PERSPECTIVE

# Toward Improved Understanding of Streamflow Effects on Freshwater Fishes

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Understanding the effects of hydrology on fish populations is essential to managing for native fish conservation. However, despite decades of research illustrating streamflow influences on fish habitat, reproduction, and survival, biologists remain challenged when tasked with predicting how fish populations will respond to changes in flow regimes. This uncertainty stems from insufficient understanding of the context-dependent mechanisms underlying fish responses to, for example, periods of reduced flow or altered frequency of high-flow events. We aim to address this gap by drawing on previous research to hypothesize mechanisms by which low and high flows influence fish populations and communities, identifying challenges that stem from data limitations and ecological complexity, and outlining research directions that can advance an empirical basis for prediction. Focusing flow ecology research on testing and refining mechanistic hypotheses can help narrow management uncertainties and better support species conservation in changing flow regimes.

## INTRODUCTION

Biologists and managers widely acknowledge the importance of streamflow regimes in shaping the structure and function of lotic ecosystems, including the abundance and diversity of stream fishes. Stream fishes exhibit a variety of ecological, life history, and behavioral adaptations to flow variability in systems where they evolved (Lytle and Poff 2004; Mims and Olden 2012). Human societies, however, have substantially modified the natural flow regimes of most rivers, while also altering and fragmenting habitats, further contributing to the decline of many fish species (Reid et al. 2019; Tickner et al. 2020). Even in rivers unaffected by dams, human actions may alter streamflow via land cover changes, direct surface and groundwater withdrawals, water transfers, wastewater discharges, and, increasingly, climate-driven changes in precipitation and water temperature (Reid et al. 2019). Although some native fishes persist in rivers with varying degrees of flow alteration (including persistence in reservoirs), many others are reduced in distribution and abundance and face uncertain futures (Tickner et al. 2020).

As human alteration of streams and rivers intensifies, managers and stakeholders are under increasing pressure to restore





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aspects of natural flow regimes to minimize or reverse undesirable ecological outcomes, including loss of stream fishes (Olden et al. 2014). For example, relicensing of Federal Energy Regulatory Commission dams often includes studies relating flows to fishes, through which state agencies, the U.S. Fish and Wildlife Service, and other stakeholders seek changes in management to minimize detrimental effects on species. Similarly, the U.S. Bureau of Reclamation and U.S. Army Corps of Engineers (Warner et al. 2014) may consider modifying operations of water control structures to benefit downstream ecosystems, including native stream fishes (Box 1). Municipal water managers may seek management strategies to lessen effects of water withdrawals on river biota, particularly during naturally low-flow periods (Box 2). Manager and stakeholder concerns about flow alteration effects on biota extend even to smaller streams, which often provide habitat for a wide variety of fishes including migratory and imperiled species (Colvin et al. 2019), and where flows may be indirectly altered by dispersed groundwater wells, impervious cover, and other changes in land cover.

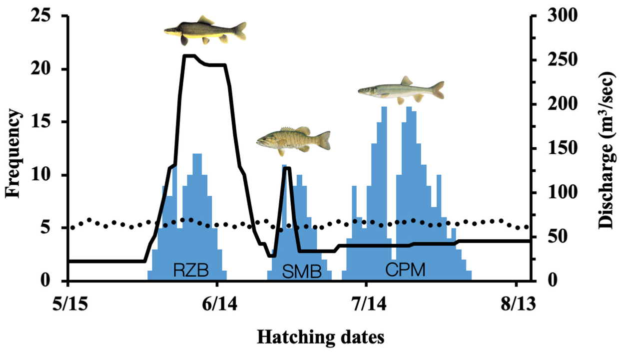
Streamflow management could be substantively improved if it were guided by a more general and transferable understanding of the mechanisms by which specific aspects of the flow regime shape fish communities composed of species with diverse traits. Ecologists currently have extensive literature on environmental flows (Arthington 2012), which offers a powerful tool for informing outcomes that jointly benefit native biodiversity and other societal needs for water. However, environmental flow assessments often focus on functions (e.g., sediment transport, habitat provision) or values (ecological status, water quality protection) that may only indirectly relate to dynamics of fish populations. The ability of scientists to make accurate predictions about population or community responses to environmental flows remains limited (Poff and Zimmerman 2010; Davies et al. 2014), confounded by inconsistent outcomes that may reflect complex interactions among flow timing, temperature, biotic interactions, and antecedent flows (King et al. 2016; Walters 2016; Chen and Olden 2018). Alteration in temperature and sediment regimes may in fact override flow regulation effects downstream from dams (McManamay et al. 2015), or flow effects may be exacerbated by interactions with nonnative species (Stefferud et al. 2011). To better inform the decisions that managers must make when balancing competing water demands, scientists need a deeper understanding of how, why, or even whether specific flows will affect fundamental biological and ecological mechanisms that mediate a species' survival, growth, or reproductive success (Rolls et al. 2013; Tonkin et al. 2019).

Flow alteration–ecological response (hereafter, "flow–ecology") relationships (Poff et al. 2010) are empirically based models that allow managers to predict ecological outcomes of alternative degrees of flow alteration. Flow–ecology models are based on hypothesized or known mechanisms linking specific flow regime changes to ecological variables. This flow–ecology approach contrasts with the more traditional hydraulic simulation approach to instream flow management, where the biological model (habitat suitability curves) is less directly linked to specific mechanistic drivers or to population dynamics (Beecher et al. 2010). However, current understanding of flow–ecology relationships is based largely on correlative studies that establish linkages between a measured population attribute (e.g., estimated abundance) and a flow condition (e.g., low-flow frequency downstream from a dam relative to the pre-dam regime) based on long-term statistical averages (Poff 2018; Wheeler et al. 2018). These relationships are generally "noisy," in part because at any given time, a measure such as population abundance may be more strongly influenced by recent flows that promoted juvenile recruitment, than by long-term average flow conditions. Similarly, although aspects of community composition may correlate with long-term flow conditions (Mims and Olden 2012; McManamay and Frimpong 2015), these relations are typically weak, reflecting multiple potential flow-mediated mechanisms operating over differing timeframes. As a result, correlations based on degree of flow alteration have an inherently limited capacity to specify environmental flow timing and quantities needed to achieve management or conservation goals such as aiding the recovery of an imperiled species, enhancing recreational fishing opportunities, or sustaining native fish diversity.

Focused cause and effect hypotheses that specify how aspects of a flow regime affect organisms with specific, mediating traits are likely cornerstones of more effective and efficient environmental flow management. By focusing on responses of individuals and populations (e.g., change in abundance, colonization or extirpation, survival, reproduction, growth) relative to a specific flow event or series of events (Konrad et al. 2011), biologists can derive a mechanistic understanding that renders flow–ecology relationships more predictable (e.g.,

**Box 1. Fish-flow mechanisms inform managed-flow releases in the Green River.**

Current and proposed flow management practices in the Green River downstream of Flaming Gorge Dam, in Utah and Colorado, are designed to promote native fish conservation. Mean daily flows post-impoundment were historically (1964–1991: dotted line; summer months only) relatively flat, and implemented mainly for hydropower production. However, since 2012, higher releases from Flaming Gorge Dam (solid line) during snowmelt runoff have been implemented to benefit Razorback Sucker *Xyrauchen texanus* (RZB) in spring by inundating floodplain nursery habitat, timed to correspond with emergence of larvae (conceptual frequencies of larval emergence for all species shown as blue bars). Managed summer baseflow releases (e.g., 34–45 $m^3$/s, July–August) when tributary Yampa River flows decline assist with backwater nursery habitat maintenance in the main channel of the Green River to benefit early life stages of native Colorado Pikeminnow *Ptychocheilus lucius* (CPM). A proposed action, a short-term early summer flow spike (shown as late June peak), is designed to reduce survival of eggs and larvae of nonnative Smallmouth Bass *Micropterus dolomieu* (SMB) that presently limit recruitment of native fishes. Ongoing studies evaluate effects of those streamflow patterns on the fish community (Bestgen 2018).



Box 2. Identifying fish-flow mechanisms to support management of a free-flowing river.

The Flint River in Georgia is one of a handful of rivers in the continental United States that still flows unimpeded by dams or channel alterations for >200 km. The upper, Piedmont portion of the river contains extensive bedrock shoal habitats that host at least five basin-endemic fishes, including the recreationally popular Shoal Bass *Micropterus cataractae*, but are vulnerable to drying from reduced flows. The upper Flint River is also an important water source for a growing population in metropolitan Atlanta, Georgia. Responding to concerns about the impacts of increasingly severe droughts on water for humans and the river, the Upper Flint River Working Group formed as a collaboration among water authorities, local governments, and environmental nongovernmental organizations, "to keep the upper Flint River and its tributary streams flowing to protect the social, ecological, recreational, and economic values the river system provides." Their members have the combined capacity to adjust the timing and volume of withdrawals and discharges to achieve ecological outcomes; however, the group has also articulated a need for better scientific information to guide these decisions. Decisions such as whether to divert rainfall-driven flow pulses to offstream reservoirs or let them pass by during low-flow periods hinge in part on understanding when pulses are most likely to benefit river ecosystems and fishes. Biologists can help inform these decisions by identifying how and when low flows and flow pulses are likely to affect shoal fishes with differing life histories (https://bit.ly/33d075R).

Photo: Alan Cressler, U.S. Geological Survey.

Bond et al. 2018; Wheeler et al. 2018) and even transferable to other streams or novel management contexts, such as those projected given climate change (Horne et al. 2019; Tonkin et al. 2019). Mechanistic hypotheses can be confronted with data and either refuted or supported, and thus, contribute to both long-term learning and short-term adaptive management.

Our goal is to highlight the complexity associated with predicting fish population and community responses to flow variability and propose a hypothesis-driven approach to address the gap created by more traditional correlative approaches. We draw on a growing number of studies, predominantly from North America, but considering other literature where appropriate, to offer a list of mechanistic hypotheses for how low and high flows affect stream fishes, either generally or for species having particular suites of traits or occurring in specific environmental contexts. We discuss challenges associated with linking streamflow and biotic data to assess hypothesized mechanisms and then consider research directions that could advance understanding of fish–flow relationships in support of water resource management.

## MOVING FROM CASE STUDIES TO PREDICTION

We focus on fish responses to high- and low-flow conditions that deviate in magnitude, duration, or frequency from typical seasonal flows under natural regimes. Water management actions, including flow regulation and water withdrawal, frequently create novel flow regimes with seasonally higher or lower flows than pre-management conditions (Poff et al. 2007; Richter and Thomas 2007). Climate change will further alter frequency, timing, magnitude, and duration of low- and high-flow events in many areas (van Vliet et al. 2013). Growing a more robust capacity to predict ecological responses accurately, including how stream fish populations and communities are likely to change given these types of altered flow regimes, is considered paramount for ecologically sustainable water management (Stoeffels et al. 2018; Tonkin et al. 2019).

Deriving testable predictions of flow effects on fishes requires identifying the mechanisms that shape population responses (Bond et al. 2018; Tonkin et al. 2019), which will depend on the timing, magnitude, and duration of flow events in relation to species-specific requirements or sensitivity at different life stages. For example, whereas an anomalous high-flow event in autumn may not measurably affect a spring-spawning species, the same event could cause nest destruction and egg and larval mortality for a species that spawns in the late summer (Figure 1, upper panel). By contrast, flows of a similar magnitude in spring, more consistent with the natural flow regime in this hypothetical system, may have few population-level consequences for either species. Similarly, an anomalous early season drought (Figure 1, lower panel) might lead to reproductive failure for early spawning species that lose access to spawning habitat or whose eggs are smothered by silt, while fishes that spawn later are less affected. A summer drought may similarly result in crowding and resource limitation for some species (Rolls et al. 2012), or concentrate prey for early life stages of others (Humphries et al. 2020).

The challenge for ecologists involves deriving generalizable predictions despite this inherent complexity and potential for diverse outcomes. Case studies from a variety of species, climates and geomorphic contexts illustrate the potential for opposing effects of low- and high-flow conditions on fish reproduction, growth or survival (Tables 1 and 2). Ecologists generally expect that the mechanisms underlying diverse fish responses involve mediating effects of species characteristics and physical context (Craven et al. 2010; Chen and Olden 2018; Humphries et al. 2020; Figure 2). For example, high- and low-flow effects on age-0 recruitment may depend on the interplay between early life history characteristics (i.e., larval size at hatching, time to first feeding, and swimming ability, corresponding to the opportunistic, equilibrium, and periodic strategies described by Winemiller and Rose 1992) and habitat-specific effects of flow magnitude on larval retention and food concentration (Humphries et al. 2020). Traits other than life history strategies may also mediate flow effects on fishes. Spawning mode, for example, may differentiate sensitivity to low flows among co-occurring, opportunistic fishes in dryland rivers (Perkin et al. 2019). Tolerance for warmer temperatures along with plasticity in foraging mode are likely to mediate responses of, for example, headwater, drift feeding fishes to low flows (Letcher et al. 2015). Stream context also matters. Local geomorphology influences flow–habitat relations (Poff et al. 2010; Humphries et al. 2020); proximity to habitats that dry or scour during extreme flows may drive dynamics of local fish abundances (Koizumi et al. 2013;

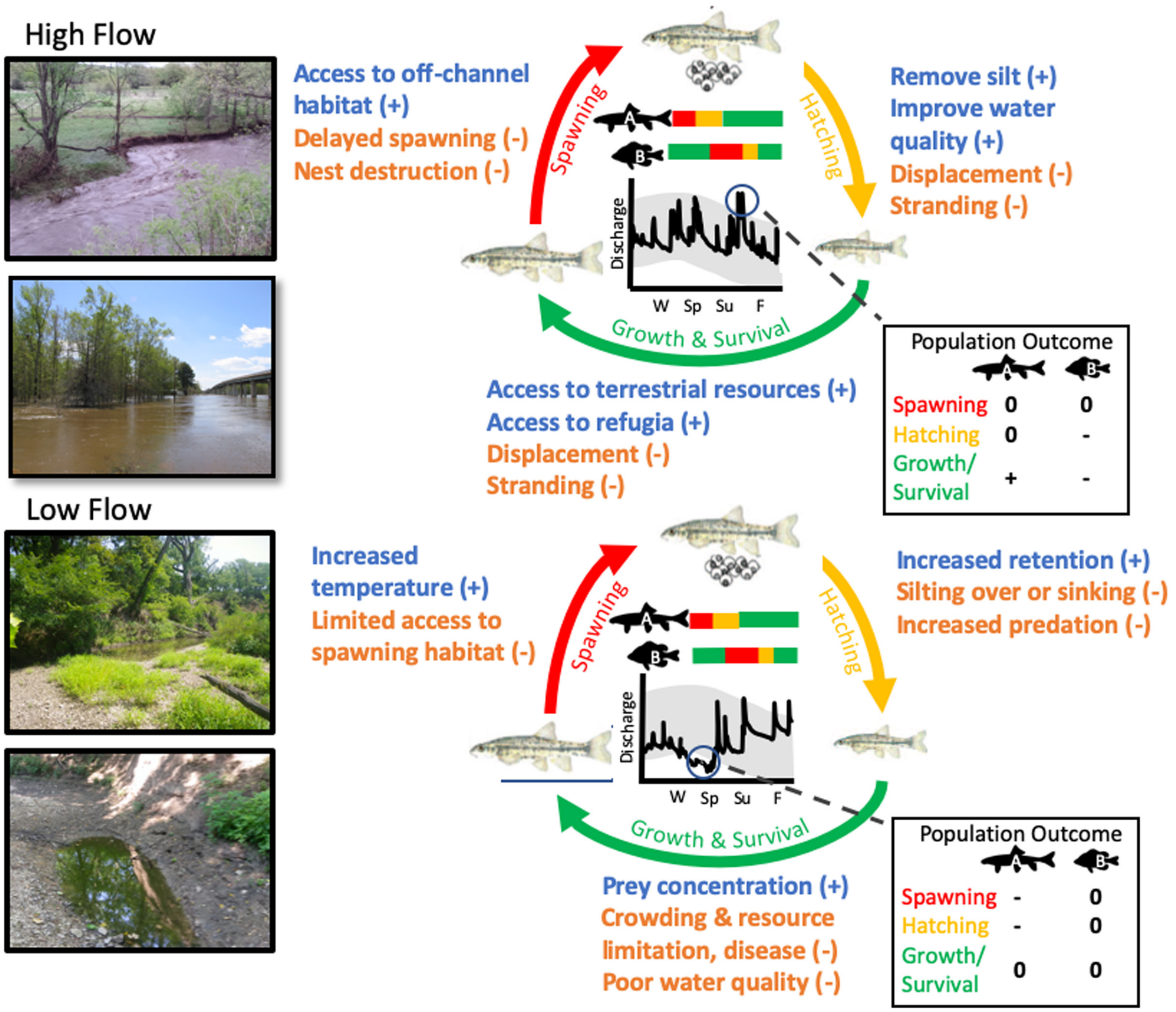



Figure 1. Life stage-specific mechanisms that might elicit positive or negative responses of fish populations to high- and low-flow events. Each example contrasts population outcomes for two hypothetical fish species (**A** and **B**) that differ in timing of critical life stages (spawning, red; hatching, yellow; growth and survival, green). Upper example: an anomalous summer high-flow event (relative to normal range of flow variation, represented by the gray shaded area on the hydrograph) has no effects (0) on spawning for either species, is detrimental (-) to hatching and early life stage survival of the late spawning species (**B**), and benefits (+) growth and survival of the early spawning species (**A**). In contrast, an anomalous early season drought (lower example) is detrimental to the early spawning species. Fish illustration: W. H. Brandenburg. Photos: K. Gido and M. Freeman.

Hedden and Gido 2020); and climatic regime may precondition species tolerances and population responses to flow events (Lytle and Poff 2004).

Importantly, alternative mechanisms may drive opposing outcomes. This is particularly clear with respect to flow effects on fish reproduction. Prolonged low flows during spawning and growing seasons can result in failed reproduction and recruitment from mechanisms such as thermal stress, crowding, egg and larval mortality, and loss of access to floodplain or nursery habitats (supporting studies cited in Table 1). Conversely, periods of unusually low flows also can provide warmer conditions that allow for earlier spawning and enhance or concentrate invertebrate prey production, increasing recruitment and growth of species able to spawn and forage in warmer, shallower, or lower-velocity habitats (Humphries et al. 2020; other studies cited in Table 1). High flows can similarly have opposing effects on reproductive success. High-flow pulses can directly depress young-of-year (YOY) abundances through mortality of eggs and larvae, an effect exacerbated by hydropeaking flow regimes where flow releases frequently also depress water temperature (McManamay et al. 2015; Shea et al. 2015; Irwin 2019). Indeed, appropriately timed flow pulses can be used in regulated systems to reduce reproductive success of invasive nest-spawning fishes (Box 1). Conversely, channel scouring flows that occur prior to spawning, and sustained high flows or flooding during spawning and growing seasons may increase YOY abundances through effects on habitat (e.g., cleaning fine sediments from spawning gravels; providing access to productive off-channel habitats), enhanced migration and spawning cues, and suspension of drifting eggs and larvae (studies cited in Table 1). Some of these mechanisms (e.g., larval mortality from high-flow pulses) apply broadly

Table 1. Hypothesized effects of low- and high-flow conditions on young-of-year (YOY) fish abundance, growth, and survival. Examples of species traits associated with observed responses are listed with hypothesized mechanisms and selected supporting case studies (Table S1).

| Hydrologic driver | Population response | Species traits | Mechanisms |
|---|---|---|---|
| Prolonged low flows during spawning and growing season | Decreased YOY abundance, growth and survival | Cold or coolwater adapted<br>Lithophilic spawner<br>Pelagic broadcast spawner<br>Migratory spawner<br>Floodplain, backwater spawner | Thermal stress[1]; nest superimposition; egg and larval mortality[2]; impeded migration; reduced YOY habitat, floodplain access, productivity[3]; greater nonnative predation[4] |
| Prolonged low flows during spawning and growing season | Increased YOY abundance, growth and survival | Warmwater adapted<br>Early season spawner<br>Nest guarding spawner<br>Opportunistic life history type | Increased warm season temperatures[5]; prey availability[6], shallow-water refuge and spawning habitat; decreased mortality from high-flow pulses[7] |
| Frequent high flows during spawning and growing season | Decreased YOY abundance | Open substrate spawner<br>Lithophilic spawner<br>Short spawning duration | Interrupted spawning, redd dewatering, nest abandonment[8]; egg or larval displacement and mortality[9]; lower feeding efficiency and growth[10] |
| Channel scouring flows prior to spawning | Increased YOY abundance | Lithophilic spawner<br>Cavity nester | Spawning and juvenile habitat rejuvenation through fine sediment removal, wood recruitment[11] |
| Bed scouring flows postspawning, prior to or soon after fry emergence | Decreased YOY abundance | Lithophilic spawner | Egg, larval or fry displacement and mortality[12] |
| High flow pulses during spawning season | Increased YOY abundance | Pelagic broadcast spawner<br>Migratory spawner | Suspend pelagic eggs and larvae[13]; provide migration and spawning cues[14] |
| Flooding during spawning and growing seasons | Increased YOY abundance | Periodic life history type | Increased access to and prey productivity in floodplain habitats[15] |

[1] Jones and Petreman 2013; Letcher et al. 2015; [2] Perkin et al. 2019; [3] Beecher et al. 2010; Falke et al. 2010; [4] Gido and Propst 2012; [5] Nunn et al. 2003, 2007; Gido and Probst 2012; Walton et al. 2017; [6] Zeug and Winemiller 2008; Patrick et al. 2019; [7] Freeman et al. 2001; [8] Lukas and Orth 1995; Grabowski and Isely 2007; [9] Harvey 1987; Fausch et al. 2001; Weyers et al. 2003; [10] Haworth and Bestgen 2016; [11] Cattaneo et al. 2001; Craven et al. 2010; [12] Warren et al. 2009; Kanno et al. 2015; [13] Rodger et al. 2016; [14] Amtstaetter et al. 2016; King et al. 2016; Lopes et al. 2018; [15] Balcombe and Arthington 2009; Robertson et al. 2018.

across taxa and contexts, while others vary depending on species traits (e.g., spawning mode; Table 1) and system context (e.g., flow regulation, floodplain access; Figure 2).

Juvenile and adult life stages appear most strongly affected by flows that alter individual growth or that influence fish movements (supporting studies cited in Table 2). Low flows may depress prey availability and thus potentially growth, particularly for drift feeding fishes (Harvey et al. 2006; Letcher et al. 2015; Rosenfeld 2017). Crowding and enhanced recruitment during low flows may also increase competition for prey, resulting in lower growth (Grossman et al. 2016), whereas high flows that provide access to productive off-channel foraging habitats may enhance fish growth (studies cited in Table 2). Flow effects on fish movements and thus local abundances are more nuanced. Prolonged low flows may prompt fish to emigrate in response to shrinking habitat, resulting in lower abundances or local extirpation (Table 2). However, habitats that become more accessible or serve as refugia may support higher local fish richness or abundances during drought conditions, followed by dispersal during high-flow periods (Table 2; Franssen et al. 2006; Peterson and Shea 2015; Hedden and Gido 2020).

The diversity of outcomes from fish–flow studies underscores the potential for contrasting population responses to flow events, but also provides a foundation for predicting responses conditional on context and species characteristics. Some predictions, for example, that low spawning season flows will depress YOY recruitment of broadcast spawning minnows in dryland rivers, have a clear mechanism (e.g., sinking and mortality of pelagic eggs and larvae) and are supported by studies in multiple systems (Perkin et al. 2019). We suggest that by focusing future research on testing other hypothesized mechanisms underlying fish responses to flow events (Tables 1, 2), ecologists can develop a basis for quantitatively forecasting outcomes of projected or alternative flow conditions.

## CHALLENGES FOR TESTING MECHANISTIC FISH–FLOW HYPOTHESES

Incomplete data—both flow and biological—coupled with ecological complexity create significant challenges for testing hypothesized flow effects on fish populations and communities (Figure 2). Some observations allow direct and unambiguous inferences of mechanistic flow effects; for example, YOY entrainment by floods (Harvey 1987) or flow–pulse stimulation of spawning migration (Amtstaetter et al. 2016). In many cases, however, the available data are estimates of population variation, in time or space, along with estimated flow conditions, which are used to evaluate evidence that fishes respond to flows as expected given species traits and context. Uncertainty regarding elements of flows and population responses can introduce errors that degrade power to detect a signal of flows on fishes. Ideally, streamflow and temperature data are available for sites with fish data. However, most streams are ungaged, particularly smaller streams, limiting the availability of measured flow (or temperature) data. Hydrologic and temperature models are increasingly capable of filling this gap, although not without limitations. For example, rainfall–runoff models may not accurately simulate extreme flow events, such as extended low flows, unless the models are specifically calibrated for that purpose (Parker et al. 2019). Supplementary data collection, for example, documenting periods of intermittency, may be necessary to improve modeled estimates of extreme flows in ungaged systems. Weather data may also provide useful proxies for occurrence of extreme events (e.g., bed

Table 2. Hypothesized effects of low- and high-flow conditions on juvenile and adult fish abundance, growth, and survival. Examples of species traits associated with observed responses are listed with hypothesized mechanisms and selected supporting case studies (Table S1).

| Hydrologic driver | Population response | Species traits | Mechanisms |
|---|---|---|---|
| Prolonged low flows during growing season | Decreased abundances, growth, or apparent survival | Drift feeder<br>Fluvial specialist<br>Coldwater adapted | Lower drifting prey availability[1]; emigration or mortality in response to diminished flowing water habitat[2]; higher competition[3], predation, disease, thermal stress[4] |
| Prolonged low flows during growing season | Increased local abundances | Fluvial specialist | Low-flow dispersal to high-gradient habitats[5]; refuge seeking from habitats with diminished streamflow[6] |
| Above-average flows during growing season | Colonization; increased growth | Larger size (e.g., >100 mm TL)<br>Dryland adapted<br>Potomadromous | High-flow dispersal[7]; increased connectivity to isolated and off-channel foraging habitats[8] |

[1]Harvey et al. 2006; Letcher et al. 2015; [2] Matthews and Marsh-Matthews 2003; McCargo and Peterson 2010; Magoulick and Kobza 2003; [3] Grossman et al. 2016; [4] Closs and Lake 1996; Letcher et al. 2015; [5] Grossman et al. 2010; [6] Katz and Freeman 2015; Hedden and Gido 2020; [7] Peterson and Shea 2015; Koster et al. 2021; [8] Franssen et al. 2006; Balcombe and Arthington 2009.

scouring flows in headwater streams; Kanno et al. 2015) and are available at a greater extent and resolution than flow data.

Biological data, typically comprising periodic samples to estimate fish abundances, also impose practical limitations on hypothesis testing (Chen and Olden 2018). Even long-term data (10 years or more) may include at best a few extreme flow events, limiting replication for assessing effects on fishes. Annual fish counts also integrate flow effects on multiple demographic processes, complicating tests of specific hypotheses (Letcher et al. 2015). This challenge is exacerbated by the mismatch between fish counts, typically at local sites (e.g., tens to hundreds of meters in length), and the larger spatial scale of processes affecting local fish abundance. In particular, fish movement may obscure flow effects on fish populations. For example, fish may evade adverse flow conditions in a mainstem habitat by seeking refuge in adjacent tributaries (Koizumi et al. 2013) or disperse to perennial reaches as intermittent tributaries dry (Hedden and Gido 2020). Finally, fish counts themselves often require correction, using sampling efficiency to provide accurate measures of abundance. Variable sampling efficiency in relation to habitat conditions and species characteristics is expected and especially problematic (Price and Peterson 2010; King et al. 2016). For example, if flow conditions affect capture efficiency, then fish counts may reflect artifacts of sampling rather than true flow-related variation. Moreover, if capture efficiency varies unevenly across taxa, then even relative species abundances (i.e., apparent community composition) will be biased (Price and Peterson 2010).

In addition to challenges in quantifying flow and fish variables individually, there are also uncertainties about the best approaches for linking the two. Both the choice of appropriate flow metrics and the functional form of flow–ecology relationships will affect interpretation (Webb et al. 2017). Flow may affect fishes primarily through indirect and interactive pathways, for example, by modifying temperature and prey availability (Rolls et al. 2013), and those effects often vary among organism life stages (Lester et al. 2020). For example, flows that provide good spawning conditions may not be optimal for providing fish cover (macrophytes) or prey habitat, potentially confounding the linkage between flow and recruitment (Garbe et al. 2016). Finally, whatever flow and response variables are most appropriate for building predictions, it is unlikely that the relationships will be consistent across varying magnitudes of flow variation (Rosenfeld 2017; Tonkin et al. 2019) or stream size, limiting model transferability in both time and space (Chen and Olden 2018).

## RESEARCH DIRECTIONS

Despite challenges, studies conducted in a variety of freshwater contexts have provided a wealth of observations that allow development of hypothesized flow effects on fish populations and communities (Tables 1, 2). Going forward, we think progress will be greatest where biologists can devise tests of these and other specific hypotheses, thereby building an empirical basis for probabilistic prediction. Here, we highlight four broadly defined research directions to advance our understanding of mechanistic relations between flow and fish populations.

(1) **Spatial analysis** of distribution data is a well-established approach for identifying species-specific habitat associations, including hydrologic variables as predictors. Spatial analyses will be most usefully applied to data sets with many sites spanning large geographic areas. For example, analysis of fish collection data at stream sites across the interior western United States supported the hypothesis that fall spawning trout species are less likely to occur in streams with more frequent winter high flows that may scour eggs and larvae (Wenger et al. 2011). Similarly, ecologists have demonstrated predictable differences in trait composition of fish communities among stream locations (Mims and Olden 2012) and regions (Tedesco et al. 2008; McManamay and Frimpong 2015) that differ in flow-regime characteristics. Given the multiple factors that influence fish distributions and abundances, correlations between species occurrence or community composition and hydrologic variables across broad landscapes provide compelling evidence of directional effects based on inferred mechanisms. Wide availability of fish collection records and sampling data, coupled with increased availability of modeled flow data, ensure that spatial analyses will remain useful as one line of evidence for evaluating hypothesized flow effects on fishes.

(2) **Time-series analysis** of abundance indices, flow, and flow-covariate (e.g., temperature) data collected annually over multiple years provides a means of testing many hypothesized, context-specific mechanisms of flow effects by relating changes in fish abundance or occurrence to antecedent flows. Historical time-series data collected in diverse systems offers opportunities for observing responses to flow variability by species characterized by divergent traits (Craven et al. 2010; Chen and Olden 2018). Moving forward, we may learn more from monitoring efforts that support direct tests of flow and flow covariates on recruitment, survival, individual growth, and dispersal,

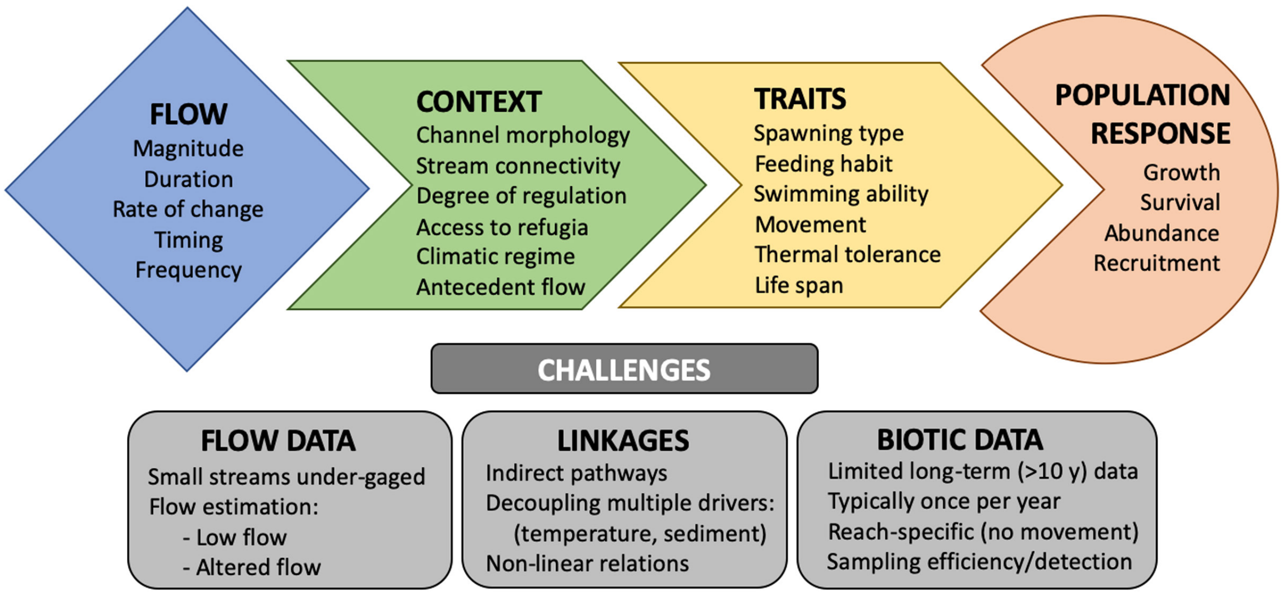



Figure 2. Flow effects on fish populations are mediated by the physical context and species traits. Scientific understanding of relationships between flow and fish are limited by flow data, biotic data, and our understanding of the linkages between them.

processes otherwise represented by cumulative effects in time–series of annual counts. Approaches include quantifying abundances of distinct life stages (e.g., YOY, juveniles, adults) in annual counts (Bond et al. 2015; Kanno et al. 2015; Letcher et al. 2015), and targeted studies of specific demographic rates in relation to flow-related drivers (Katz and Freeman 2015; Letcher et al. 2015; Merciai et al. 2018).

(3) **Flow experiments** can provide a relatively rapid and less confounded means to test hypothesized mechanistic relationships between fish ecology and flows. At a minimum, experiments entail manipulating an aspect of the flow regime (e.g., pulsed flow releases to influence fish reproduction) or fish population (e.g., releases of marked larvae to study dispersal and recruitment), with adequate subsequent monitoring of outcomes (Box 1). Flow experiments have been conducted in many regulated systems, although rarely with sufficient monitoring of outcomes to allow strong tests of hypothesized mechanisms (Konrad et al. 2011; Olden et al. 2014). Nonetheless, there is substantial potential for understanding responses linked directly to flow in the context of adaptive management. For example, stakeholders on the flow-regulated Tallapoosa River, Alabama agreed to experimentally increase nonpower-generating flows below a hydropower dam for 12 years. Annual monitoring of fish communities revealed that lower temperatures corresponding to higher flows likely limited colonization and recruitment of many species, pointing to the need for alternative management approaches (Irwin 2019). A major obstacle in experimental assessment of links between flows and fish populations is building the necessary management, research, and stakeholder commitments to monitoring as well as manipulation. Relicensing of hydroelectric dams and environmental flow negotiations provide opportunities to build adaptive management directly into management processes. "Natural experiments," such as opportunistically timed flow events hypothesized to affect fish growth or recruitment, accompanied by targeted monitoring, may also inform flow management strategies aimed at species conservation (Bestgen et al. 2006).

(4) **Comparing multiple lines of evidence** can facilitate comprehensive evaluation of support for hypothesized flow–ecology mechanisms (Kennedy et al. 2016). By pursuing multiple lines of evidence—for example, combining life history research, data on individual survival and population dynamics, and observations of community differences in relation to flow regimes—researchers can evaluate support for hypothesized mechanisms using observations that individually could be inconclusive. Inferences will be strongest when stressors are measured as directly as possible, rather than using indirect indicators. For example, high-flow metrics are frequently used as a surrogate for scour that displaces benthic eggs or larvae, yet directly estimating flow effects on bed sediments may provide a better understanding of causal relationships. Given that flow variables commonly covary with other stressors, research to discern mechanisms may require multiple stressor experiments, along with measurements of habitat-scale abiotic conditions, prey and predator interactions, and associated fish behavior, growth, or survival.

## CONCLUSIONS

New insights into how flows affect fishes across all levels of ecological organization are essential to advance our ability to predict outcomes of management actions taken in response to flow regulation and water abstraction, climate and land use change, and the spread of nonnative species. The ability to incorporate improved scientific understanding into decision making depends on our capacity to manage the flow regime or otherwise restore river habitat, which may be limited by infrastructure and regulatory constraints. Nevertheless, even in situations where management control is limited (e.g., Box 2), making and testing predictions of fish responses to flow events represents a productive path toward informed decision making. Testing hypotheses that link flow events to demographic processes—juvenile recruitment, survival, growth, dispersal—underpins development of a predictive capability and potentially improved management for stream fishes in a rapidly changing world.

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Supplementary Material AFS