-independence may confer additional extinction risk to the species [26].

Other analyses have indicating declines of aquatic animals in the Upper Coosa Basin and in the Conasauga River in particular, including the rapid decline of the mussel fauna there [177]. Numerous efforts have been made to identify the drivers of declines, but these remain enigmatic. Understanding the declines of organisms in any one location may be difficult unless those declines can be placed within a broader context. For example, it may not be clear 1) if trends in a location are anomalous or if similar dynamics are occurring elsewhere, 2) whether the particular combination of stressors and environmental variation in a location is unique, and 3) whether the taxa declining in that location share commonalities with taxa elsewhere. The inability to answer these questions about the Conasauga declines was in part what motivated the analysis of trends across the contiguous U.S. conducted in Chapter 3.

In Chapter 3, I showed that fishes at the subwatershed scale across the contiguous U.S. declined by a median of -0.3% annually, a rate comparable to recent declines of macroinvertebrates across the U.S. [119]. I also found large differences in the magnitude and spatial variability of trends: the largest declines were concentrated in the arid Southwest, while in the East, few trends were negative and many North Carolina trends were positive. All but one stressor covariate across regions did not have a significant effect on trends. However, there was some evidence in Eastern Forest sites that a general shift toward drier, warmer conditions may be favoring cosmopolitan species. The identity of declining and increasing taxa showed important variation among regions. Many taxa that declined in the Dry West and Great Plains have life histories tightly linked to long-term patterns of environmental variation found in those regions, such as fishes requiring pulses of flow and unfragmented stretches of river to spawn. On the other hand, increasing fauna in the East appear to be cosmopolitan species tolerant of anthropogenic activity. Consequently, the patterns that I observed may indicate that Eastern and Western sites are at different points in an ecological degradation trajectory. Many Eastern sites may have lost non-cosmopolitan species prior to the onset of fish monitoring, and now sustain communities that can co-exist with human development.

In Chapter 4, I found that riffle-dwelling and nest-building fishes largely did not respond in guild-specific ways to metrics representing high, low, and variable flow. Where responses were shared among guild members, they were often in contrast to my hypotheses that stable, low flows would benefit nest fishes while riffle fishes would favor higher—but not extreme—levels of flow. Flow effects were also not consistently predicted by life-history traits, and some of the stronger relationships documented between flow and life-history traits—such as the positive relationship between length-at-maturity and variable summer flows—contrast with expectations from life-history theory. Overall, my results suggest that uncovering flow-ecology relationships that are generalizable and can be used to predict the response of fishes in poorly-studied locations may be difficult—or that general relationships do not exist. Ultimately, my findings suggest that most fish may be fairly tolerant to a wide range of flow conditions.

The analyses in Chapter 3 and 4 provide some context with which to interpret the declines in the Conasauga River.. Decline estimates in two Conasauga subwatersheds were among the most substantial in the Eastern Forest ecoregion, approximately 5% annually. This is more than 15 times the rate of declines in the median subwatershed in my analysis, and is especially notable given that the Eastern Forest ecoregion had fewer declining subwatersheds than the other ecological regions. When comparing stressor variables in the Conasauga to those of other Eastern Forest sites, one category is most notable. Out of the 133 Eastern Forest subwatersheds, two Conasauga subwatersheds experienced the largest increases in agricultural land cover. Furthermore, starting agriculture land cover percentages of these subwatersheds were 28% and 29%. Chen and Olden [178] estimated that thresholds of agricultural land cover at which the species richness and community compositions of fishes change in the U.S. are 26% and 31%. Agriculture has long been a candidate cause of declines in Conasauga fishes, and viewing the Conasauga declines in the context of other fish populations throughout the East suggests that this may be the most parsimonious explanation, although it still does not provide a proximate mechanism through which agriculture might be affecting fish. Conasauga subwatersheds also had among the greatest increases in temperature, which could exacerbate potential agriculture-related stressors.

Low flow has also been implicated as a potential driver for declines in Conasauga taxa, as some extreme droughts have co-occurred with fish declines [16]. However, my results in Chapter 4 suggest that riffle fishes—a guild that includes most of the declining taxa in the Conasauga—are largely resilient to low flows. Furthermore, drought levels in the Conasauga were intermediate compared to other Eastern Forest sites as a whole. This indicates that drought in the absence of other factors is unlikely to have caused such pronounced fish losses. However, drought conditions may have exacerbated the effect of other factors such as agriculture. Groundwater pumping associated with agriculture has worsened drought elsewhere and led to declines of fishes assemblages in the Great Plains [179, 180]. On the other hand, if fish are being harmed most by contaminants and poor water quality related to agriculture, drought conditions that generate warmer, less-oxygenated water that is not flushed as frequently from the system could exacerbate these problems. Exceptional low flows have been shown to concentrate harmful contaminants in other systems [181].

My analyses demonstrate some of the benefits of jointly analyzing datasets using hierarchical models. Results from Chapter 2 indicate that modeling the distinct populations of endangered taxa together provides the ability to explore different hypothesized relationships among populations, and allow the data to determine whether parameters should be shared or estimated separately. In the context of evaluating populations of protected species for status assessments, doing so provides information that may alter our understanding of the resiliency and vulnerability of a species. My other analyses also show the value of jointly analyzing datasets with hierarchical models. In both cases, parameters at the count level of the model were used to inform estimates of parameters representing broader phenomena: the central trend of species in each subwatershed, or the mean response of fish guild members to hydrologic drivers. Some analyses estimate individual-level parameters in one model and then treat those estimates as independent variables in subsequent analyses, but doing so fails to properly account for uncertainty in estimates at all levels.

The analyses in Chapter 3 and 4 required the compilation of a large number of fish time-series datasets. The original impetus for each dataset is unique, with several initiated to monitor species with protected status, while others were carried out to augment broad-based assessments of water quality. Still, each dataset represents the substantial effort by individuals across the country to sample fish annually, and in many cases, the foresight to understand the future value of long-term datasets when they were less ubiquitous. These analyses also would not have been possible without a large number of datasets featuring relatively fine-scale predictor information from across the United States, including data for streamflow, land use, temperature, hydrologic alteration, and several other variables. These datasets represent large investments from both individual scientists, organizations and government agencies, particularly USGS and the EPA.

Continued effort to collate datasets at the national scale should improve analyses such as these. For example, spatial datasets indicating where taxa have already been extirpated could augment trend analyses and indicate taxa overlooked when using only contemporary data records.

While my combined dataset may represent the largest collection of fish time series assembled for the U.S., its spatial and temporal coverage pales in comparison to the scope of the macroinvertebrate data used in a recent trend analysis (6,131 sites) [119], and to the 4,500 routes surveyed annually that comprise the Breeding Bird survey. That degree of spatial coverage enables powerful inferences, such as the estimate that three billion birds have been lost in North America since 1970 [79]. Increasing the coverage of fish monitoring in the United States could provide substantial benefits, but even if implemented now, it might take 10-20 years before the data could generate meaningful inferences [182]. This suggests that additional efforts should be made to leverage data from “data-rich” organisms to inform our understanding of the status of organisms with comparatively less data. Evaluating the circumstances under which bird or macroinvertebrate trends are correlated with fish trends—and the cases where they are not—could generate additional insight into processes governing trends of all taxa. Furthermore, areas with pronounced changes in one group of organisms might be investigated for similar changes in understudied species. The datasets that I have assembled and the analyses I have demonstrated lay the groundwork for such multi-taxa analyses and other future studies that could collectively lead to greater understanding of organismal population trends, which are needed to solve the biodiversity crisis.

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APPENDIX A

CHAPTER 2 SUPPLEMENTARY INFORMATION

Table A1. Mean parameters values from the top five MARSS models. Values in parentheses represent 95% confidence intervals generated using parametric bootstrapping implemented within the MARSS package.

Rank	Growth	Growth, Conasauga	Growth, Etowah	Process variance	Process covariance	Observation Variance
1	-0.086 (-0.119, -0.049)	NA	NA	0.005 (0, 0.015)	NA	0.368 (0.288, 0.410)
2	-0.086 (-0.119, -0.053)	NA	NA	0.005 (0, 0.017)	0.005 (-0.002, 0.015)	0.368 (0.290, 0.411)
3	-0.086 (-0.119, -0.051)	NA	NA	0.005 (0, 0.019)	0.005 (0, 0.019)	0.368 (0.289, 0.415)
4	NA	-0.095 (-0.129, -0.061)	-0.080 (-0.113, -0.047)	0.005 (0, 0.013)	0.004 (0, 0.012)	0.368 (0.285, 0.409)
5	NA	-0.095 (-0.127, -0.059)	-0.080 (-0.111, -0.047)	0.005 (0, 0.014)	0.004 (0, 0.014)	0.367 (0.288, 0.414)

APPENDIX B

CHAPTER 3 SUPPLEMENTARY INFORMATION

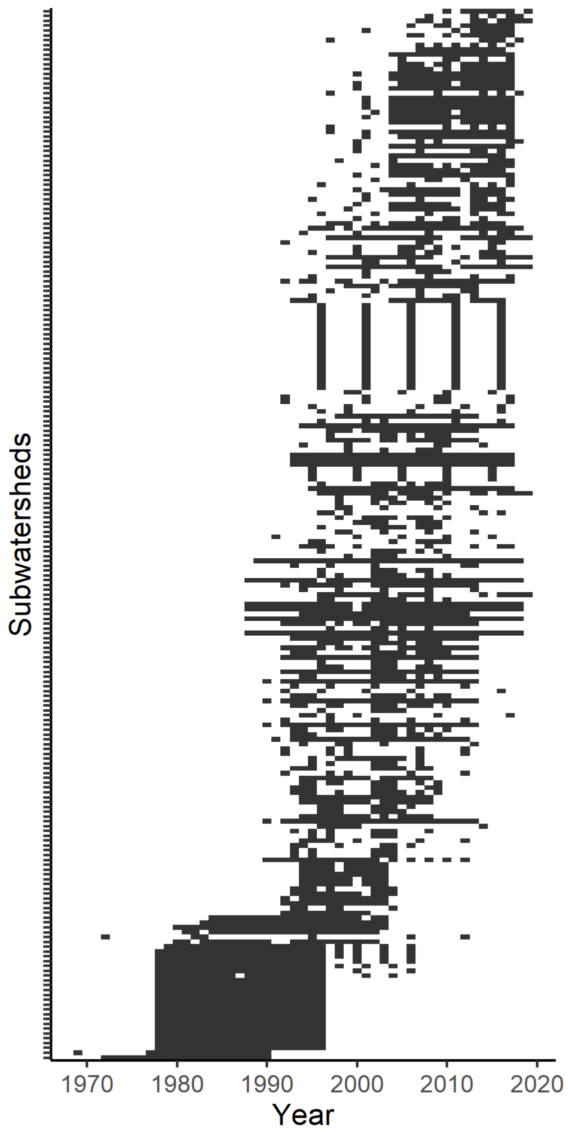

Figure B1. Years of in which fish sampling occurred within each subwatershed.

Table B1. Data sources for fish count data.

Dataset	Num. sites	Num. species	First yr.	Last yr.	Num. yr.	States	Dry West sites	Eastern Forest sites	Great Plain sites
Conasauga R.	14	33	1996	2019	19	TN,GA	0	3	0
Etowah R.	9	31	1997	2019	21	GA	0	3	0
Gila R.	4	7	1988	2018	31	NM	4	0	0
Iowa DNR	17	54	1994	2017	23	IA	0	4	12
Kings Creek	4	6	1995	2018	22	KS	0	0	1
Little TN. R.	11	33	1990	2013	24	NC,GA	0	6	0
MassWildlife	57	14	1997	2017	18	MA	0	22	0
Maryland	18	24	1992	2017	25	MD	0	4	0
MN. PCA	13	44	1992	2018	20	MN	0	11	2
MT. FWP	1	10	2001	2010	5	MT	0	0	1
NAWQA	40	154	1993	2019	25	24 States	5	23	12
NC DEQ	40	54	1991	2016	25	NC	0	39	0
OH	11	34	1993	2016	23	5 States	0	7	0
OK DEQ	22	85	1978	2006	25	OK,TX	0	7	15
OK,_Matthews	1	15	1972	2012	6	AR	0	1	0
OK,_Pyron	2	25	1969	1990	20	OK	0	2	0
Pecos R.	14	14	1992	2013	22	NM	8	0	4
Big Raccoon Cr	8	31	1981	2002	21	IN	0	1	0
San Fran. R.	2	5	1988	2018	31	NM	2	0	0
San Juan R.	3	3	1993	2017	25	UT,NM	3	0	0
Verde R.	7	6	1994	2012	19	AZ	5	0	0
Virgin R.	12	6	1980	2003	24	UT,NV	11	0	0

APPENDIX C

CHAPTER 4 SUPPLEMENTARY INFORMATION

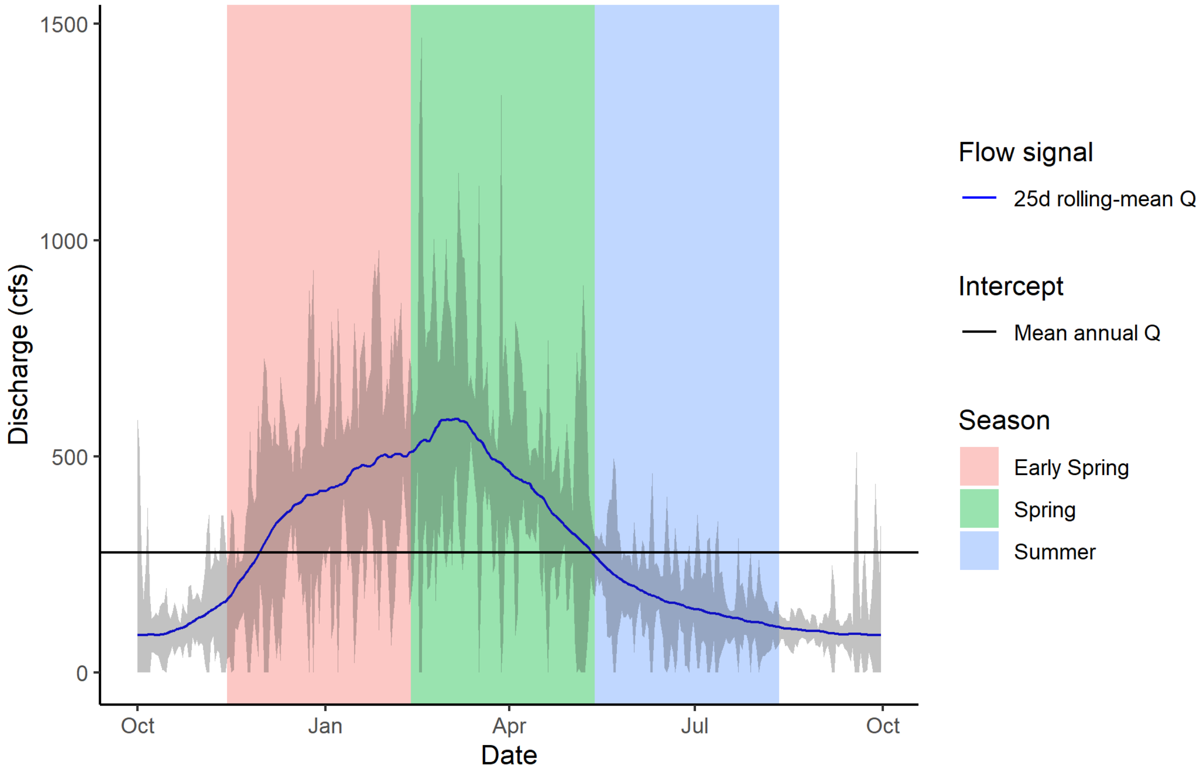

Figure C1. Example hydrograph depicting how seasons were determined in order to calculate seasonal flow metrics, using data from USGS streamgage 02384500, Conasauga River at GA 286, near Eton, GA. The date at which the 25-day rolling-mean discharge (Q) falls below the mean annual discharge (Q) represents the transition from spring to summer. Spring and summer are each 60 days in duration. Early spring is the 60 days preceding spring. The shaded area represents flow variability and is calculated as the mean daily flow on each date ± 0.25*standard deviation of the mean daily flow on that date.

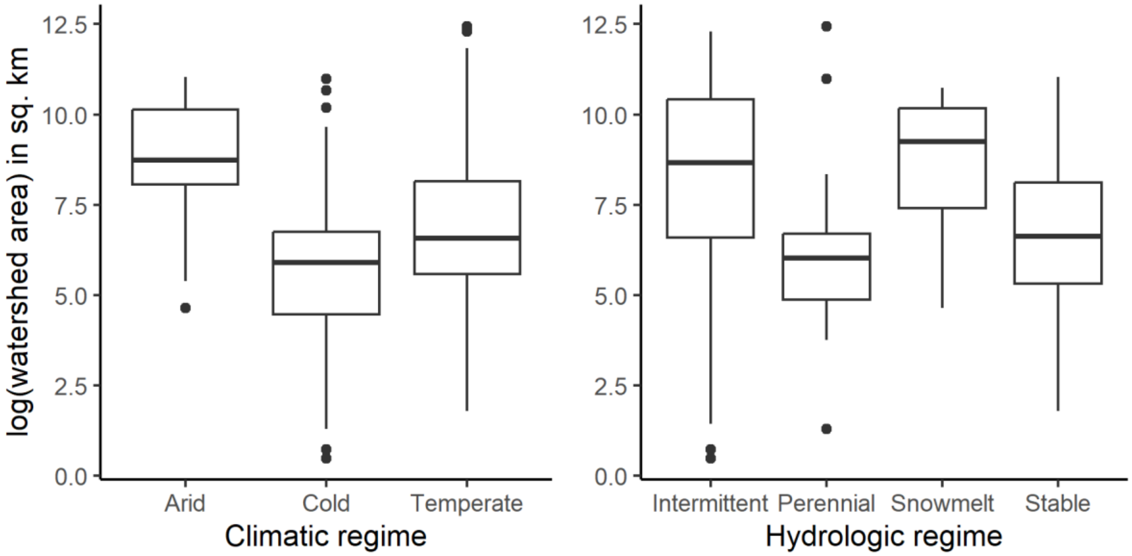

Figure C2. Watershed area of fish sampling sites comprising different hydrologic and climatic regimes.

Table C1. Data sources used in the analysis of fish-flow relationships.

Dataset	Num. Sites	First year	Last year	States
Conasauga	14	1996	2019	GA, TN
Etowah	10	1997	2019	GA
Fox Creek	4	2008	2018	KS
Gila River	4	1988	2018	NM
Kings Creek	4	1995	2018	KS
Little Tennessee	11	1990	2013	GA, NC
MassWildlife	6	2004	2017	MA
Maryland	1	2006	2017	MD
Minnesota Pollution Control Agency	6	1992	2018	MN
Montana Fish, Wildlife and Parks	2	1971	1997	MT
NAWQA	41	1993	2019	25 States
Ohio River	4	1997	2016	IN, PA
Oklahoma Department of Environmental Quality	19	1978	2006	OK
OK, Matthews	1	1991	2004	OK
OK, Pyron	1	1973	1990	OK
Pecos River	4	1992	2013	NM
Big Racoon Creek	8	1981	2002	IN
San Francisco River	1	1988	2018	NM
San Juan River	2	1993	2017	NM, UT
San Pedro River	1	1989	2007	AZ
Verde River	7	1994	2012	AZ
Virgin River	11	1976	2003	AZ, NV, UT

Table C2. Trait guilds for each Genus in the fish-flow analysis.

Genus	Number of species	Riffle dwelling	Nest building
Acantharchus	1	0	1
Acipenser	2	0	0
Acrocheilus	1	0	0
Agosia	1	0	0
Alosa	2	0	0
Ambloplites	4	0	1
Ameiurus	6	0	1
Amia	1	0	1
Ammocrypta	2	0	0
Anguilla	1	0	0
Aphredoderus	1	0	1
Aplodinotus	1	0	0
Astyanax	1	0	0
Atractosteus	1	0	0
Campostoma	3	1	0
Carassius	1	0	0
Carpiodes	3	0	0
Catostomus	11	1	0
Centrarchus	1	0	1
Chrosomus	3	0	0
Clinostomus	3	1	0
Cottus	12	1	1
Couesius	1	0	0
Crystallaria	1	0	0
Ctenopharyngodon	1	0	0
Culaea	1	0	1
Cycleptus	1	0	0
Cyprinella	19	1	0
Cyprinodon	2	0	0
Cyprinus	1	0	0
Dionda	1	0	0
Dorosoma	2	0	0
Elassoma	1	0	0
Enneacanthus	2	0	1
Entosphenus	1	0	1
Erimystax	3	1	0

Erimyzon	1	0	0
Esox	4	0	0
Etheostoma	51	1	0
Exoglossum	2	0	1
Fundulus	11	0	0
Gambusia	2	0	0
Gasterosteus	1	0	1
Gila	5	0	0
Hemitremia	1	0	0
Herichthys	1	0	1
Hiodon	2	0	0
Hybognathus	6	0	0
Hybopsis	5	0	0
Hypentelium	2	1	0
Hypophthalmichthys	2	0	0
Hysterocarpus	1	0	0
Ichthyomyzon	4	1	0
Ictalurus	2	0	1
Ictiobus	3	0	0
Labidesthes	1	0	0
Lampetra	1	1	0
Lavinia	1	0	0
Lepidomeda	1	0	0
Lepisosteus	3	0	0
Lepomis	12	0	1
Lethenteron	1	0	0
Lota	1	0	0
Lucania	1	0	0
Luxilus	8	1	1
Lythrurus	7	0	0
Macrhybopsis	4	1	0
Margariscus	1	0	1
Meda	1	0	0
Menidia	2	0	0
Micropterus	5	0	1
Minytrema	1	0	0
Morone	4	0	0
Moxostoma	15	1	0
Mugil	1	0	0
Mylocheilus	1	0	0
Mylopharodon	1	0	0
Neogobius	1	0	1
Nocomis	5	0	1

Notemigonus	1	0	0
Notropis	56	0	0
Noturus	12	1	1
Oncorhynchus	5	0	0
Opsopoeodus	1	0	1
Oreochromis	1	0	0
Orthodon	1	0	0
Paralichthys	1	0	0
Perca	1	0	0
Percina	21	1	0
Percopsis	1	0	0
Petromyzon	1	0	0
Phenacobius	3	1	0
Pimephales	4	0	1
Plagopterus	1	0	0
Platygobio	1	0	0
Poecilia	2	0	0
Pogonichthys	1	0	0
Polyodon	1	0	0
Pomoxis	2	0	1
Prosopium	1	0	0
Pteronotropis	2	0	0
Ptychocheilus	3	0	0
Pylodictis	1	0	1
Rhinichthys	6	1	0
Richardsonius	1	0	0
Rutilus	1	0	0
Salmo	2	0	0
Salvelinus	2	0	0
Sander	2	0	0
Scaphirhynchus	1	0	0
Scardinius	1	0	0
Semotilus	3	0	1
Trinectes	1	0	0
Umbra	2	0	0

Table C3. Gages selected for each fish sampling site.

Dataset ID	Site ID	Gage ID	Gage name	Number of missing days	Same HUC8	Site watershed Area (km^2)	Gage watershed area (km^2)	Watershed ratio	Euclidean distance (m)
Con	con001	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	300	653	0.46	19421
Con	con015	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	671	653	1.03	2444
Con	con131	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	471	653	0.72	10174
Con	con135	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	478	653	0.73	9005
Con	con138	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	478	653	0.73	8775
Con	con146	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	605	653	0.93	4134
Con	con148	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	610	653	0.94	1891
Con	con152	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	658	653	1.01	504
Con	con153	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	658	653	1.01	1126
Con	con213	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	593	653	0.91	5705
Con	con214	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	487	653	0.75	7787

Con	con216	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	600	653	0.92	5311
Con	con217	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	794	653	1.22	5295
Con	con251	02384500	CONASAUGA RIVER AT GA 286, NEAR ETON, GA	0	TRUE	605	653	0.93	3847
Eto	eto055	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	1007	1588	0.63	19239
Eto	eto057	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	968	1588	0.61	21751
Eto	eto066	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	1033	1588	0.65	18820
Eto	eto085	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	1506	1588	0.95	11361
Eto	eto278	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	730	1588	0.46	26911
Eto	eto285	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	461	1588	0.29	31762
Eto	eto294	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	718	1588	0.45	30975
Eto	eto295	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	722	1588	0.45	29393
Eto	eto298	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	718	1588	0.45	30323
Eto	eto301	02392000	ETOWAH RIVER AT CANTON, GA	0	TRUE	785	1588	0.50	25590
Fox	Fox Creek	07182250	COTTONWOOD R NR PLYMOUTH, KS	1	TRUE	85	4507	0.02	17342
Fox	Gashouse Creek	07182250	COTTONWOOD R NR PLYMOUTH, KS	1	TRUE	2	4507	0.00	20268
Fox	Palmer Creek	07182250	COTTONWOOD R NR PLYMOUTH, KS	1	TRUE	15	4507	0.00	22446
Fox	Schoolhouse Creek	07182250	COTTONWOOD R NR PLYMOUTH, KS	1	TRUE	4	4507	0.00	18854
Gila	East Fork	09430500	GILA RIVER NEAR GILA, NM	0	TRUE	1803	4828	0.37	49180

Gila	Middle Fork	09430500	GILA RIVER NEAR GILA, NM	0	TRUE	885	4828	0.18	33038
Gila	Riverside	09430500	GILA RIVER NEAR GILA, NM	0	FALSE	6267	4828	1.30	14934
Gila	West Fork	09430500	GILA RIVER NEAR GILA, NM	0	TRUE	283	4828	0.06	31565
Kings	K2A	06879650	KINGS C NR MANHATTAN, KS	0	TRUE	5	11	0.47	1733
Kings	N1B	06879650	KINGS C NR MANHATTAN, KS	0	TRUE	2	11	0.16	2487
Kings	N4D	06879650	KINGS C NR MANHATTAN, KS	0	TRUE	2	11	0.16	2465
Kings	NT	06879650	KINGS C NR MANHATTAN, KS	0	TRUE	18	11	1.71	1116
LilTN	CARRP-087	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	149	148	1.01	581
LilTN	CRAEM-061	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	6	148	0.04	3347
LilTN	CULPC-075	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	155	148	1.05	9020
LilTN	CULWG-067	03500000	LITTLE TENNESSEE RIVER NEAR PRENTISS, NC	0	TRUE	235	363	0.65	2430
LilTN	LTRBP-086	03500000	LITTLE TENNESSEE RIVER NEAR PRENTISS, NC	0	TRUE	513	363	1.42	1585
LilTN	LTRNE-005	03503000	LITTLE TENNESSEE RIVER AT NEEDMORE, NC	0	TRUE	1126	1129	1.00	1028
LilTN	LTRSL-136	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	145	148	0.98	18287

LilTN	MIDHE-126	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	36	148	0.24	13392
LilTN	RABRC-055	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	26	148	0.18	6805
LilTN	SKEWC-107	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	18	148	0.12	5168
LilTN	WAYCR-093	03500240	CARTOOGECHAYE CREEK NEAR FRANKLIN, NC	0	TRUE	37	148	0.25	8655
MA	east_br_north_r_1	01169000	NORTH RIVER AT SHATTUCKVILLE, MA	0	TRUE	130	231	0.56	9357
MA	green_r1_1	01170100	GREEN RIVER NEAR COLRAIN, MA	0	TRUE	131	107	1.22	5567
MA	mill_river2	01171500	MILL RIVER AT NORTHAMPTON, MA	0	TRUE	132	136	0.97	3104
MA	north_river	01169000	NORTH RIVER AT SHATTUCKVILLE, MA	0	TRUE	233	231	1.01	1792
MA	south_river_1	01169900	SOUTH RIVER NEAR CONWAY, MA	0	TRUE	44	62	0.70	3628
MA	wb_westfield	01181000	WEST BRANCH WESTFIELD RIVER AT HUNTINGTON, MA	0	TRUE	132	243	0.54	10267
MD	LSCR202	01644375	LITTLE SENECA CREEK TRIBUTARY NEAR GERMANTOWN, MD	0	TRUE	4	3	1.04	36
MN_PCA	S10485	05132000	BIG FORK RIVER AT BIG FALLS, MN	0	TRUE	4049	3833	1.06	5773

MN_PCA	S4713	05315000	REDWOOD RIVER NEAR MARSHALL, MN	0	TRUE	799	671	1.19	14117
MN_PCA	S5806	05330000	MINNESOTA RIVER NEAR JORDAN, MN	0	TRUE	42875	41958	1.02	14274
MN_PCA	S6476	05280000	CROW RIVER AT ROCKFORD, MN	0	TRUE	6809	6838	1.00	253
MN_PCA	S9102	05333500	ST. CROIX RIVER NEAR DANBURY, WI	0	TRUE	6943	4092	1.70	27638
MN_PCA	S9480	05227500	MISSISSIPPI RIVER AT AITKIN, MN	0	TRUE	15708	15903	0.99	19381
MT_FWP	S2359	06090300	Missouri River near Great Falls MT	0	TRUE	62121	59262	1.05	12775
MT_FWP	S8221	12303000	Kootenai River at Libby MT	0	TRUE	26461	26364	1.00	4433
NAWQA	ACCOTINK CREEK NEAR ANNANDALE, VA	01654000	ACCOTINK CREEK NEAR ANNANDALE, VA	0	TRUE	62	62	1.01	10
NAWQA	Auglaize River near Fort Jennings OH	04186500	Auglaize River near Fort Jennings OH	0	TRUE	860	860	1.00	2
NAWQA	CAHABA VALLEY CREEK AT CROSS CR RD AT PELHAM, AL.	0242354750	CAHABA VALLEY CREEK AT CROSS CR RD AT PELHAM, AL.	0	TRUE	71	66	1.07	49
NAWQA	CLINTON RIVER AT STERLING HEIGHTS, MI	04164000	CLINTON RIVER NEAR FRASER, MI	0	TRUE	811	1150	0.71	7413
NAWQA	COLORADO RIVER NEAR COLORADO-UTAH STATE LINE	09163500	COLORADO RIVER NEAR COLORADO-UTAH STATE LINE	0	TRUE	46123	46229	1.00	377
NAWQA	CONTENTNEA CREEK AT	02091500	CONTENTNEA CREEK AT HOOKERTON, NC	2	TRUE	1897	1898	1.00	18

	HOOKERTON, NC								
NAWQA	COW CASTLE CREEK NEAR BOWMAN, SC	02174250	COW CASTLE CREEK NEAR BOWMAN, SC	0	TRUE	64	61	1.06	106
NAWQA	Clear Ck nr Sanger, TX	08051500	Clear Ck nr Sanger, TX	0	TRUE	768	764	1.01	39
NAWQA	DUCK CREEK AT SEMINARY ROAD NEAR ONEIDA, WI	04072150	DUCK CREEK NEAR HOWARD, WI	0	TRUE	251	280	0.90	10397
NAWQA	Dismal River near Thedford, Nebr.	06775900	Dismal River near Thedford, Nebr.	0	TRUE	1553	2502	0.62	57
NAWQA	French Creek near Phoenixville, PA	01472157	French Creek near Phoenixville, PA	0	TRUE	158	153	1.03	23
NAWQA	Frio Rv at Concan, TX	08195000	Frio Rv at Concan, TX	0	TRUE	1009	1008	1.00	25
NAWQA	GILLS CREEK AT COLUMBIA, SC	02169570	GILLS CREEK AT COLUMBIA, SC	0	TRUE	164	154	1.07	54
NAWQA	GREEN RIVER AT STEWARTVILLE, MA	01170100	GREEN RIVER NEAR COLRAIN, MA	0	TRUE	97	107	0.90	1447
NAWQA	LITTLE COTTONWOOD CREEK @ JORDAN RIVER NR SLC	10168000	LITTLE COTTONWOOD CREEK @ JORDAN RIVER NR SLC	0	TRUE	105	119	0.88	220
NAWQA	LITTLE POWDER RIVER AB DRY CREEK, NEAR WESTON, WY	06324970	LITTLE POWDER RIVER AB DRY CREEK, NEAR WESTON, WY	0	TRUE	3207	3204	1.00	33
NAWQA	Little Neshaminy C at Valley Road nr Neshaminy PA	01464907	Little Neshaminy C at Valley Road nr Neshaminy PA	0	TRUE	71	69	1.03	50
NAWQA	MILWAUKEE RIVER AT MILWAUKEE, WI	04087000	MILWAUKEE RIVER AT MILWAUKEE, WI	0	TRUE	1810	1803	1.00	0

NAWQA	MUDDY CREEK AT MOUNT CLINTON, VA	01621050	MUDDY CREEK AT MOUNT CLINTON, VA	0	TRUE	43	37	1.16	13
NAWQA	Mad R. nr Hwy. 41 nr Springfield, OH	03269500	Mad River near Springfield OH	0	TRUE	819	1269	0.65	3557
NAWQA	Maple Creek near Nickerson, Nebr.	06800000	Maple Creek near Nickerson, Nebr.	0	TRUE	962	953	1.01	85
NAWQA	NORWALK RIVER AT SOUTH WILTON, CT	01209700	NORWALK RIVER AT SOUTH WILTON, CT	0	TRUE	78	78	1.01	11
NAWQA	North Sylamore Creek near Fifty Six, AR	07060710	North Sylamore Creek near Fifty Six, AR	0	TRUE	152	150	1.01	459
NAWQA	ORESTIMBA CR AT RIVER RD NR CROWS LANDING CA	11274538	ORESTIMBA CR AT RIVER RD NR CROWS LANDING CA	0	TRUE	465	NA	NA	23
NAWQA	Ouiska Chitto Creek Near Oberlin, LA	08014500	Ouiska Chitto Creek Near Oberlin, LA	0	TRUE	1325	1321	1.00	36
NAWQA	PALOUSE RIVER AT HOOPER, WA	13351000	PALOUSE RIVER AT HOOPER, WA	0	TRUE	6219	6475	0.96	67
NAWQA	POPPLE RIVER NEAR FENCE, WI	04063700	POPPLE RIVER NEAR FENCE, WI	0	TRUE	373	360	1.04	38
NAWQA	ROCK CREEK AB HWY 30/93 XING AT TWIN FALLS ID	13092747	ROCK CREEK AB HWY 30/93 XING AT TWIN FALLS ID	0	TRUE	632	671	0.94	31
NAWQA	River Raisin near Manchester, MI	04175600	RIVER RAISIN NEAR MANCHESTER, MI	0	TRUE	335	342	0.98	18
NAWQA	SALT CREEK AT WESTERN SPRINGS, IL	05531500	SALT CREEK AT WESTERN SPRINGS, IL	0	TRUE	306	298	1.03	21
NAWQA	SAN JOAQUIN R NR VERNALIS CA	11303500	SAN JOAQUIN R NR VERNALIS CA	0	TRUE	35855	35066	1.02	93

NAWQA	SNAKE RIVER AB JACKSON LAKE AT FLAGG RANCH WY	13010065	SNAKE RIVER AB JACKSON LAKE AT FLAGG RANCH WY	0	TRUE	1227	1259	0.98	63
NAWQA	SNAKE RIVER AT KING HILL ID	13154500	SNAKE RIVER AT KING HILL ID	0	TRUE	62321	92722	0.67	96
NAWQA	SOPE CREEK NEAR MARIETTA, GA	02335870	SOPE CREEK NEAR MARIETTA, GA	0	TRUE	86	80	1.09	30
NAWQA	SOUTH PLATTE RIVER NEAR KERSEY, CO	06754000	SOUTH PLATTE RIVER NEAR KERSEY, CO	0	TRUE	25021	25022	1.00	40
NAWQA	SUGAR CREEK AT CO RD 400 S AT NEW PALESTINE, IN	03361650	SUGAR CREEK AT NEW PALESTINE, IN	0	TRUE	248	243	1.02	1604
NAWQA	Salado Ck at Loop 13, San Antonio, TX	08178800	Salado Ck at Loop 13, San Antonio, TX	0	TRUE	490	490	1.00	31
NAWQA	South Fork Iowa River NE of New Providence, IA	05451210	South Fork Iowa River NE of New Providence, IA	0	TRUE	583	580	1.00	37
NAWQA	THORNTON CREEK NEAR SEATTLE, WA	12128000	THORNTON CREEK NEAR SEATTLE, WA	0	TRUE	31	31	0.99	57
NAWQA	Trinity Rv bl Dallas, TX	08057000	Trinity Rv at Dallas, TX	0	TRUE	16253	15815	1.03	10770
NAWQA	WEST CLEAR CREEK NEAR CAMP VERDE, AZ	09505800	WEST CLEAR CREEK NEAR CAMP VERDE, AZ	0	TRUE	627	624	1.00	27
OH	OH026.0LDB	03086000	Ohio River at Sewickley, PA	0	TRUE	58974	50505	1.17	17273
OH	OH026.3LDB	03086000	Ohio River at Sewickley, PA	0	TRUE	58974	50505	1.17	17261
OH	OH751.5RDB	03303280	OHIO RIVER AT CANNELTON DAM AT CANNELTON, IN	0	TRUE	251089	251230	1.00	32208

OH	OH751.8RDB	03303280	OHIO RIVER AT CANNELTON DAM AT CANNELTON, IN	0	TRUE	251089	251230	1.00	32563
OK	7152000	07152000	Chikaskia River near Blackwell, OK	0	TRUE	4877	4859	1.00	355
OK	7152500	07152500	Arkansas River at Ralston, OK	0	TRUE	137007	140399	0.98	228
OK	7159100	07159100	Cimarron River near Dover, OK	0	TRUE	34537	40945	0.84	23
OK	7165570	07165570	Arkansas River near Haskell, OK	0	TRUE	219856	195009	1.13	52
OK	7196500	07196500	Illinois River near Tahlequah, OK	0	TRUE	2463	2461	1.00	7
OK	7198000	07198000	Illinois River near Gore, OK	0	TRUE	4184	4183	1.00	30
OK	7228500	07228500	Canadian River at Bridgeport, OK	0	TRUE	61882	63968	0.97	81
OK	7231500	07231500	Canadian River at Calvin, OK	0	TRUE	68918	71010	0.97	281
OK	7237500	07237500	North Canadian River at Woodward, OK	0	TRUE	30499	30777	0.99	51
OK	7241550	07241550	North Canadian River near Harrah, OK	0	TRUE	35398	35677	0.99	25
OK	7242000	07242000	North Canadian River near Wetumka, OK	0	TRUE	37418	37682	0.99	124
OK	7300500	07300500	Salt Fork Red River at Mangum, OK	0	TRUE	3767	3766	1.00	84
OK	7301500	07301500	North Fork Red River near Carter, OK	0	TRUE	6228	6869	0.91	73
OK	7305000	07305000	North Fork Red River near Headrick, OK	0	TRUE	11155	11810	0.94	767
OK	7331000	07331000	Washita River near Dickson, OK	0	TRUE	18574	18575	1.00	113
OK	7335500	07335500	Red River at Arthur City, TX	0	TRUE	112423	115113	0.98	189
OK	7335700	07335700	Kiamichi River near Big Cedar, OK	0	TRUE	104	103	1.02	49
OK	7336200	07336200	Kiamichi River near Antlers, OK	0	TRUE	2935	2924	1.00	39

OK	7338500	07338500	Little River blw Lukfata Creek, nr Idabel, OK	0	TRUE	3186	3181	1.00	25
OK Matthews	S6019	07335790	Kiamichi River near Clayton, OK	0	TRUE	1811	1810	1.00	195
OK Pyron	S2674	07335700	Kiamichi River near Big Cedar, OK	0	TRUE	128	103	1.25	3779
Pecos	Pecos12	08395500	PECOS RIVER NEAR LAKE ARTHUR, NM	0	TRUE	31217	38228	0.82	24217
Pecos	Pecos13	08395500	PECOS RIVER NEAR LAKE ARTHUR, NM	0	TRUE	35698	38228	0.93	1064
Pecos	Pecos14	08396500	PECOS RIVER NEAR ARTESIA, NM	0	TRUE	37329	39627	0.94	29
Pecos	Pecos15	08399500	PECOS RIVER (KAISER CHANNEL) NEAR LAKEWOOD, NM	0	TRUE	41499	49632	0.84	11100
Racc	F1	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	8933
Racc	F2	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	6681
Racc	F3	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	4705
Racc	F4	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	3091
Racc	F5	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	3118
Racc	F6	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	2170

Racc	F7	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	564
Racc	F8	03340800	BIG RACCOON CREEK NEAR FINCASTLE, IN	0	TRUE	365	360	1.01	658
SF	SanFran	09444000	SAN FRANCISCO RIVER NEAR GLENWOOD, NM	0	TRUE	4189	4281	0.98	7209
SJ	4	09368000	SAN JUAN RIVER AT SHIPROCK, NM	1	FALSE	37475	33411	1.12	44954
SJ	5	09368000	SAN JUAN RIVER AT SHIPROCK, NM	1	TRUE	32803	33411	0.98	6178
SP	sp1	09471000	SAN PEDRO RIVER AT CHARLESTON, AZ.	0	TRUE	3175	3196	0.99	924
Verd	Verde1	09503700	VERDE RIVER NEAR PAULDEN, AZ	0	TRUE	6239	6493	0.96	7828
Verd	Verde2	09503700	VERDE RIVER NEAR PAULDEN, AZ	0	TRUE	6475	6493	1.00	15697
Verd	Verde3	09503700	VERDE RIVER NEAR PAULDEN, AZ	0	TRUE	5221	6493	0.80	5339
Verd	Verde4	09503700	VERDE RIVER NEAR PAULDEN, AZ	0	TRUE	5363	6493	0.83	5247
Verd	Verde5	09503700	VERDE RIVER NEAR PAULDEN, AZ	0	TRUE	5267	6493	0.81	3029
Verd	Verde6	09503700	VERDE RIVER NEAR PAULDEN, AZ	0	TRUE	6449	6493	0.99	12602
Verd	Verde7	09504000	VERDE RIVER NEAR CLARKDALE, AZ	0	TRUE	7834	9073	0.86	1568
Virg	BeDaWa2	09413900	BEAVER DAM WASH NEAR ENTERPRISE, UT	0	TRUE	217	150	1.45	9998

Virg	EaFoVi1	09404900	EAST FORK VIRGIN RIVER NEAR SPRINGDALE, UT	0	TRUE	828	888	0.93	1119
Virg	NoFoVi1	09405500	NORTH FORK VIRGIN RIVER NEAR SPRINGDALE, UT	0	TRUE	795	891	0.89	3329
Virg	Virg1	09415000	VIRGIN RV AT LITTLEFIELD, AZ	0	TRUE	12859	13183	0.98	16544
Virg	Virg2	09415000	VIRGIN RV AT LITTLEFIELD, AZ	0	TRUE	12291	13183	0.93	493
Virg	Virg3	09413500	VIRGIN RIVER NEAR ST. GEORGE, UT	0	TRUE	10411	10679	0.98	12968
Virg	Virg4	09413200	VIRGIN RIVER NEAR BLOOMINGTON, UT	0	TRUE	9710	9979	0.97	3779
Virg	Virg6	09406000	VIRGIN RIVER AT VIRGIN, UT	0	TRUE	3850	2476	1.56	23229
Virg	Virg7	09406000	VIRGIN RIVER AT VIRGIN, UT	0	TRUE	3850	2476	1.56	20816
Virg	Virg8	09406000	VIRGIN RIVER AT VIRGIN, UT	0	TRUE	3563	2476	1.44	15974
Virg	Virg9	09406000	VIRGIN RIVER AT VIRGIN, UT	0	TRUE	3275	2476	1.32	9470