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Article

Developing generalized flow ecology relationships for stream salmonids: Providing a clearer empirical basis for minimum flow regulations

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ABSTRACT

Objective: To provide a clearer empirical basis for guiding minimum flow regulations, we tested for a consistent relationship between the magnitude of stable flows and correlates of productive capacity for stream salmonids.

Methods: We extracted and analyzed data from 35 flow–ecology relationships related to salmonid productive capacity (defined by diverse ecological responses including abundance, density, growth, or survival) from 25 streams ranging in flow from 0.4 to 750 m^3/s mean annual discharge (MAD). To facilitate comparison among studies, we rescaled flow to percentage of MAD and rescaled ecological responses to a 0–1 range (dividing by the largest value in each study) or units of standard deviation (dividing by the SD). To control for effects of season and flow regime, we classified studies into four common hydroecological contexts: summer low flows (rainfall dominant streams with dry summers), summer high flows (snowmelt/glacial runoff streams), winter low flows, and migration or spawning flows. Standardized ecological response was then modeled as a function of percent MAD, ecological context, and their interaction.

Results: The slope of ecological response–flow relationships was positive for summer or winter low-flow regimes and migration flows but negative in summer high-flow regimes, consistent with expectations from habitat simulation models of a unimodal relationship between flow and habitat availability. Generalized additive models and logistic regression indicated peak salmonid productive capacity at 57% MAD (approximate 95% CIs 39–93% MAD), and average low-flow regressions indicate an 82% loss of capacity from 57% MAD (optimal flow) to flow cessation (0% MAD).

Conclusions: Standardizing response and flow axes while controlling for context dependence (i.e., seasonal hydrology) provides a useful approach for extracting cryptic flow–ecology relationships from diverse data sets, allowing detection of generalized flow–ecology relationships with optimal rearing flows at intermediate discharge. These generic relationships can be used to predict population-average flow effects in data-deficient salmonid streams and guide landscape-level flow policy.

KEYWORDS: context dependence, environmental flow needs, flow–ecology relationships, minimum flows, salmonid flow requirements

LAY SUMMARY

Standardizing diverse metrics of biological response (e.g., fish growth, survival, or abundance) and absolute discharge (*y* and *x* axes, respectively) can help identify generalized flow–ecology relationships to guide flow management, reducing ambiguity around the negative effects of low flow.

INTRODUCTION

Flow is a master variable controlling the quantity and quality of stream habitat, with cascading effects on stream function, production, and organism diversity (Acreman et al., 2014; Poff et al., 1997; Yarnell et al., 2015). The magnitude of stable flow determines the availability of habitat to fish and other organisms (Rolls et al., 2012), and flow variation sets the disturbance regime that shapes productivity and community

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structure (Blum et al., 2013; Lytle & Poff, 2004). However, the natural flow regime is becoming increasingly disrupted by human appropriation of freshwater resources associated with economic growth (Albert et al., 2021; Postel et al., 1996; Richardson et al., 2023), which is pushing local and global water systems beyond the safe operating space for humanity (Steffen et al., 2015; Zipper et al., 2020). Establishing environmental flows to maintain the productive capacity of streams remains an ongoing scientific challenge for natural resource management agencies (Castleberry et al., 1996; Stoffels et al., 2018; Tickner et al., 2020; note that our use of productive capacity is intended in the broad sense of the number or biomass of individuals that can be supported per unit area rather than the narrow sense of the slope of the stock–recruit curve at low density). Although maintaining diverse components of the natural flow regime—including both stable flows and variation associated with seasonality and storm events—is essential for maintaining biodiversity and stream ecosystem function (Grantham et al., 2022; King et al., 2008; Poff et al., 1997), in this study we focus exclusively on the effects of relatively stable flows. This is not to diminish the importance of other components of the natural flow regime (e.g., the essential role of flow variation); rather, it reflects a desire to focus on the effects of low flows when human demand for water is in greatest conflict with flow needs for salmonid production.

Historically, scientific advice to guide instream flow management has relied on a combination of detailed studies for high-profile rivers (e.g., PHABSIM; Bovee, 1982; Gopal, 2013) and generic rules (desktop methods) for setting instream flows in myriad other lower priority streams that are subject to water withdrawals. Desktop methods typically use inferred thresholds of habitat degradation that are associated with hydrologic metrics like flow exceedance or relative discharge (e.g., Caissie et al., 2015; Gopal, 2013). For example, Tennant (1976) developed a streamflow habitat quality classification using flow expressed as a percentage of mean annual discharge (MAD), with habitat quality ranging from degraded (below 10% MAD) to optimal in the range of 60–100% MAD. By expressing flow as a percentage of the annual average, Tennant and other desktop approaches generate rules that are intended to be scale independent and generalizable across streams of different sizes to facilitate their application in data-deficient systems.

However, the transferability of generic rules of thumb across multiple streams remains poorly validated, and traditional reliance on habitat simulation models has also been questioned (Mathur et al., 1985; Railsback, 2016). More recently, flow–ecology relationships have emerged as a new approach to establish instream flow requirements (Arthington et al., 2010; Poff et al., 2010). Flow–ecology relationships are stressor-response functions (Jarvis et al., 2024; Larned & Schallenberg, 2019) that directly relate measured ecological attributes (e.g., fish abundance) to discharge based on empirical observations rather than habitat simulations (Kendy et al., 2012). Direct measures of ecological attributes at different flows have become the gold standard for understanding the true effects of flow alteration. However, generating empirical flow–ecology relationships remains expensive, time-consuming, and notoriously difficult because of the difficulty of accurately measuring the response of fish to altered flow. Uncertainty in the transferability of flow–ecology relationships beyond the stream of origin also undermines confidence in their generality, motivating meta-analyses to develop generic flow–ecology relationships across a diversity of streams. Unfortunately, success at generating robust general relationships to altered flows has been limited. For example, an early meta-analysis by Poff and Zimmerman (2010) found that both increased or decreased stream flow could trigger a reduction in fish or benthic invertebrate abundance, leading them to conclude that "our analyses do not support the use of the existing global literature to develop general, transferrable quantitative relationships between flow alteration and ecological response" (p. 194).

However, failure to identify a generalizable response may simply reflect cryptic context dependence that drives divergent responses to altered flows (Freeman et al., 2022; Rosenfeld et al., 2022; Walters, 2016). For instance, a nonlinear unimodal (humped) response to a stressor (e.g., flow) will display contrasting positive or negative effects (slopes) over low- and high-flow ranges on opposite sides of the optimum, respectively (Figure 1A); failure to recognize this context dependence may result in deterministic variation being interpreted as random error (Catford et al., 2022; Rosenfeld et al., 2022).

Apparently chaotic and unpredictable patterns can often be resolved when the effect of ecological context is clearly defined (Catford et al., 2022). The context dependence of flow–ecology relationships is best understood by considering how the slope and intercept are expected to change along a discharge gradient. For example, habitat simulation models (e.g., PHABSIM; Bovee, 1982) are widely used to predict how available habitat (and by inference population size) changes with flow. Habitat availability for salmonids typically shows a unimodal relationship between available habitat (weighted useable area) and flow (Figure 1A), with maximum habitat at intermediate discharge and the optimal flow (peak of the curve) shifting to higher flows for larger fish (Armstrong & Nislow, 2012; Jowett et al., 2008). Insofar as many stream organisms display maximum performance over a well-defined optimal range of velocity (e.g., Bovee, 1978; Gore et al., 2001), it is reasonable to treat a unimodal relationship as the default flow–ecology model for salmonids, generating the expectation of contrasting low- and high-flow contexts defined by positive and negative slopes, respectively (Figure 1A).

These contrasting responses to flow are usually associated with discrete seasons and flow regimes. For example, summer low flows in rain-dominated streams with a Mediterranean climate result in strong habitat limitation (Figure 1B; Rolls et al., 2012; Rosenfeld et al., 2024), and a positive effect of increasing flow would be expected in this context (henceforth, the "summer low-flow context"). Winter periods in cold temperate climates when precipitation falls as snow also experience low flows that can limit habitat and promote stressful ice formation (Huusko et al., 2013), also generating the expectation of a positive relationship between available habitat and winter low flows (winter low-flow context; Figure 1B). In contrast, streams with snowmelt and glacial influences experience extended high flow during the summer growing season (Liermann et al., 2012; Neuswanger et al., 2015; Wilding & Poff, 2008), resulting in the expectation of negative effects of increasing

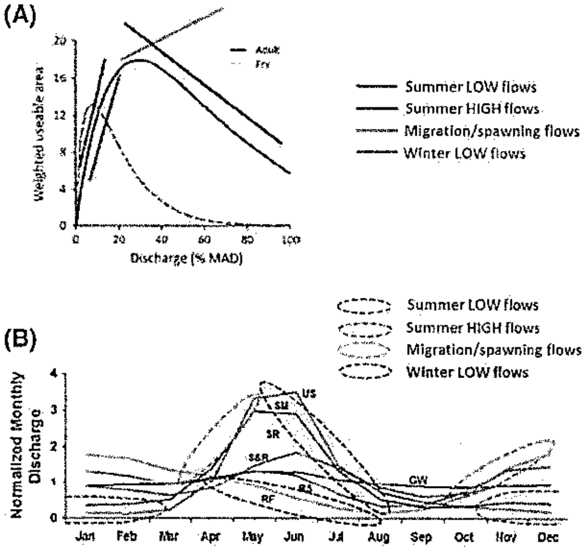

Figure 1. (A) Expected generic relationship between weighted usable area (WUA, i.e., modeled available habitat) and flow for a typical salmonid species (Brown Trout; upper solid black curve is available habitat for adults; lower broken green curve is for juveniles; after Snelder et al., 2011). Because fish growth is optimized at intermediate velocity, extremely low and extremely high flows reduce available habitat, which is optimized at an intermediate discharge that is higher for larger fish because of their greater swimming ability. Straight lines represent the expected flow–ecology relationships between discharge and salmonid abundance, growth, or survival in different hydroecological contexts (summer low flow, summer high flow, winter low flow, spawning/migration flow). For instance, summer-rearing fish in a rainfall-dominated stream (RF) may experience low summer flows and a positive effect of increased discharge on fish production, whereas summer-rearing fish experiencing high flows in a cold snowmelt (SM) or glacial stream may be on the downward leg of the WUA versus flow curve, resulting in a negative effect of increased summer discharge. (B) Illustration of how season (summer, winter) and flow regime (e.g., rainfall dominant vs. snowmelt dominant; after Liermann et al., 2012) define ecological context and therefore the expected slope of flow–ecology relationships.

flow (negative slope of the flow–ecology relationship) during a summer high-flow context. These three ecological contexts pertain to the effects of prolonged stable flows on salmonid rearing and growth; however, a fourth ecological context can be recognized related to the effects of flow on fish passage, migration, or spawning. In general, a positive flow–ecology relationship would be expected for this fourth ecological context, as barriers to fish passage (e.g., spawning migrations, smolt out-migration) usually increase as flow declines (e.g., Cunjak et al., 2013). Many other ecological contexts can be defined in association with other dimension of the flow regime (Olden & Poff, 2003)—for example, the functional effects of short-term stochastic peak flows (as opposed to stable sustained flows) on fish survival (e.g., Blum et al., 2013); however, in the interest of simplicity, in this study we focus on the effects of stable flow magnitude rather than peak flow events, which can be thought of as press versus pulse disturbances, respectively (Lake, 2000; Rolls et al., 2012).

To test for the occurrence of general salmonid flow–ecology relationships, we performed a literature review and meta-analysis of published relationships between stream flow and indices of salmonid abundance, survival, growth, or other measures of performance. To facilitate the analysis, we standardized flows and ecological responses while controlling for ecological context (low summer flows, low winter flows, higher summer flows, and migration flows). Our general goals were to determine whether accounting for ecological context and standardizing the stressor and response axes could resolve the inherent variation that is observed among salmonid flow–ecology relationships and to generate empirical reference points for establishing environmental flows. Our specific objectives were (1) to determine whether there are common relationships between correlates of salmonid productive capacity (e.g., growth, survival, abundance) and flow across a diversity of streams, salmonid species, and ecological contexts; (2) to evaluate whether empirical generic flow–ecology relationships may be useful for predicting the consequences of water withdrawals in data-deficient streams; and (3) to assess whether emergent empirical relationships are consistent with thresholds of impairment and optimal flow identified by the widely used Tennant percent MAD desktop guidelines.

METHODS

Data collection

We conducted an extensive search of the published primary and gray literature for flow–ecology relationships with a primary focus on salmonids. We included primary literature from any continent or jurisdiction, but for gray literature (e.g., government reports) we focused on studies from British Columbia, which primarily consisted of BC Hydro Water Use Plan reports (e.g., Burt, 2013); this was motivated by a mandate to develop regional flow–ecology relationships for salmonids within our jurisdiction. Databases were searched for one or more primary terms (flow–ecology relationships, environmental flows, hydroecology, flow variability, natural flow regime paradigm, river ecosystem condition, stream ecology) with the addition of any supplementary terms (biotic indices, salmonid, British Columbia, discharge), up to a date of December 2021; publications subsequent to this date are not included. Search platforms included Google, Google Scholar, and the University of British Columbia Library academic search engine. Candidate studies were also identified through citation searches and reference lists of relevant articles. A data source required a figure or table reporting a relationship between discharge and an ecological response variable such as salmonid biomass, abundance, density, survival, growth, recruits, or smolt production and had to include original data (Table S1; see online Supplementary Material).

Mean annual discharge (MAD) was also required for each study to standardize flows and scale streams of different sizes to a common discharge axis; MAD had to be reported in the article or readily available from other credible sources such as the Water Survey of Canada or the U.S. Geological Survey for inclusion. One consequence of the requirement for MAD to rescale absolute flows was to exclude most flow studies either because MAD was not available or because reported fish responses (e.g., biomass data points) could not be associated with a specific discharge. Apart from gray literature from British Columbia, we also extracted data only from published studies and excluded data from online databases or other sources where the quality of collected data or potential confounding factors was unclear or required additional validation. Although some studies represented before–after monitoring from flow diversion experiments or hydroelectric facilities ($n = 5$; e.g., Ovidio et al., 2008), most studies represented multiyear monitoring where annual variation in flow was the driver of interannual variation in the measured biological response, typically with one observation per year across multiple years in each study ($n = 20$ studies). The number of data points in each data set ranged from 4 to 70, with a median of 14 and a total combined sample size of 675 observations. We included only studies on salmonids and excluded warmwater or other species to focus the analysis on a single data-rich high priority taxon that is often considered a keystone species for managing ecosystem health (Hyatt & Godbout, 1999).

A primary focus of this study was to define flow–ecology relationships in the lower range of discharge, when out-of-channel demands for water are in the greatest conflict with instream flow needs and therefore most contentious. Studies related to summer low flows, summer high flows, and winter low flows were thoroughly searched and included in the database. Although our literature review was extensive, some studies were likely missed because of their obscurity or simply the volume of available studies. In contrast with the first three ecological contexts, it is important to note that studies relating flow to spawning and migration were not as thoroughly searched; they were only included opportunistically when they co-occurred in publications documenting stable low- or high-flow relationships, which were the primary focus of this review (e.g., Cunjak et al., 2013; Warkentin et al., 2022). We nevertheless include this incomplete class in the meta-analysis, as it represents an additional ecological context for comparison with the low-discharge flow–ecology relationships. However, the lack of a systematic search for spawning/migration flow studies means that the slope and intercept of the average spawning/migration versus flow regression may not be representative of the population of available studies (although the general trend should be accurate).

Except for spawning and migration flows, we assume that studies meeting our criteria were representative of salmonid streams and broader responses to flow alteration. This is probably a reasonable assumption, as studies came from six countries (primarily in North America and Europe) and represent nine salmonid species including Rainbow Trout *Oncorhynchus mykiss* (steelhead), Coastal Cutthroat Trout *Oncorhynchus clarkii*, Brown Trout *Salmo trutta*, European Grayling *Thymallus thymallus*, Atlantic Salmon *Salmo salar*, Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *Oncorhynchus kisutch*, Pink Salmon *Oncorhynchus gorbuscha*, and Brook Trout *Salvelinus fontinalis* (Table S1). This diversity of species likely increases variation among flow–ecology relationships that could obscure a common signal of flow effects but also ensures that any detectable pattern is likely to be generalizable. Streams also ranged over three orders of magnitude in size (i.e., 0.4–750 m^3/s MAD). In total, 25 studies that met our inclusion criteria were found, including data from 35 flow–ecology relationships (i.e., several studies included data from multiple streams or ecological response variables).

Engauge Digitizer software (Mitchell et al., 2023) was used to extract ecological response and flow data from figures, and data from tables were directly transcribed into a database (see online data repository; Table S1). We identified four ecological contexts as described in the introduction and outlined in Table 1: summer low rearing flows; summer high rearing flows; winter low rearing flows; and high flows associated with fish out-migration, passage, or spawning.

Because the focus of this review is on the ecological consequences of stable flow (i.e., prolonged press disturbances) for correlates of salmonid production (e.g., density, or average growth or survival), studies related to pulse disturbance events (e.g., spates and floods) were explicitly excluded. Periodic high-flow events are critical components of the natural flow regime and have both positive and negative effects on salmonid production (e.g., positive: maintenance of channel structure through pool scour and sediment transport; Death et al., 2015; negative: redd scour and fry mortality; Carline & McCullough, 2003). However, disturbance flows represent a separate discrete driver of productive capacity that is characterized by a different set of flow–ecology relationships and underlying mechanisms, which precludes their analysis here.

Overview of analytic approach

We used a sequence of linked steps to generate the final composite flow–ecology relationship (Figure 2). First, we converted all discharge axes to the same relative scale (%MAD) to facilitate comparison and standardized all biological response variables to shared units of standard deviation (SD) for each of the 35 relationships. The average peak (optimum) of the 35 standardized biological response versus flow relationships was then determined based on the transition from a positive to a negative slope (i.e., using logistic regression) and by fitting a generalized additive model (GAM). However, very low SD can inflate standardized slopes; normalization generates unbiased slopes, but only when the flow range overlaps with the peak of the curve (Supplementary Methods and Figure S2 [see online Supplementary Material]). The optimal range determined by the analysis of standardized regressions was then used to identify the subset of studies with flow ranges that overlapped the optimum. Normalized regressions were then applied to this subset to generate unbiased slopes and intercepts for separate empirical predictive regressions for low flows, high summer flows, and very low flows to create a final composite model as described below and illustrated in Figure 2.

Data standardization

To enable a comparison of studies with diverse ecological responses and flows, both discharge and ecological response axes were rescaled. Absolute discharge (m^3/s) was converted to a percentage of mean annual discharge (%MAD) by dividing absolute flow by MAD for each stream; %MAD represents an index of the relative fullness of the stream channel that is largely independent of stream size, as noted in the introduction (see Rosenfeld, 2017; Tennant, 1976; or Rashidabady et al., 2022, for a more detailed explanation). The flow metrics that were used across individual studies ranged from measurements of

Table 1. Ecological context classes and associated hydrology attributes to which the different salmonid flow–ecology studies were assigned. The summer low-flow context includes studies in rainfall-driven streams over the summer low-flow recession when juveniles or adults are rearing in the stream and represents the lower end of the discharge spectrum (average flow range of the 15 studies from 7% to 35% MAD). Summer high flows are summer-rearing relationships in snow or glacial melt streams experiencing much higher summer flows (average range from 50% to 260% MAD). Winter low flows represent studies where salmonids were responding to low winter flows (26–71% MAD average range) and are relevant to minimum overwinter flows. High (migration or spawning) flows represent salmonid responses (smolt out-migration, fish passage, or spawning) to higher flows.

Hydrologic and ecological context	Biological response	Flow–ecology hypothesis	Predicted slope	Average flow range (%MAD)	Flow metrics	Season	*N*
SUMMER LOW FLOWS							
Mediterranean (rainfall dominant) streams (prolonged low flows beginning in early summer)	Juvenile or adult: rearing	Abundance, survival, or growth *decline* at lower flows	+	7–35% (min 0.06–3.3%) (max 27–99%)	7 or 30 d average minimum flows; mean or median summer monthly low flows	Summer	15
SUMMER HIGH FLOWS							
Colder glacial, snowmelt, or high elevation/latitude streams	Juvenile or adult: rearing	Abundance, survival, or growth *decline* at higher flows	–	50–260% (min 40–115%) (max 18–798%)	Average (Jun–Sep) summer flows, mean monthly flows	Summer	7
WINTER LOW FLOWS							
Stable winter low flows	Juvenile or adult: rearing/overwintering	Abundance, survival, or growth *decline* at lower flows	+	26–71% (min 7–46%) (max 74–99%)	7 or 30 d minimum average or monthly flows	Winter	7
HIGH (MIGRATION OR SPAWNING) FLOWS							
Spring/summer freshet fall or winter flows	Smolt: out-migration, fish passage, *or* spawning migration flows	Survival, passage success, or availability of spawning habitat *increase* with flow	+	65–325% (min 12–91%) (max 241–1,522%)	Monthly or average flows; flows during migration or spawning	Spring (smolt out-migration) Fall or winter (spawning)	6

daily duration ($n = 6$) to a 5-month average flow ($n = 1$), with a median of 1 month and an average of 2.1 months for the 35 relationships (Table S1). In principle, flows of monthly duration may better predict average fish growth integrated over a growing season rather than a single daily or weekly minimum flow value.

Ecological response variables differed greatly among studies and encompassed a range of state and rate variables (Wheeler et al., 2018), often diverging by orders of magnitude (Figure S2). Responses were dominated by measures of abundance ($n = 12$ studies) and fish density (9 studies), but also included survival (5), biomass (3), smolt production (2), catch per unit effort (1), growth (1), redd abundance (1), and egg survival (1). Different units and scales make it extremely difficult to compare responses across studies without first standardizing the response variables (i.e., the y-axis). We standardized responses in two separate ways: first, by dividing by the standard deviation (SD), which rescales all the studies to common units of SD (Figure 2A, B; henceforth, "standardization"; Schielzeth, 2010; Smith & Ward, 2000) and second, by dividing responses with the maximum observed value in each study, which rescales them from 0 to 1 (Figure 2C, D; henceforth, "normalization"; e.g., Rosenfeld & Lee, 2022; Wilding & Poff, 2008). Both approaches have strengths and limitations. As noted earlier, standardized relationships were used to identify the optimal flow (peak ecological response) but can generate inflated slopes when SD is unusually low. Normalization was used to generate more reliable slope estimates as described below (see Supplementary Methods and Figure S1 for additional detail).

Statistical analysis

Analysis of standardized data

Hydraulic modeling predicts that the slope of flow ecology relationships should decline with average discharge, based on the expected unimodal (hump-shaped) response to increasing flow (Figure 1A). Slopes of flow–ecology relationships should therefore be steepest at very low flows (i.e., low-flow context), approach zero slope over the optimal flow range, and become negative at higher flows (high-flow context). To test for differences in slope across the four hydroecological contexts, we used mixed-model analysis to model standardized ecological response as a function of context (four classes: summer low flows, summer high flows, winter low flows, and migration/spawning flows), median discharge range for each flow–ecology relationship (as %MAD), and an interaction between median discharge and context, with individual flow–ecology relationships ($n = 35$) treated as a random effect. A significant interaction between discharge and context is diagnostic of context-dependent differences in the slopes of flow–ecology relationships, as predicted by hydraulic modeling (Figure 1A).

Separate models of standardized ecological response versus %MAD were fit for each of the four ecological contexts, again treating flow–ecology relationship as a random effect. Mixed-model regressions were performed using SAS proc mixed (Littell et al., 2006), using a Kenward–Roger approximation for degrees of freedom. Standardized ecological response data were log + 1 transformed to ensure normality and homogeneity of variance, which was assessed using a Shapiro–Wilk test of regression residuals and a plot of residuals against predicted values. Note that all

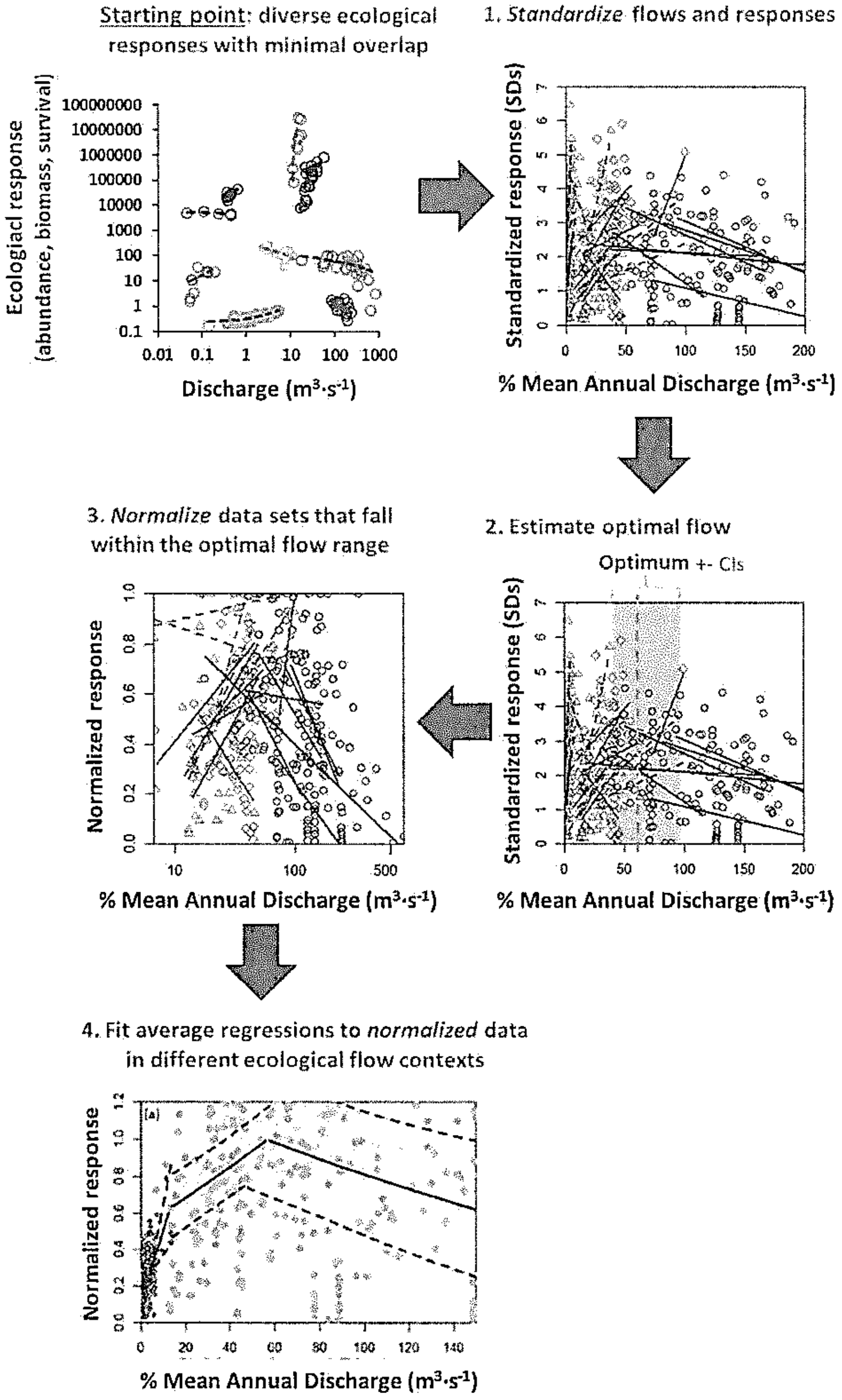

Figure 2. Graphic illustrating the data analysis workflow (see Methods for details). The starting point is represented by a set of flow–ecology relationships from streams that differ in units of measured ecological response (survival, density, smolt production, population size) and absolute flow magnitude by orders of magnitude, making it difficult to identify generalized responses to flow. (1.) Disparate individual flow–ecology responses were first standardized by their standard deviation, and flows were normalized to mean annual discharge (%MAD) to place them on similar scales. (2.) The optimal flow range was then determined using logistic regression and generalized additive models. (3.) To avoid biases associated with standardization, the subset of flow–ecology relationships with flow ranges falling within the estimated optimal range were normalized to a 0–1 scale. (4.) Average mixed-model regressions were fit to normalized data to estimate average flow–ecology relationships for different ecological flow contexts.

mixed models were fit as random slope and intercept regressions, with the explicit intent of treating different studies as a random subset of the population of all streams to widen the scope of inference beyond the specific subset of sampled streams.

We estimated the peak (optimum) of any common hump-shaped flow–ecology relationship using two approaches (Figure 2). First, we fit a GAM to standardized response data for all studies combined, modeling ecological response as a function of standardized flow (%MAD) and treating flow–ecology relationship ($n=29$) as a random effect using gam in the MGCV package (Wood, 2017; R version 4.2.2) with k (knots) evenly spaced and set to a default value of 10. To improve the smoothing of the GAM and generate a less jagged model fit, we also estimated the optimum flow using a GAM with $k=10$ knot locations specified to maximize smoothing.

Second, we used logistic regression as an additional method to estimate the peak of the generic flow–ecology curve based on the transition from positive to negative slopes (Figure 1A). The slope of each standardized flow–ecology relationship was determined using linear regression ($n=29$, excluding the spawning/migration flow context), which provided a superior fit to log (nonlinear) regression in most cases. Positive and negative slopes were then treated as binary states (1 and 0), with the probability of a positive slope modeled as a function of median study discharge (expressed as %MAD), with the discharge at 50% probability treated as the average transitional flow between positive and negative slopes (i.e., the peak of the habitat availability curve illustrated in Figure 1A). Logistic regression was performed using proc logistic in SAS (SAS Institute, 2015).

Analysis of normalized data

Because of concerns over the sensitivity of standardized slopes to variation in SD among studies (Figure S1), normalized data were considered more likely to generate reliable empirical flow–ecology relationships. However, prediction of maximum ecological response at an unrealistically low flow is a concern for studies with a narrow flow range (Figure S1D–F). To avoid generating biased flow–ecology curves, we excluded low-flow studies whose maximum flow was below the lower 95% confidence interval (39% MAD) for the predicted optimal flow (peak) of the generic flow–ecology curve (57% MAD; see results); this criterion excluded 11 very low-flow studies. Similarly, high-flow studies whose lowest flow exceeded the upper 95% confidence interval for the optimum (93% MAD) were also excluded; because all seven summer high-flow studies met this criterion, all were retained (see Figure 2 and Figures S1 and S2 for a visual illustration of this filtering process).

Normalized ecological response data were $(\text{response}+c)^d$ transformed to normalize regression residuals, with the transformation constant c ranging from -0.03 to -0.01 and the exponent d ranging from 0.43 to 0.75 depending on the subset of studies included in each mixed-model regression. Because there was no significant difference in slope between normalized summer and winter low-flow regressions ($t_9=-0.68, P<0.51$), both summer and winter low-flow studies were combined into a single low-flow relationship to maximize replication. Separate mixed-model regressions to predict normalized ecological response as a function of %MAD were then generated for combined summer and winter low flows ($N=11$ flow–ecology relationships) and summer high flows ($N=7$ relationships), treating study as a random effect. In addition to the full low-flow regression using all 11 studies, we also performed a reduced regression ($n=9$), dropping the two low-flow relationships with negative slopes. To ensure that average normalized empirical flow–ecology models covered a full range of ecological response (i.e., 0–1), average regressions for the low-flow and high-flow contexts were renormalized to generate a maximum predicted value of 1 at the estimated optimal flow of 57% MAD.

Dropping the nine studies with maximum flows below 39% MAD is problematic because the truncated data range limits the ability to predict ecological responses at very low flows. Fortunately, normalizing data to a shared common value other than the maximum can also generate a normalized relationship when studies share a common underlying functional response (e.g., Poorter et al., 2010). To generate a normalized regression for studies in the very lowest flow range, we identified six of the nine studies with overlapping flows ranging from 0.5% to 13.7% MAD (Table S1) to generate a very low-flow regression to complement the low- and high-flow regressions. Because the flow range of all six studies included 3% MAD, we normalized data from each study to the predicted value at 3% MAD (i.e., effectively rescaling each study so that the observed value at 3% MAD is 1) and fit a separate linear regression between ecological response and %MAD for each study. A mixed-model analysis was then used to predict the ecological response standardized to 3% MAD as a function of discharge, again treating flow–ecology relationship ($n=6$) as a random effect; this model was fit using the lme4 package in R (version 4.2.2), with a Kenward–Roger approximation for degrees of freedom, which was better able to fit a random slope and intercept model than SAS proc mixed. Finally, to generate a linked set of empirical regressions that covered the full range of discharge, the very low-flow regression was rescaled to link it to the low- and high-flow regressions that were normalized to a maximum of 1 (see Supplementary Methods for additional detail).

To test whether study attributes explained additional variation in flow–ecology relationships, we also modeled slope as a univariate function of stream size (MAD), species, duration of the flow metric, or life stage of the response variable (e.g., juveniles, adults). Finally, to assess how well the qualitative Tennant desktop criteria matched the empirically derived flow–ecology relationships for salmonids, the Tennant summer-rearing flow categories were superimposed on the derived regressions for direct visual comparison (severe degradation < 10% MAD; 10% = poor or minimum habitat; 30% = fair or degrading; 40% = good; 50% = excellent; 60% = outstanding; 60–100% = optimal range; Tennant, 1976).

RESULTS

The mixed-model analysis with data from all 35 flow–ecology relationships showed that the slope of standardized flow–ecology relationships was significantly positively related to median study discharge (%MAD; $F_{1,647}=31.1, P<0.0001$; Figure 3A), with a significant effect of ecological context on slope ($F_{3,37.7}=2.91$, $P<0.05$) and a significant interaction between discharge and context ($F_{3,653}=32.6, P<0.0001$). As expected, increasing flow had a positive effect on the correlates of salmonid production

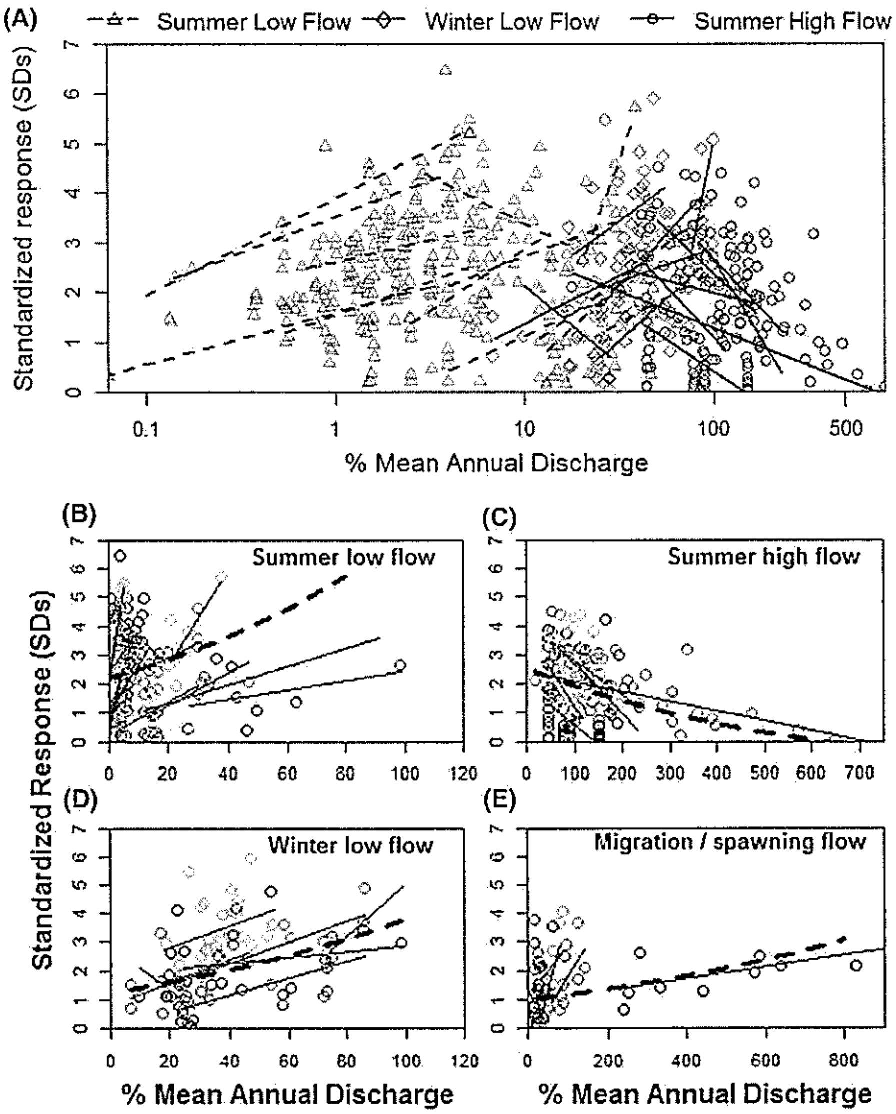

Figure 3. (A) Flow–ecology relationships for different ecological contexts (summer low flow, broken green lines; winter low flow, solid red lines; summer high flow, solid blue lines) standardized to a similar response scale by dividing by the standard deviation of each data set. Note the log scale x-axis (% Mean Annual Discharge). The remaining panels show standardized response versus discharge for (B) summer low-flow context, (C) summer high-flow context, (D) winter low flows, and (E) spawning/migration flows. The thick broken lines represent the average relationship within a context, and the thin black lines are individual relationships.

and individual performance in the summer and winter low-flow and spawning/migration contexts (Figure 3A, B, D, E) and a negative effect during higher discharge summer flows in snowmelt and glacial streams (Figure 3C).

The GAMs fit to the standardized response data showed a hump-shaped curve ($F_{7.1}=16.1$, $P<0.0001$) as predicted by hydraulic geometry, with an optimum at 51% MAD (37–69% approximate 95% CIs) for the default $k=10$ model and 53% MAD (38–75% approximate 95% CIs) for the second GAM ($F_{5.8}=15.5$, $P<0.0001$) with uneven knot spacing to produce a smoother model fit (Figure 4A, B; Supplementary material). The logistic regression model for the transition from a positive to negative slope identified a flow of 67% MAD (43–134% CIs) as the discharge with a 50% probability of a positive slope (i.e., the peak of the hump-shaped curve corresponding to a change in sign of the regression slope from positive to negative; Figure 4C; $\lambda^2_{1,27}=6.6$, $P<0.01$). The optimal flow and 95% CIs averaged across these three estimation methods was 57% MAD (39–93%).

When the slopes of the empirical flow–ecology regressions were normalized to a maximum of 1, they showed patterns that were similar to those of the standardized flow–ecology regressions but with somewhat less variation in slope (Figure 5) and a more easily interpretable response metric (proportion of maximum response rather than units of SD). Flow effects were statistically significant in both the low- and high-flow contexts ($F_{1,9.3}=24.8$, $P<0.0007$ and $F_{1,7.1}=13.5$, $P<0.008$, respectively; Figure 5B–E). The low-flow regression with all studies

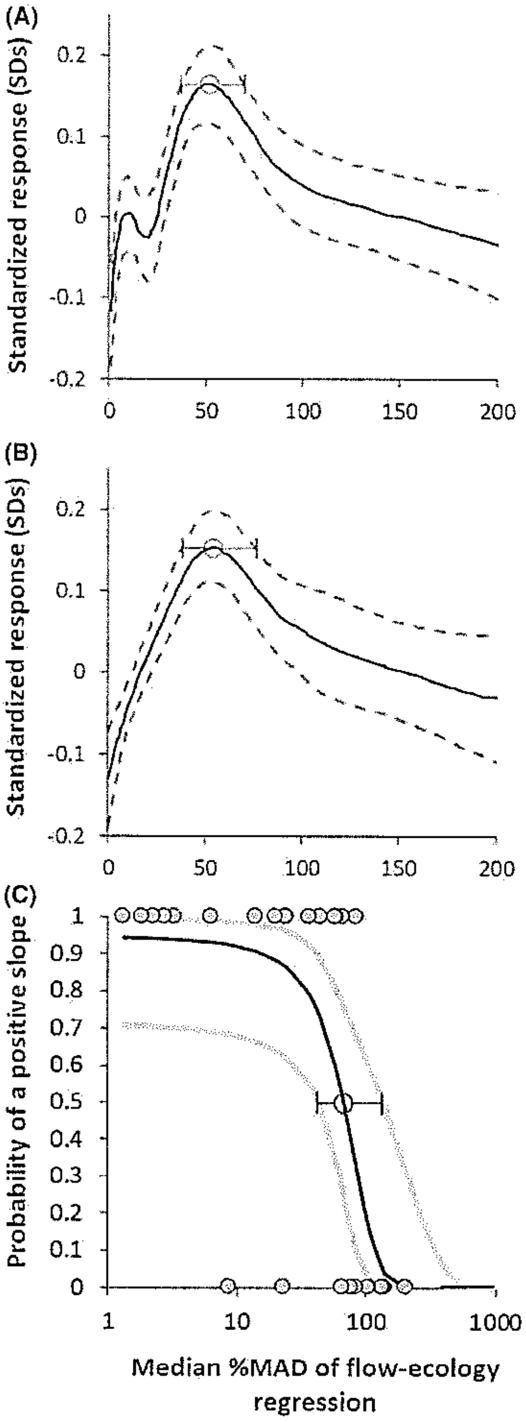

Figure 4. (A) Generalized additive model predictions for standardized ecological response as a function of the median %MAD for 29 flow–ecology relationships (migration/spawning flows excluded) for evenly spaced knots (optimum flow 51% MAD; 37–69% approximate 95% CIs) and (B) uneven knot spacing to maximize smoothing (53% MAD optimum; 38–75% approximate 95% CIs). (C) Shows the logistic regression of the probability of a positive slope as a function of median %MAD, with the optimal flow (%50 probability of a positive slope—that is, transition from a positive to negative slope) at 67% MAD (43–134% CIs). Logistic regression equation: $P(\text{positive slope}) = 1 / 1 + \{e^{-[(-0.0426 \cdot \%MAD) + 2.881]}\}$.

retained ($n = 11$) had a lower slope and intercept than the low-flow regression with the two negative slope studies removed ($n = 9$; Figure 5B; Table 2). Normalization to a maximum of 1 required dropping the low-flow studies that fell below the lower 95% CI of the optimal flow; normalizing a subset of these studies to 3% MAD generated a very low-flow regression, which also showed the expected positive slope ($F_{1,3.7} = 20.8$, $P < 0.02$; Figure 6). However, when the very low-flow regression was rescaled to match the intermediate low-flow regression, a relatively steeper slope is apparent at very low flows (Figure 7A), indicating an incrementally greater effect of flow reduction at lower flows. Overall, a clear pattern emerges in predicted ecological response that broadly matches the expectations from hydraulic habitat modeling of a unimodal flow–ecology relationship, with a positive effect of increasing flow at low discharge transitioning to a negative effect at higher flows. Nevertheless, the variation in slopes within ecological contexts remains considerable (Figure 7A), highlighting the need to interpret any empirical thresholds with caution. Note that the file Flow–ecology_equations (see Supplementary material) provides a simplified spreadsheet for applying the generic equations to data-deficient systems. We recommend that any application of these generic regressions be associated with a flow metric of monthly or similar duration, as this was the median duration used in the underlying flow–ecology relationships.

Our empirical flow–ecology relationships provide a useful quantitative reference point for evaluating desktop flow criteria. For example, qualitative Tennant flow criteria are broadly consistent with the composite flow–ecology relationship (Figure 7B), although the empirically derived optimal flow of 57% MAD falls below the optimal flow range identified by Tennant (60–100% MAD), suggesting that Tennant criteria may somewhat overestimate optimal rearing flows. However, this inference should be tempered by the wide confidence intervals on the empirically derived optimum (36–96% MAD), which overlap with the Tennant optimal flow range. Tennant categories at lower flows are generally consistent with the empirical data, with the severe degradation category closely matching the steepest rate of decline in ecological response of the composite flow–ecology relationship, with a predicted average decline from 63% to 18% of maximum response between flows of 13% and 0% MAD (Figure 7B).

Despite an expectation that juvenile life stages should have lower optimal flows and therefore steeper flow–ecology relationships than adults (Figure 1A), slopes of normalized flow–ecology relationships were not significantly different among life stages ($F_{3,13} = 0.51$, $P < 0.68$). Similarly, there were no significant relationships between slope and the other study covariates, including stream size (absolute MAD in m^3/s; $F_{1,16} = 1.2$, $P < 0.29$), species ($F_{7,10} = 0.86$, $P < 0.55$), or duration of the flow metric ($F_{1,16} = 0.54$, $P < 0.55$). However, these results need to be tempered by the relatively low replication in normalized slopes ($n = 18$).

DISCUSSION

Our analysis shows strong evidence for a consistent response of salmonids to altered flows. This consistency was revealed, in part, by controlling for the effects of context dependence

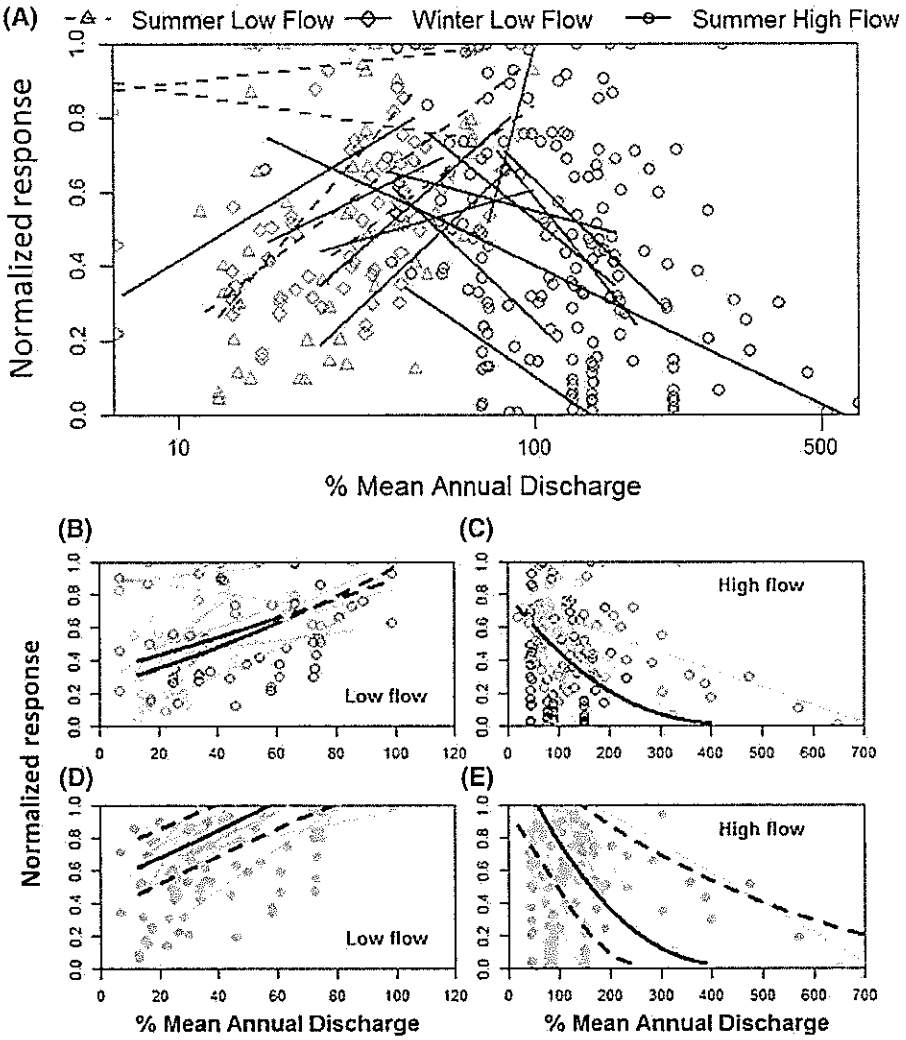

Figure 5. (A) Flow–ecology relationships normalized to a maximum of one for different ecological contexts (summer low flow, broken green lines; winter low flow, solid red lines; summer high flow, solid blue lines). (B) Average summer and winter low-flow relationship (solid black line) including all studies ($n = 11$, lower slope line) and only relationships with a positive slope ($n = 9$, higher slope line). The broken red lines represent inappropriate extrapolation beyond the optimal flow at 57% MAD. The fine gray lines and colored points represent different individual relationships. (C) Average summer high-flow relationship (solid black line). (D) Average low-flow relationship (solid black line) from panel B (all low-flow studies) standardized to a maximum of 1 at 56% MAD. The broken blue lines represent 95% confidence intervals. (E) Average high-flow relationship (solid black line) from panel C standardized to a maximum of 1 at 57% MAD. The broken blue lines represent 95% confidence intervals.

(e.g., low vs. high flows) on the slope of flow–ecology relationships. Failure to account for the hydroecological context may have contributed to the low power of earlier meta-analyses to detect a consistent signature of flow alteration on ecological response (e.g., Poff & Zimmerman, 2010). Normalizing ecological responses (i.e., the y-axis) to a common scale (0–1) also facilitated comparison among diverse response metrics, and normalization of flows (the x-axis) to MAD generated scale independence, resolving the disruptive effect of orders of magnitude differences in absolute discharge across streams. The successful application of these scaling and normalization approaches to salmonids suggests their useful application to resolving ambiguity in flow–ecology relationships among other taxonomic groups as well.

The overall shape of the salmonid flow–ecology relationship (transition from a positive to negative slope with increasing flow) is consistent with expectations from habitat simulation models—that is, a unimodal relationship between salmonid abundance and flow (e.g., Armstrong & Nislow, 2012; Jowett et al., 2008). This highlights the foundational importance of both theory and basic ecology in guiding the development and analysis of flow–ecology relationships, including the appropriate choice of covariates (e.g., flow regime) to define context dependence, as originally suggested by Poff et al. (2010). It also highlights the value of empirical flow–ecology relationships in confirming underlying theory and mechanism of flow effects. The expression of a unimodal curve is therefore not surprising; however, from an applied management perspective the goal

Table 2. Salmonid habitat capacity flow–ecology relationships (normalized to a maximum of 1 corresponding to maximum capacity) for discrete ranges of flow, expressed as a percentage of mean annual discharge (MAD). If reference data are available for the ecological response variable of interest for a particular stream (e.g., it is known that juvenile density is 2 fish/m^2 at 30% MAD), then *i*) the equation that covers the appropriate flow range is first identified (in this example, the first or second equations). The normalized value for the first equation is 0.76 at 30% MAD (refer to Figure 5A or the Supporting Information worksheet Flow–ecology_equations), and the first equation is then rescaled to the reference data by multiplying by 2 fish·m^{-2}·0.76^{-1} (i.e., setting maximum capacity at 57% MAD to 2.7 fish/m^2, assuming that the response to flows is linear). As another example, if the stream in question is completely data deficient but is assumed to have a maximum population size of 600 adults based on data from other similar streams, then the first three equations and the last equations would be multiplied by 600 to convert a maximum capacity of 1 to an ecological response of population size with a maximum of 600. To use the fourth equation that is standardized to a maximum of 3% MAD, the equation needs to be multiplied by the measured or estimated value of the ecological response at 3% MAD (which may be available for streams that experience very low flows) or rescaled as described above from any other value in the 0–13% MAD range. Please refer to the Excel spreadsheet Flow–ecology_equations in the Supplementary Material for a worked example.

Context	Range of flow application (%MAD)	Equation	*N*	Average MAD of streams (m^3/s)	Range of stream MAD (m^3/s)	Figure
Summer and winter low flows (all studies)	13–57%	$[(0.00681\cdot\%\text{MAD})+0.589]^{1.33}+0.03$	11	17.1	0.4–48	4C, 7
Summer and winter low flows (+'ve slope only)	13–57%	$[(0.00697\cdot\%\text{MAD})+0.587]^{1.82}+0.03$	9	20.8	0.4–48	4C, 7
Extreme low flows (standardized to 1)	0–13%	$\{[(0.105\cdot\%\text{MAD})+0.713]^{1.25}-0.06\}\cdot 0.257$	6	7.6	1.1–480	7
Extreme low flows (standardized to 3% MAD)	0–13%	$[(0.105\cdot\%\text{MAD})+0.713]^{1.25}-0.06$	6	7.6	1.1–480	5
Summer high flows	57–249%[a]	$[(-0.00247\cdot\%\text{MAD})+1.137]^{2.33}+0.01$	7	154	5.8–900	4E, 7

[a] 249% MAD is the average upper limit of flow data in the seven substituent flow studies used to generate the equation. Projected responses in excess of this flow should be done with caution.

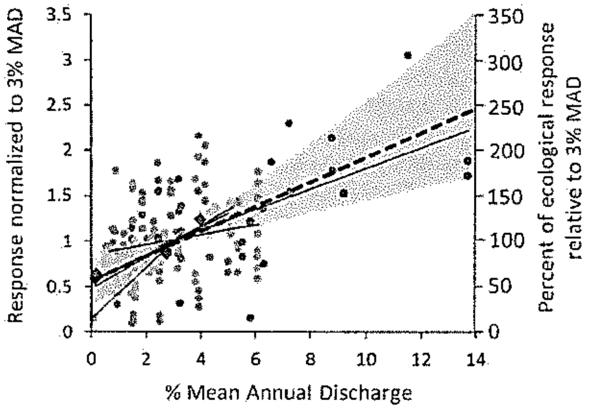

Figure 6. Ecological responses normalized to 3% mean annual discharge ($n = 6$) for very low-flow relationships (0–13%MAD).

is not merely to confirm the underlying ecological hypothesis (i.e., the shape of the flow–ecology curve), but to develop empirical relationships that can be directly used to predict the consequences of altered flows to guide management decisions.

However, the utility of general empirical relationships will ultimately depend on their uncertainty and scope of inference. The generic flow–ecology relationships that we derived here should reasonably predict the average response of a population of streams across a landscape, given the diversity of species and streams represented in the underlying data. However, confidence intervals on the regressions remain substantial, and extrapolation of the predicted responses to any specific stream needs to be done with caution or at least a solid appreciation of the inherent uncertainty driven by site-specific attributes. Refining empirical flow–ecology relationships to better capture the detailed ecological context associated with local variation in channel structure, fish community, and hydrology is an obvious need to improve empirical prediction of flow effects (Freeman et al., 2022; Göthe et al., 2019). Ecologists and managers know that channel size, gradient, confinement, and aggradation likely affect the strength of ecological responses to flow variation (Buchanan et al., 2017; Reid et al., 2020; Walker et al., 2020), but a lack of stream-specific data (other than MAD as a surrogate of channel size) precluded the inclusion of these covariates in our analysis. Even were these data available, it is unclear whether the analytic approach used here has sufficient power to detect these nuances. Determining the interactive effects of additional stressors (e.g., aggradation, loss of large wood) on ecological response to flow may be better suited for paired watershed experiments or targeted flow manipulations, where variation associated with extraneous factors can be better controlled. Ultimately, flow manipulations or thoughtfully designed regional studies that measure flow effects on salmonid abundance in contrasting channel types or flow regimes offer the best prospect for fully resolving habitat effects on instream flow requirements (e.g., Göthe et al., 2019).

Publication bias—that is, the greater likelihood that significant flow–ecology relationships will be reported and published—is a potential concern for our generic regressions. Publication bias is common in science, and excluding streams where flows minimally effect salmonid production could presumably lead to an overestimation of the average slope of flow–ecology relationships. The degree of publication bias in our data set is unclear, but studies with nonsignificant results are more likely to be rejected and less likely to be submitted to a journal (Thornton & Lee, 2000), potentially inflating the general strength of published fish–flow relationships. On the other hand, there may also be hidden biases that undermine

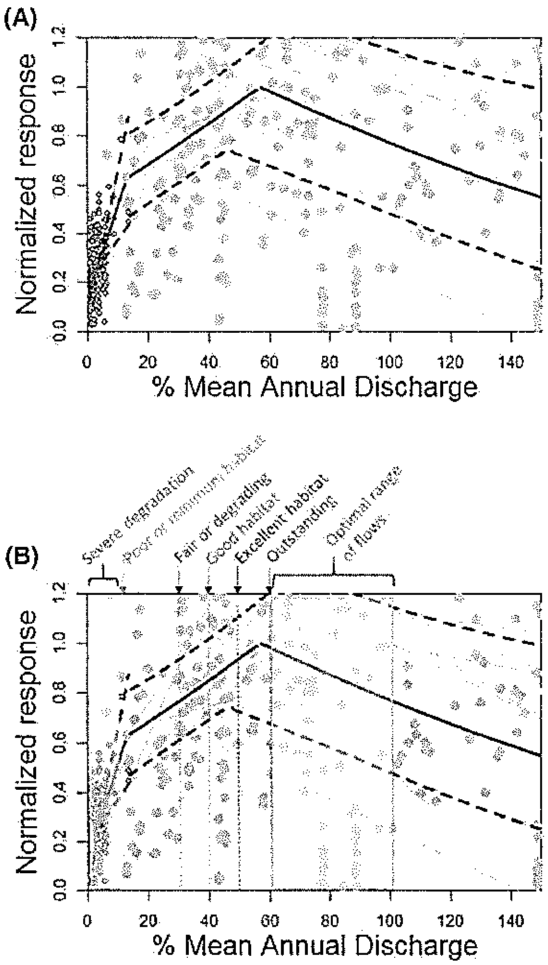

Figure 7. (A) Average normalized regressions of ecological responses plotted against mean annual discharge for very low-flow studies (red line on extreme left, $n = 6$), low-flow studies (central solid black line with positive slope, $n = 11$), and summer high-flow studies (solid black line on right with negative slope, $n = 7$). Broken lines represent 95% confidence intervals. Large gray circles and lines represent data and regression lines for individual low- and high-flow studies, small circles with a black outline represent data for the very low-flow studies illustrated in Figure 6 (regression lines hidden by the data points). See Table 2 for regression equations. (B) Superimposition of the Tennant flow categories on top of the composite salmonid flow–ecology regressions.

the ability to detect flow effects (e.g., poor study design and low power, often in unpublished studies), resulting in the opposite bias—that is, an underestimation of the generality of flow effects. For instance, when studies fail to detect a significant effect of flow, it may be due to the true absence of flow effects (i.e., fish abundance is limited by factors other than flow such as temperature, habitat bottlenecks, sediment inputs, marine survival, etc.) or because low replication or confounding factors reduce statistical power to detect a flow effect even when present (Bisson et al., 2024; Christie et al., 2020). The net outcome of contrasting publication and detection biases is unclear, but the strength and consistency of the signals that we observed and the breadth of studies included suggests that our results are fairly representative. Probably the best way to interpret and apply the insights from this meta-analysis is to recognize that the observed biological response to altered flows can be expected in any salmonid stream where flow is likely to be a limiting factor. Flow effects will be less likely to manifest in streams where fish abundance is known or strongly suspected to be limited by factors other than flow (e.g., fish passage barriers, pollution, predation, poor marine survival, etc.). It is also important to again emphasize that our results pertain primarily to average flows of monthly or longer duration rather than short-term disturbance flow events (i.e., spates and floods).

Our flow–ecology relationships provide an empirical basis for evaluating qualitative desktop tools that are widely used in data-deficient flow management contexts. For example, categorical Tennant instream flow guidelines are broadly consistent with empirical predictions, at least in the lower range of flows (Figure 7B), providing a partial validation of this widely used flow-setting approach. However, the recommended Tennant optimal flow range of 60–100% MAD exceeds the predicted optimum of 57% MAD from our empirical analysis. Although this apparent mismatch is worth noting, the upper confidence interval on the empirical optimum of 96% MAD falls within the Tennant optimal flow range, which is intended as a simple rule to capture wide variation among streams with a categorical guideline. Another commonly used desktop threshold for setting instream flows that can be referenced against our empirical regressions is 95% flow exceedance (Q95; Acreman et al., 2008). The value for Q95 for a representative set of 52 eastern Canadian streams averaged 5.8% MAD (Caissie et al., 2015), corresponding to 35% of optimal habitat capacity (Figure 7) and indicating that flow exceedance criteria in the lower range are not very protective of instream values (although this will depend strongly on regional hydrology and natural duration of low flows).

Ultimately, flow effects on adult population size and persistence are the most consequential ecological responses for management purposes. However, many of the ecological responses in our data set represent component parameters of population dynamics (e.g., growth or survival) rather than the population response itself, and this also has the potential to introduce bias (Minns et al., 2011). For example, Warkentin et al. (2022) showed that Chinook Salmon smolts per spawner (i.e., stock productivity at low spawner abundance) in the Nicola River, British Columbia, is below replacement in years with August flows that are less than 40% MAD; this indicates that the population will eventually go extinct if late summer rearing flows are consistently below a 40% MAD threshold. However, our simplified flow–ecology relationship using the same data (but expressed as a linear regression of normalized recruits vs. August flows) infers 50% of total adult recruitment at 40% MAD and a positive value for adult recruitment even at 20% MAD, suggesting substantial residual capacity even at these lower flows despite stock productivity being below replacement. This example illustrates how flow–ecology relationships fit to individual parameters like growth or survival, as analyzed in this study, may underrepresent the consequences of decreased vital rates for actual population persistence. Therefore, our generic regressions should be interpreted with caution and are not necessarily precautionary with respect to salmonid conservation—that is, interpreting a positive intercept for growth or survival as indicative of stock productivity above replacement may be misleading. Our combined analysis therefore likely underestimates the negative population-level consequences of very low flows. Similarly, a positive intercept may also occur as a partial artifact of fitting a linear relationship to a nonlinear function.

In the absence of local habitat information in data-deficient systems, the generic flow–ecology regressions presented here can reasonably be applied to predict flow effects (for an example, see the caption in Table 2). However, if local knowledge is available concerning habitat constraints, flow regime, or other conditions, then the generic relationships can be treated as a starting point for modification based on local knowledge (MacMillan & Marshall, 2006; MacPherson et al., 2020). For example, stream channels that are severely aggraded by coarse sediment inputs from poor forestry practices may experience considerable subsurface flow at low discharge, reducing the volume of available instream habitat at low flow relative to a nonaggraded channel (e.g., Reid et al., 2020); this would mean that the appropriate flow–ecology regression should have a reduced intercept (and potentially steeper slope) relative to the generic equations presented here (i.e., a severely aggraded stream would manifest lower habitat capacity at low flow than expected relative to the general population of streams). The effects of land use from oil and gas exploration can similarly exacerbate the negative effects of low flow on benthic fishes (Walker et al., 2020). Temperature effects on salmonid growth are also known to have a strong interaction with flow, with thermally marginal transitional coolwater streams being especially sensitive to warming at reduced flows (Korman et al., 2023; McKenna et al., 2018; Zorn et al., 2012; lower intercept, steeper slope). In general, if there is strong inference that populations are severely flow limited, it may be reasonable to force the intercept of the flow–ecology relationship through zero. In contrast, if a stream is known to be extremely cold to the extent that temperature is limiting salmonid growth and production, then reduced flows could have less negative effect than expected if they result in warmer stream temperatures (Donadi et al., 2021; Tschaplinski & Pike, 2017), resulting in a higher intercept and lower slope. Although deviations from the generic flow–ecology equations presented here can be posited based on local data, modifications should be clearly rationalized and documented in flow assessments. Ultimately, the goal of adaptive flow management and regional monitoring is to measure these deviations to allow a transition from the realm of qualitative inference to quantitative prediction (Webb et al., 2017). Caveats are also warranted when interpreting any break points that might be implicit in the composite flow–ecology regressions in Figure 7. Although nonlinearities in population responses to reduced flows can be expected (e.g., when recruitment falls below replacement), any apparent break point at 13% MAD should be understood to be a consequence of fitting linear segments to nonlinear responses. Treating slope and intercepts as continuous variables results in the expected smooth univariate flow–ecology relationship (Figure S4C).

Ultimately, uncertainty in instream flow needs for fish undermines efforts to ensure adequate flows because water users are reluctant to bear lost opportunity costs when the benefits of flow retention are unclear (Bunn & Arthington, 2002; Poff et al., 2003; Rosenfeld & Ptolemy, 2017). Reducing uncertainty by investment in programs to develop regional flow–ecology relationships (e.g., Buchanan et al., 2017; McKenna et al., 2018) therefore needs to be a priority for natural resource management agencies (Arthington et al., 2024; Castleberry et al., 1996; Stoffels et al., 2018). In the interim, qualitative desktop methods like Tennant flow guidelines or the empirical flow–ecology relationships presented here can provide a credible foundation for environmental flow policy and decision making. The continuum of approaches ranging from qualitative guidance like Tennant rules, to generic empirical flow–ecology regressions like those presented here, to detailed regional or stream-specific relationships generates the information hierarchy that is needed to protect instream values (Opperman et al., 2018). The contribution of each of these approaches to flow decisions will ultimately depend on the scope of the flow assessment and where the responsible management agency is situated on the data-deficient to data-rich information spectrum constraining regional flow management.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

Data used in this study are available on Figshare (https://doi.org/10.6084/m9.figshare.25962184) and as Supplementary Material to this article.

Supplementary Material includes the original data set and supplementary analyses and figures.

ETHICS STATEMENT

No ethical guidelines were applicable to this study.

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CONFLICTS OF INTEREST

None declared.

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Conceptualization: J.S.R. Developing methods: D.E., J.S.R. Data analysis: J.S.R., D.E. Preparation of figures and tables: J.S.R., D.E. Conducting the research, data interpretation, writing: J.S.R., D.E.

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APPENDIX: STUDIES USED IN THE META-ANALYSIS

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