Colorado State University

Flow-ecology relationships for the watershed flow evaluation tool

A project funded by the Colorado Water Conservation Board

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Contents

1. Introduction

Background

The Colorado Water Conservation Board is assisting the Interbasin Compact Roundtables with their NCNA (Non-Consumptive Needs Assessments). The NCNA will (1) identify priority areas and reaches for environmental and recreational attributes, and (2) based on Roundtable direction and needs, identify the quantities of seasonal flows necessary to maintain priority areas and reaches. A component of goal 2 is the Watershed Flow Evaluation Tool (WFET), a coarse screening tool that can be applied by stakeholders in selected watersheds to assess the potential status of biological resources under existing hydrologic conditions. WFET pilot studies are underway for the Roaring Fork River and Fountain Creek (Colorado Springs) watersheds. After the pilot study is complete, results will be shared with the Basin Roundtables who may then decide to apply the tool in their basin. The goal of this report is to develop relationships (quantitative where possible) between measures of environmental condition and levels of stream flow for Colorado. These relationships will support the development of the WFET.

ELOHA

The WFET is a specific application under the broader framework known as The Ecological Limits of Hydrologic Alteration (ELOHA). The hallmark of this new framework is that it offers a flexible, scientifically defensible approach for broadly assessing environmental flow needs when in-depth studies cannot be performed for all streams or rivers in a region (Arthington et al. 2006; Poff et al. *In Press*). ELOHA builds upon the wealth of knowledge gained from decades of river-specific studies, and applies that knowledge to geographic areas as large as a state, province, nation, or large river basin (see the TNC Factsheet for more information, TNC 2008).

Determining Non-Consumptive Flow Needs

This report is intended to assist the assessment of the potential status of aquatic, riparian and recreational resources for Colorado streams, and we are concerned with the flow-dependence of ecosystems. Flow is sometimes called a master variable because it limits the distribution and abundance of riverine species and influences other important environmental features such as water quality (Figure 1). It is important to understand the wide range of direct and indirect effects of flow on river ecosystems. The area of stream that is wet limits how many fish can survive day-to-day. This is an example of the direct importance of flow, but indirect effects may be less intuitive. Floods mobilize sand and cobbles and shape the stream-bed, and this process indirectly determines the area of pool and riffle habitat. Fast-water animals specifically require riffle habitat and fish need pools that are deep enough to avoid freezing solid in winter. Animals show an immediate response to drying or freezing, but it may take years for stream ecosystems to respond to loss of channel maintenance flows. For this reason it is easy to overlook the importance of flow beyond basic life support. Flow does not act alone in determining the types of animals and plants living in a stream. For example, steep, mountainous streams are cooler than plains rivers, and will support different communities because of these differences alone. The effects of flow change in Colorado rivers therefore need to be considered within the context of other key environmental variables, such as water temperature and channel geomorphology (shape).

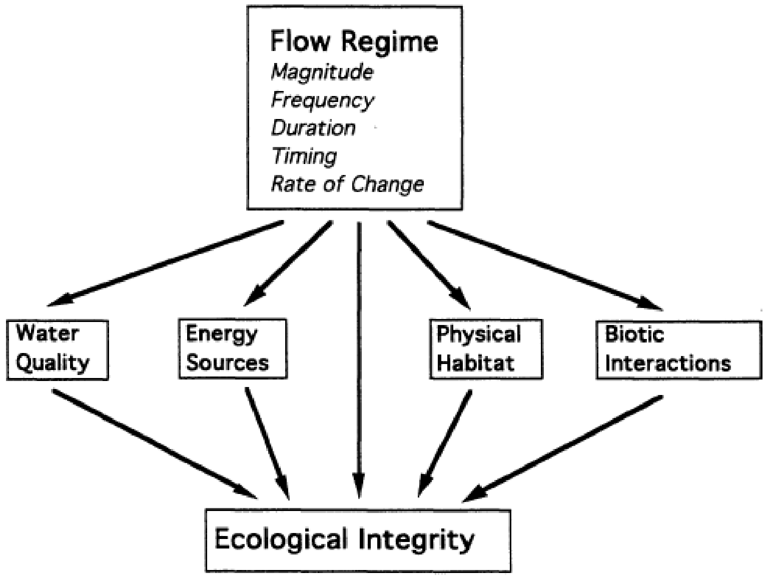


Figure 1 The flow regime, and its components, are of central importance in sustaining the ecological integrity of rivers (Poff et al. 1997).

Producing relationships that are specific to a stream type and biological community, as recommended by Arthington et al. (2006), specifically incorporates key environmental variables and therefore improves the precision of relationships with flow. Major river types in Colorado include the Rocky Mountains, Western Interior and Great Plains (see Methods section). Stream communities can be broadly classed as riparian vegetation, fish, invertebrates and so on. Each of these stream communities is sensitive to particular flow parameters such as the size of floods or the duration of extreme low flows (Richter et al. 1996). The number of combinations of stream type, community and flow parameter would be unwieldy for Colorado. We have focussed on specific combinations that represent an important component of ecosystem function, and for which data exist to provide a basis for flow-ecology relationships (published data sources). Relationships with flow are detailed in this report for riparian vegetation, stream invertebrates, warm-water fish, trout and recreation. Most of these attributes featured among valued non-consumptive uses identified by roundtable groups, with the exception of invertebrates. They were incorporated in this assessment because fish and birds depend on invertebrates for food, directly or indirectly (Allan 2007; Binns and Eiserman 1979; Jowett 1992).

Here, we describe the response of stream communities to flow change to provide a basis for analysis of non-consumptive flow needs by roundtable groups. This report provides information to answer the question: for a given change in flow, what amount of stream community response can be expected? Deciding what is an acceptable level of change, or risk of change, is a social process that can be informed by (not necessarily resolved by) the scientific information that we seek to gather (Poff et al. *In Press*). This document will enable informed decision-making about the impacts of flow alteration on non-consumptive attributes. Applied at a broad level, it is hoped this tool will aid in the identification of stream segments or subwatersheds where aquatic and riparian resources are at risk due to high water demand and, further, distinguish which non-consumptive users of the water are most at risk (e.g. cottonwoods versus trout). One application of this tool would be to identify places where more detailed site-specific investigations are needed.

2. Methods

Information on responses to flow change was sourced from a range of scientific literature (journal articles, technical reports and theses). The database of Poff and Zimmerman (*In Press*) was used as a starting point, with additional publications sought to improve coverage of Colorado stream types. Equivalent stream types from neighboring states were incorporated to bolster relationships. Literature searches were based on keywords, cross-references and scanning the publications of leading authors in each field. Discussions with relevant experts provided additional information sources and avenues of investigation. An expert-panel was assembled to provide comment on trout of the Rocky Mountains and fish communities of the Great Plains (see Acknowledgements section for participants). We did not seek endorsement or consensus from the panel, though major revisions of the draft were made to incorporate more relevant research and a broader understanding of critical issues.

Location data were extracted for most sources (Latitude and Longitude). Site descriptions were often limited but adequate for identifying the state, river system and geomorphic setting. Streams were nominally classified as one of three broad types; Rocky Mountains, Western Interior and Great Plains. Site descriptions were helpful, as was aerial photography from Google Earth ®.

Stream Types

Relationships of stream communities were investigated for individual stream types to increase the precision of relationships. Colorado was divided into three major stream types: Rocky Mountains, Interior Western and Great Plains (after Graf 2006 and Fausch and Bestgen 1997).

Great Plains rivers flow east from the Rocky Mountains, crossing the semi-arid plains. Snowmelt is a shaping feature of the natural hydrograph for mainstem rivers that have Rocky Mountain headwaters, such as the South Platte and Arkansas Rivers (Fausch and Bestgen 1997). Spring rain and summer convective-storms produce high flows (and occasional intense flood events) for all waterways of the Great Plains, with marked inter-year variability. Graf (2006) reported more variable flow regimes for Great Plains rivers compared to Interior Western rivers. Baseflows in tributary streams that originate on the plains are dependent on groundwater, which sustain perennial flow in some tributaries (e.g. historically for the Arikaree River). Channels are typically wide sandy beds (in natural settings), sometimes forming rock canyons and arroyos (incised earth channels). Historically, riparian trees may have been rare or cyclical features of those streams that lacked stable baseflows (Fausch and Bestgen 1997). The wide and sandy braided-channels of Great Plains rivers have narrowed to single thread channels, with riparian vegetation encroachment following reduced snowmelt flows from regulation (Johnson 1994).Rocky Mountain streams have a strong snowmelt signature, clear waters and generally coarse stony substrates. Summer temperatures are relatively cool and stream gradients are steeper than both Interior Western and Great Plains streams. Headwater streams in the western half of Colorado are predominantly Rocky Mountain streams, with example rivers including the Roaring Fork, Cache Le Poudre (above Fort Collins), Big Thompson and Fountain Creek headwaters.

Interior Western streams are characterized (in natural settings) by warm temperatures in summer, high turbidity, and a geomorphological setting that varies from canyons to alluvial floodplains. A degree of snowmelt-runoff pulses through Interior Western rivers (often sourced from Rocky Mountain headwaters), with increasing contributions from arid, highly-erodible landscapes further downstream. Example rivers include the non-headwater sections of the Colorado, Gunnison and Yampa.

Defining the boundaries between the above stream types is outside the scope of this report. For terrestrial systems, it is sometimes adequate to draw lines on maps to delineate ecosystem classes. Rivers are more accurately viewed as a product of the entire watershed, and hence they make gradual transitions with inflows from different land systems and changing geomorphic settings (Snelder et al. 2005). As an example, Fausch and Bestgen (1997) describe a transition-zone for rivers flowing from the Rocky Mountains out onto the Great Plains. Along the front-range, these rivers and streams feature cool temperatures, cobble substrates and single-thread channels of moderate gradient that are shaded by riparian trees. Sections of Fountain Creek presumably fall into this category. A similar transition is expected between the Rocky Mountains and Interior Western area.

Metadata

The literature review was extensive, covering a broad field of research. Some disciplines have received more attention from researchers, and Table 1 provides a breakdown of studies by community and stream type. These numbers represent studies relevant to flow change, though not all were ideal for deriving flow-ecology relationships (see Results section). Only 34 studies were actually undertaken in Colorado. The remainder (from Wyoming, Utah, Kansas, etc.) represented equivalent stream types and were critical in achieving adequate sample sizes.

Some of the more intensively studied areas include riparian vegetation and fish of Interior Western rivers. More intensive research on the Green, Yampa and Colorado Rivers encompass much of this work. Riparian vegetation is also the focus of many studies on Great Plains streams, together with fish. Studies of Rocky Mountain streams more often focus on invertebrates and fish.

Table 1 Number of studies contributing to this report, broken down by stream type and community. The "other" category includes studies from non-Colorado stream types and other communities. This report focussed on areas highlighted in bold.

	Interior Western	Rocky Mountains	Great Plains	Total
Fish	**19**	**18**	**15**	50
Riparian vegetation	**20**	1	**8**	28
Invertebrates	9	**9**		18
Vertebrates (birds, beaver)	4			4
Terr. Invertebrates	2		1	3
Algae	2			2
Total	56	25	24	105
Other				44

Data Analysis

Within the confines of available data formats, some general guidelines were followed in determining what should represent an individual response (i.e. data points for flow-response plots). For example, sites were used as individual data points for diverse invertebrate communities, with community information summarized using abundance and diversity metrics. The response of less diverse communities was sometimes represented using individual species as data points (e.g. biomass of Colorado pikeminnow).

Ecological responses were limited to species that are indigenous to the area of study, so excluding the response of potential pest species (e.g., tamarix). Combining the two groups in the same plot would complicate interpretation of the output in terms of assessing responses of valued native species or community types (e.g., cottonwood). Trout were an exception to this rule. Introduced species (brown, rainbow and brook trout) were included in the response analysis because of their recreational value.

The flow parameters used by researchers were not consistent across the literature. Our investigations focused on the effects of peak flow and low flows. Duration, magnitude and timing were occasionally reported in the source literature but not often enough to derive relationships. We attempted to standardize peak flow to 24-hour average annual peak flow, helped by the consistent use of this parameter in many studies. Likewise, estimates of low flow were typically standardized to 24-hour average annual low flow (this was sometimes limited to the summer/autumn period). Dividing flow by watershed area or mean annual flow to produce a specific discharge was attempted where percent flow alteration (relative to a pre-management baseline) was not used. Producing relationships both derived from and applied to different sized rivers can benefit from standardization by some correlate of channel size (mean annual flow or, failing that, watershed area). Although attempted for low flows, only relationships with peak flow benefited from such standardization.

By comparing measured ecosystem parameters across a range of flow conditions (varying levels of modification), emerging patterns provide a basis for quantifying ecosystem response (Figure 2). Analysis methods were tailored to suit the available data, and these are described in the results for each community. The mechanisms by which flow alteration affect stream ecosystems are complex, so a simple response to flow (1-dimensional) was not anticipated. A community could be limited by the chosen flow-parameter (e.g. peak-flow), but other parameters (sometimes unmeasured) often constrain the ecosystem and limit its response to flow. For example, cutthroat trout may reach higher biomass in deeper channels, but if introduced competitors (brook trout) are present then the trout population will be small regardless of depth (Dunham et al. 2002). Using quantile regression to define the upper bound is therefore expected to better represent the potential response to the chosen flow parameter (see Cade and Noon 2003). This also expresses complex relationships in an easily digestible form for end-user application, as compared to multi-dimensional models.

Quantile regression was used to identify these upper bounds, providing a coarse filter to isolate the potential response to each flow parameter (using Blossom statistical software, Cade and Richards 2007). This method minimizes the sum of absolute deviations (least absolute deviation), which are asymmetrically weighted by the quantile (e.g. 90%) for positive residuals and one minus the quantile for negative residuals (e.g. 1-0.9=0.1). Using absolute deviations (cf. squared deviations for conventional regression) reduces the effect of outliers. In most cases, 90% quantiles were judged as representing the upper-bound response adequately. Transformations were applied to the data, as necessary, before carrying out linear quantile regression.

The significance of the relationships was tested (null hypothesis: slope =0) using a quantile rank score test to minimize assumptions regarding error distributions (cf. higher power parametric alternatives). The rank score test provides P-values that are calculated from the sign of the residuals (+ve or –ve), not their magnitude. The permutation version uses an F statistic with its sampling distribution approximated by permutation (Cade et al. 2006), with 1000 permutations used here. In cases where both flow and the response parameter were quantified as a percent-change, relative to some reference condition, the equation intercept was assumed to be zero (where zero must be the reference condition for each data point).

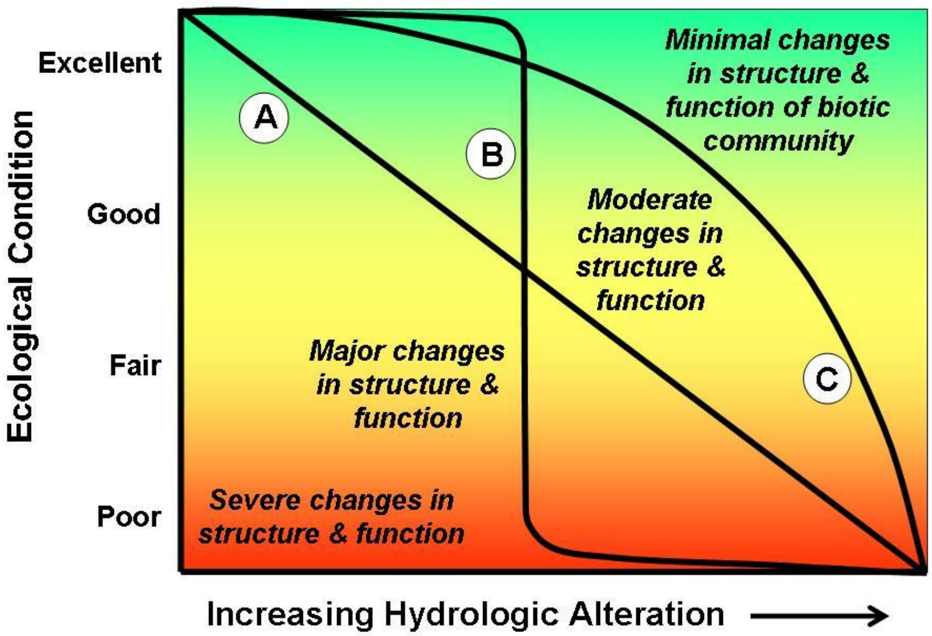


Figure 2 Three of several possible forms of flow alteration-ecological response relationships: linear (A), threshold (B), and curvilinear (C). The form of the curve depends on the specific ecological and hydrological variables analyzed. (Adapted from Davies and Jackson 2006).

3. Results

Riparian Vegetation

The response of riparian vegetation to changes in peak flow could provide a basis for generalized flow needs (Figure 3). Interior Western rivers (black dots, Figure 3) are consistent with the bounded response, but depend on riparian data from other river types (Great Plains or non-Colorado) to define the limits of the response over a wider spectrum of alteration. Different types of vegetation display a varied response to reduced disturbance by peak flows. For example, wetland plants can increase under stable flow conditions without periodic floods (Merritt and Cooper 2000), providing a numerically positive response to reduced peak flows. Conversely, cottonwood numbers respond negatively to a lack of flood recruitment events (Lytle and Merritt 2004; Richter and Richter 2000). Combined, the positive and negative numerical responses to flow alteration signify a shift in community composition from the natural riparian forest, and these can be plotted as an absolute (positive) percent change (Figure 3). The absolute response is therefore a coarse representation of the complex effects of flow change. Not all species and populations are expected to be equally sensitive to flow change, so the 90% bound (quantile regression line) provides a delineation of those species that are vulnerable. The 90% quantile line approaches a 1:1 relationship for the response of riparian vegetation to peak flow alteration. This describes, for example, that a 50% change in peak flow could produce up to a 60% change in riparian vegetation (with 10% probability of greater effects). No Rocky Mountain rivers were included in the dataset, but they are expected to show a similar response. For example, willow establishment responded positively to peak flow magnitude (> 2-year return period flow) for Rocky Mountain streams with natural flow regimes (Cooper et al. 2006).

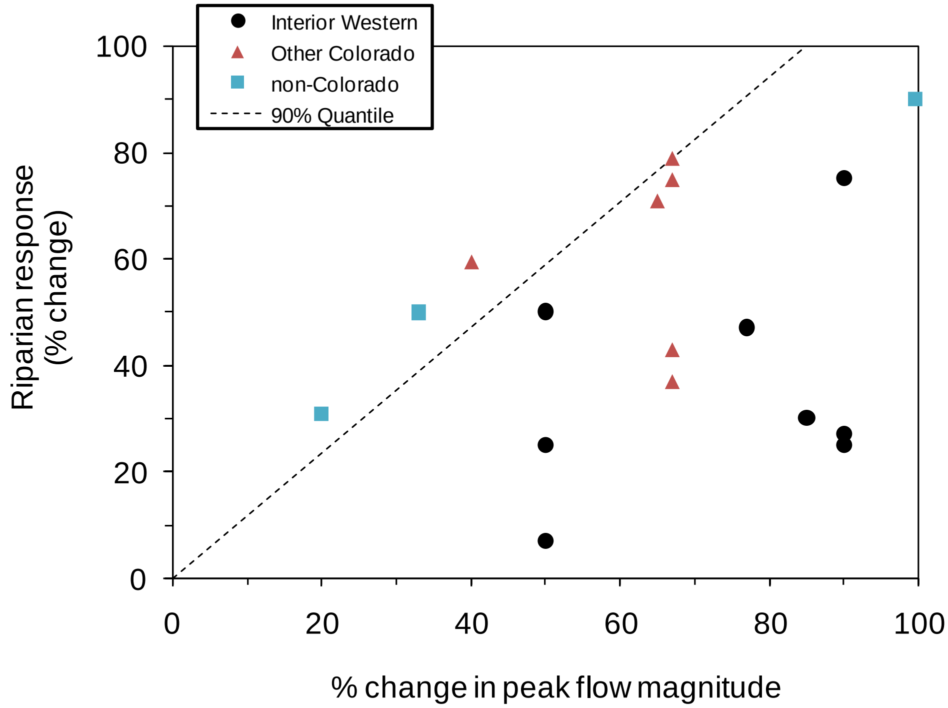
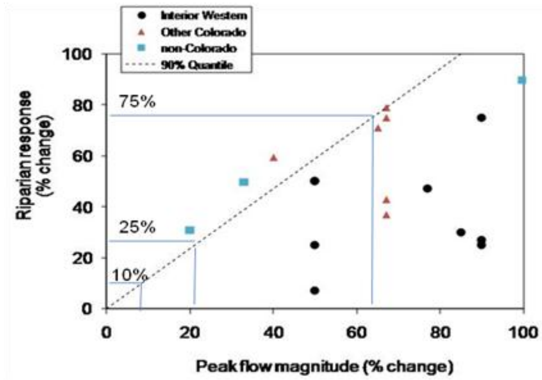


Figure 3 The response of riparian vegetation to change in peak flow. Riparian response is the percent change in riparian metrics relative to a reference condition. Percent change in peak flow is also relative to a reference condition (typically a reduction in snowmelt peak). The response for Interior Western rivers is reinforced by a similar response from riparian communities elsewhere. Quantile regression provides a 90% bound on the response (Y = 1.18 * X; forced zero intercept to reflect no riparian response to zero change in flow).

The relationship portrayed in Figure 3 indicates that the greater the change in peak flow, the greater the risk of a change in riparian vegetation (deviation from reference condition). To minimize the risk of a change in riparian vegetation, end-users might decide a small change in riparian vegetation is acceptable (e.g. 10%), and then use Table 2 to determine the corresponding change in peak-flow (8% in this case). Likewise if the acceptable level of riparian change is 50%, then the corresponding flow change is 42% (Table 2). This allows the end user to decide the level of risk that is acceptable. The riparian response values in Table 2 are based on the upper-bound response (90% quantile) to represent those populations that are susceptible to a change in peak flow. This minimizes the number of populations that will show a greater response (100% - 90% = 10% of populations, in this case).

Table 2 The change in peak-flow expected to produce five levels of riparian response (% change). This is calculated, based on data presented in Figure 3, for a 90% quantile (upper bound). The plot to the right shows the derivation of three points from the quantile regression, as an example.

Riparian Response	Peak-flow change
10%	8%
25%	21%
50%	42%
75%	64%
90%	76%



In addition to peak flow magnitude, the timing of peak flows and rates of recession are also important for maintaining riparian forests, as this determines seedling mortality (Cooper et al. 1999). Specifying hydrographs to this level of detail is beyond the scope of this document and should instead be incorporated into site-specific studies where riparian vegetation is a critical issue.

Riparian vegetation responds to peak flows (via sediment supply, disturbance, seedling establishment, etc.), but can also respond to low flow. Seedling reliance on surface water continues after seasonal peak flows have receded (Cooper et al. 1999), but extended periods of zero flow are required (>24% of the time) before changes in riparian vegetation are seen (Lite and Stromberg 2005). As flows approach zero, groundwater levels will determine water availability for riparian vegetation. This is perhaps why the majority of studies focus on response to groundwater levels, rather than river flow (Cooper et al. 2003; Scott et al. 1999; Stromberg 2001).

Significant changes in riparian vegetation are often observed where annual low-flows have actually increased due to dam operations (Merritt and Cooper 2000; Shafroth et al. 2002). The elevated low flows may increase survival of some species; however, coincident decreases in peak flow and sediment supply make it difficult to quantify what appears to be a secondary response to low flow. The importance of groundwater levels and peak flows for sustaining riparian vegetation is well established. Riparian response to change in low flow may not be a critical issue, compared to fish and invertebrate response, and so is not quantified here.

Stream Invertebrates – Rocky Mountains

Most of the invertebrate data are from Rocky Mountain streams with flow diversion structures. Here we have the luxury of a large number of diversion sites, evaluated using standard methods, with few confounding effects. By drawing data from two studies meeting these criteria (Albano 2006; McCarthy 2008), more subtle responses can be distinguished. There is a range of metrics available for summarizing invertebrate data, many of which represent the pollution tolerance of sensitive species in the community. However, when evaluating community response to flow change, the diversity and abundance of invertebrates that require riffle or fast water habitat (so-called obligate rheophiles, as designated by Poff et al. 2006) are more appropriate indicators. For Rocky Mountain streams, this group of invertebrates responded to large reductions in flow (Figure 4). This is more apparent from the McCarthy (2008) data, which focussed on a uniform group of small subalpine streams in the Fraser River basin (elevation 7,500 to 13,000 feet).

Diversity of rheophiles may show a threshold response to flow quantity (i.e. response to a specific flow rate, rather than a percent change in flow), with declining diversity below about 0.2 cfs (Figure 5). The potential density of rheophile species increased with flow (Figure 6), particularly for flows less than 2 cfs. In terms of the amount of food available to predators, such as fish and birds, density of invertebrates (number per unit area) is important, but the total number of invertebrates can limit the number of predators supported by a stream. This means a larger area of stream with the same density of invertebrates can potentially support more trout (total number of invertebrates = density x area). The area of wetted stream increases with flow beyond the thresholds mentioned above, and site specific studies could be used to describe this relationship (e.g. wetted perimeter or PHABSIM). Alternatively, the low-flow categories from Binns and Eiserman (1979) were partly based on habitat area measures and hence may represent the response of total invertebrate production to flow, if greater than 2 cfs (see Table 3 for categories).

Alteration of peak flows can affect invertebrates because flood disturbance is important in limiting algal growth (a major food source for scrapers) and maintaining habitat. Peak flows also represent a direct disturbance to invertebrates. Consequently, high disturbance streams have contrasting biota to low disturbance streams (Lytle and Poff 2004). The dataset used to evaluate the effects of baseflow (from McCarthy 2008 and Albano 2006) was not suitable for reviewing the effects of peak-flow alteration because flow was measured at the time of sampling only and not during peak flow.

Resorting to the larger Colorado dataset necessitates a broader view of the invertebrate community than just the obligate rheophiles, and consequently a more variable response is seen (Figure 7). The large response of some invertebrate metrics to reduced flood disturbance produced a strongly skewed dataset. This may be more pronounced for Interior Western rivers (e.g. density increased by an order of magnitude below Flaming Gorge Dam, Vinson 2001), where natural extremes in temperature and turbidity are potentially cut by flow regulation. Because of the skewed response, a 75% quantile was considered a more comparable indicator of response across Rocky Mountain and Interior Western streams, compared to the 90% quantile used for other datasets (Figure 7).

Timing of peak flows and water temperature are important seasonal triggers for the life cycles of many invertebrates (Lytle and Poff 2004), but are not dealt with in this report.

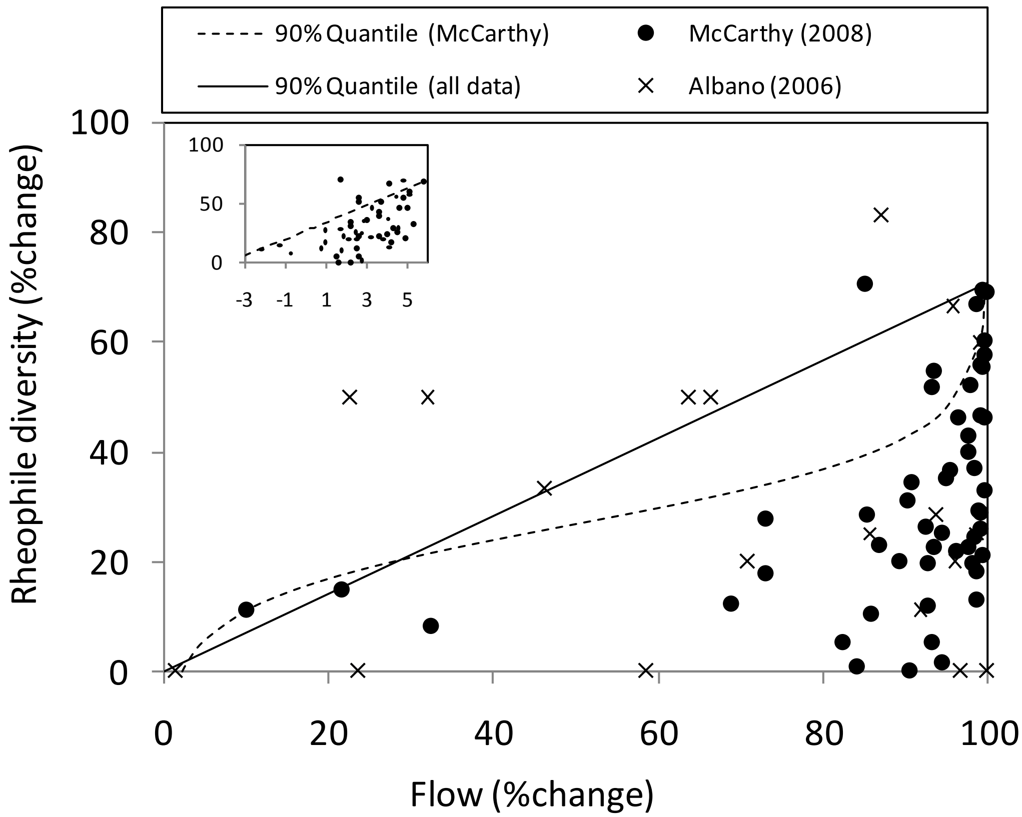


Figure 4 Response of Rocky Mountain invertebrates to change in flow (flow reduction downstream of the diversion on the day of sampling). Invertebrate response is measured as % change of rheophiles (fast-water species), compared to reference sites upstream of the diversion. Data from two literature sources are presented (Albano 2006; McCarthy 2008). Upper bounds for the data are represented as 90% quantiles. The quantile for the McCarthy (2008) data was calculated after transformation (using logit for %flow reduction) to better represent the skewed response (response function; Y = 7.2 * Ln(X/(100-X)) + 26.77, P-value = 0.0839). The inset shows the McCarthy data plotted on a logit scale. Three data points are not shown to clarify the core data pattern (Albano study x,y; 63,300; 91, 400; McCarthy 111,14).

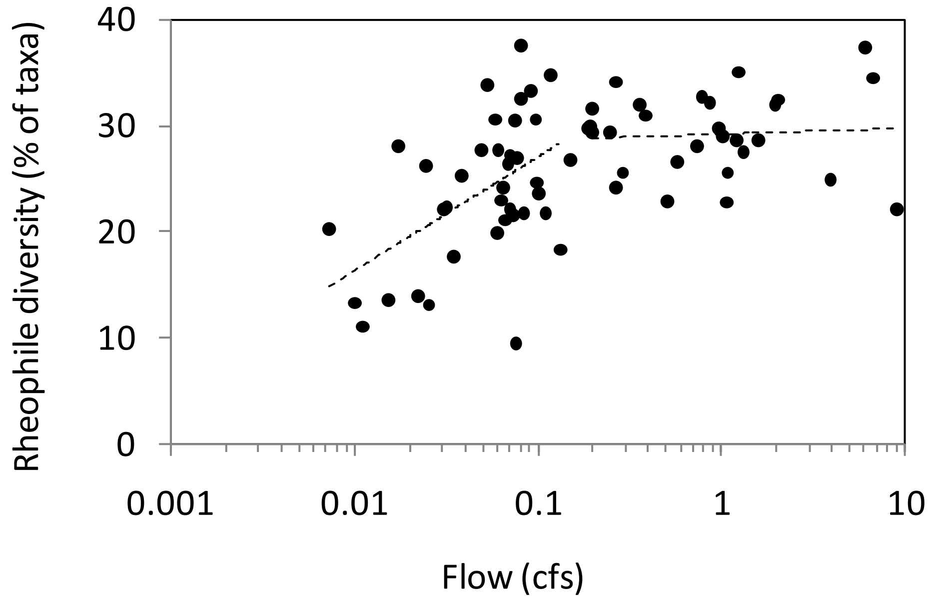


Figure 5 Response of rheophile (fast water) invertebrates to flow (log scale). The number of rheophile species is expressed as a percentage of total number of taxa per sample. Regression lines (log) are fitted to two separate bins of data to illustrate an apparent threshold response. Data are from McCarthy 2008).

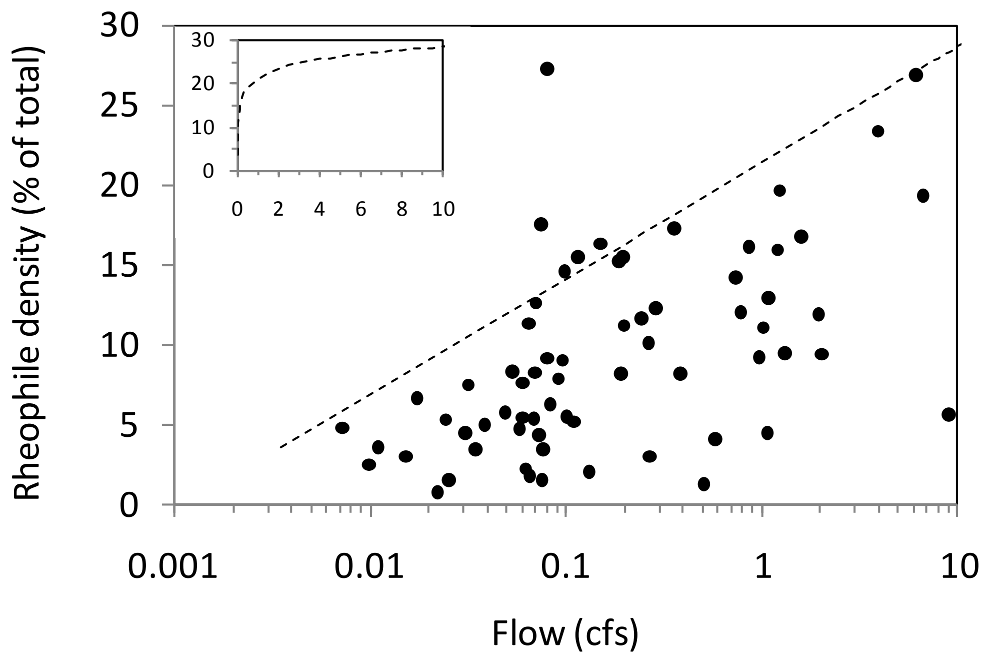


Figure 6 Response of rheophile (fast water) invertebrates to flow (log scale). The density of rheophile taxa are expressed as a percentage of total sample density. Data are from McCarthy 2008). The upper bound for the data is represented as a 90% quantile ($Y = 7.24 * Log_{10}X + 21.4$; $p = 0.001$), and the inset plot shows this on a normal (arithmetic) scale.

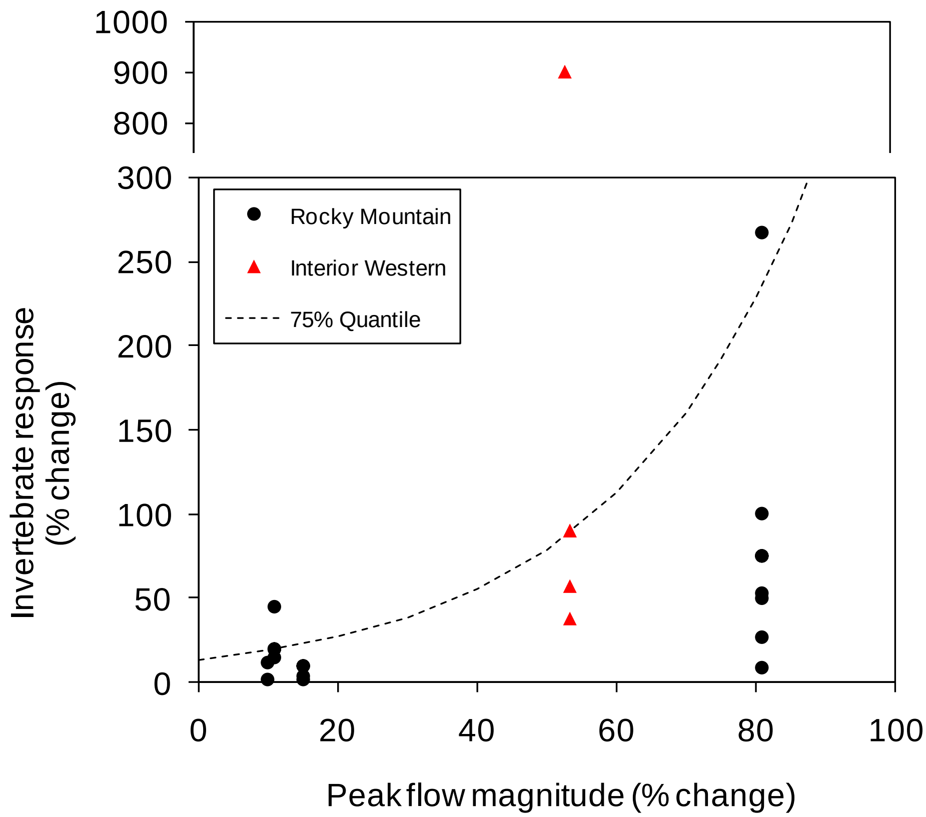


Figure 7 Response of stream invertebrates to a reduction in peak flow. The upper bound for all data is represented as a 75% quantile ($Log_{10}Y = 0.015 * X + 1.13$; $P = 0.123$). Note the discontinuous y-axis (higher scale > 300%).

Cold-water Salmonids – Rocky Mountain area

Several salmonid species are found in cold water streams and rivers of Colorado, including native cutthroat trout and three introduced species (brown trout, rainbow trout and brook trout). The introduced species represent an important recreational fishery in Colorado. Trout distributions can be explained in terms of water temperature (both upper and lower altitude limits) and interactions among species (competitive, predation). Requirements for cool temperatures create a lower altitudinal limit that largely confine trout fisheries to the Rocky Mountain area. But dams that release cool water to otherwise warm water rivers (Interior Western), sustain excellent fisheries (Merwin 2008).

An inability to reproduce successfully during short summers is expected to set the upper altitudinal limit for trout (Coleman and Fausch 2007). The order of cold-tolerance (stenothermy, from cold to warm) is cutthroat, brook, rainbow and brown trout (Raleigh et al. 1986). The order of competitive advantage is the reverse, which often excludes cutthroat and brook trout from lower elevation waters where temperatures are otherwise tolerable (McHugh and Budy 2005).

Within the confines of their temperature range and competitive exclusions, the abundance of salmonids is potentially limited by flood disturbance during critical life stages. In Colorado streams, this bottleneck is the magnitude of snowmelt coinciding with fry emergence (Fausch et al. 2001; Latterell et al. 1998; Nehring and Anderson 1993). The timing of fry emergence varies from year to year, between species and with altitude. But generally speaking, brown trout fry emerge during May and June for Colorado, with rainbow trout fry emerging in late June and July (Nehring and Anderson 1993). With snowmelt runoff often peaking in June for Rocky Mountain streams, the potential for snowmelt to overlap with fry emergence is high for brown and rainbow trout. Brook trout emerge earlier (fall spawners), but they are still vulnerable to flow disturbance (Latterell et al. 1998). Cutthroat trout fry emerge later in summer, and this native species appears better adapted for avoiding disturbance from snowmelt runoff.

Several authors have documented the negative correlation between peak flow magnitude and recruitment success in trout (Fausch et al. 2001; Latterell et al. 1998; Nehring and Anderson 1993). Data was sourced from technical reports by Nehring and Anderson (Nehring 1986; Nehring and Anderson 1985) to generate quantitative relationships for brown and rainbow trout (Figure 8). To describe relationships across multiple sites, individual site-year values for density of juvenile trout (number of age 1+ trout per unit area) were standardized by the maximum value for that site, and peak flow (monthly average) was standardized by the mean annual flow. Rivers monitored include the Arkansas, Gunnison, Rio Grande, South Platte and Cache la Poudre (mean annual flow ranged from 170 to 1400 cfs).

Density of juvenile brown trout declined steeply with peak-flow (Figure 8). The lower bound (10% quantile) gave a better response to peak flow than the upper bound (P-value 0.016 and 0.094 respectively). This suggests flow disturbance has a more consistent effect on trout recruitment in otherwise bad years (i.e. when unmeasured parameters are unfavourable). In an otherwise good year for recruitment, peak monthly flows of up to 4 times mean annual flow can still produce high recruitment (from the upper bound, Figure 8). In an otherwise bad year, 2 times mean annual flow will be sufficient to limit recruitment to less than a third of maximum (from the lower bound response). There is a greater risk of recruitment failure if the average flow for a month exceeds 6 times mean annual flow (Figure 8).

June was typically the month with the highest average flow (peak snow melt), but July flows produced a better correlation with juvenile brown trout (R^2 values for April to September respectively: 0.107, 0.220, 0.342, 0.547, 0.307, 0.451). It is not clear whether this reflects a higher susceptibility of juvenile trout to disturbance in July, or perhaps July flow better captures the duration of disturbance acting on that year class (i.e. high snow melt extending well into July). Similar conclusions regarding recruitment limitation would probably be drawn, whether predictions are based on peak flow (monthly average) or July flow, because of the similar form of the relationship (compare Figure 8 and 9).

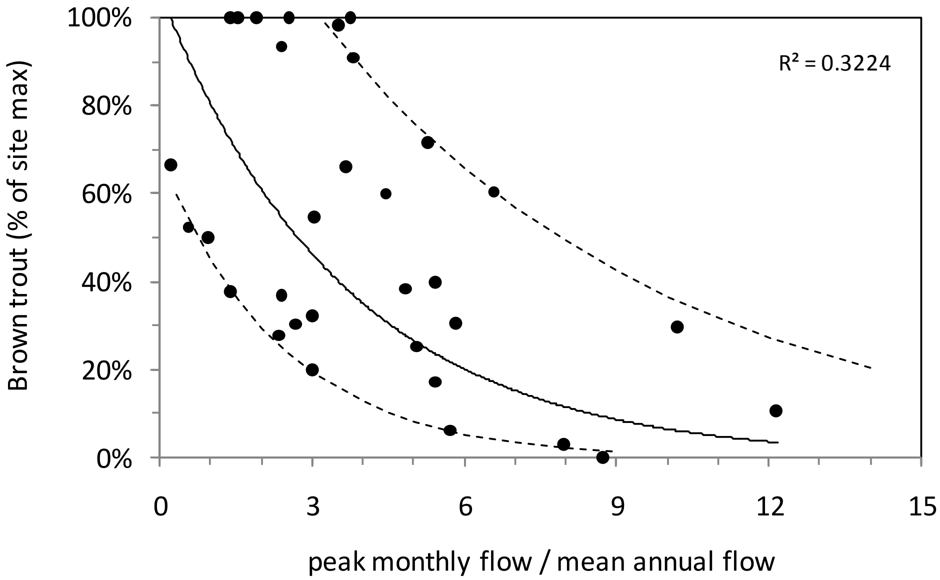


Figure 8 Response of juvenile trout to peak-flow. Recruitment success is measured in terms of the density of age class 1+ brown trout, and is standardized by the observed site maximum. Peak monthly flow was standardized by mean annual flow. The data are sourced from Nehring 1986 and Nehring and Anderson 1985. A standard regression line (solid line, exponential) and corresponding R^2 value is presented, along with 10% and 90% quantile regression lines (dashed lines, P-value 0.016 and 0.094 respectively), fitted to Log_e transformed trout data.

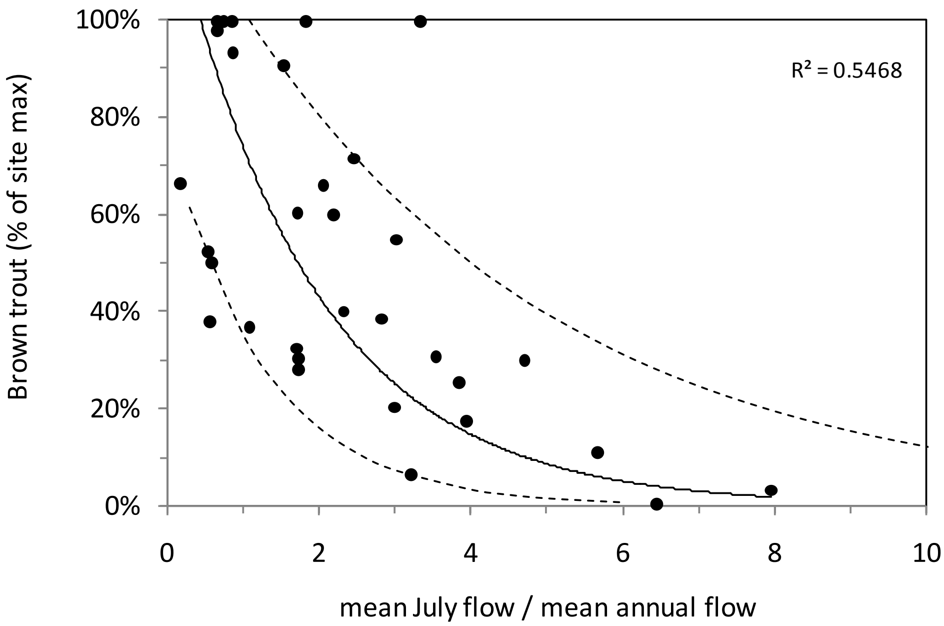


Figure 9 Response of juvenile trout to July flow. Recruitment success is measured in terms of the density of age class 1+ brown trout, and is standardized by the observed site maximum. The average flow for July was standardized by mean annual flow. The data are sourced from Nehring 1986 and Nehring and Anderson 1985. A standard regression line (solid line, exponential) and corresponding R^2 value is presented, along with 10% and 90% quantile regression lines (dashed lines, P-value 0.002 and 0.089 respectively), fitted to Log_e transformed trout data.

Rainbow trout data were also collected for the same studies (Nehring 1986; Nehring and Anderson 1985), but this species was recorded at lower densities and at fewer sites. The data were adequate to describe a similar decline in the density of juvenile rainbow trout with increasing flow, which was most pronounced for July (exponential decay, R^2 = 0.391). A similar response to peak flow is expected for brook trout, with (Latterell et al. 1998) describing a decline in the recruitment of trout in streams dominated by brook trout (relationship reproduced in Figure 10). It is possible that native cutthroat trout are less sensitive to the magnitude of snowmelt, given their later spawning.

The relationships describing juvenile trout response to peak flow are useful in assessing the potential effect of flow change on trout recruitment, but should not be used to imply reduced peak flows are always better for sustaining trout. High value trout fisheries can be degraded by excess recruitment of juveniles, because increased competition can reduce the average size of adult fish (Bohlin et al. 2002; Keeley 2001). The density of adult trout must be considered at this point. Rivers with abundant adult trout are more likely to experience negative effects from competition with increased recruitment. Conversely, increased recruitment is more likely to be beneficial in rivers with low densities of adult trout. Peak flows are essential for channel maintenance, including flushing of spawning gravels and food-producing riffle areas (Poff et al. 1997). Several members of the expert panel suggested the benefits of a sustained loss of peak flows may only last a few years, until habitat degradation and competition produces a net impact on the fishery. Maintaining inter-annual flow variability is therefore viewed as important for productive trout fisheries.

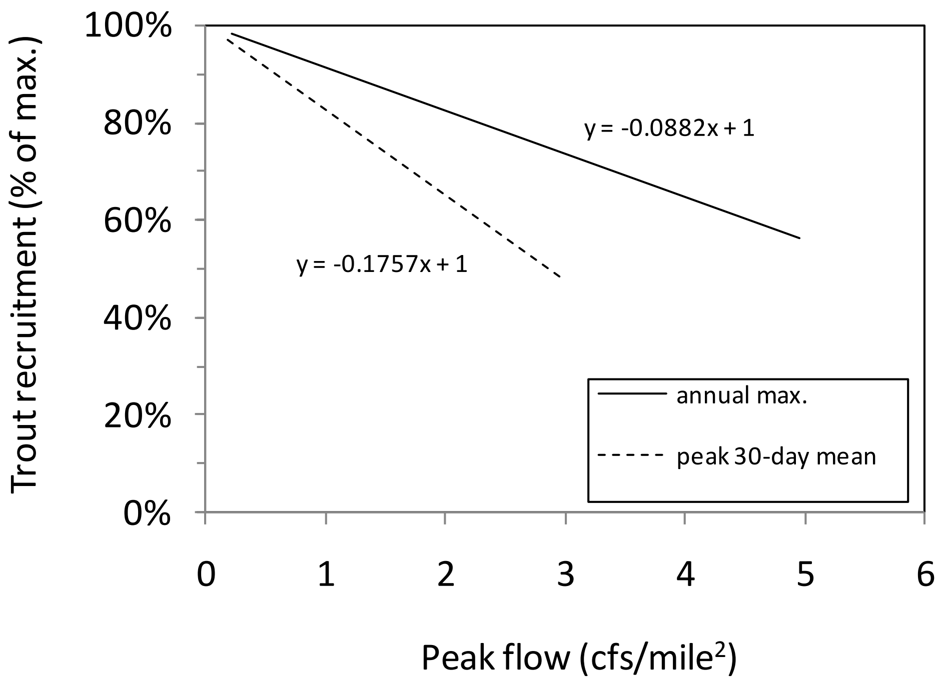


Figure 10 Response of trout recruitment to peak-flow. Recruitment success was measured in terms of the density of 1-year old fish (both brook and brown trout), and is standardized here as a proportion of theoretical maxima. Two measures of peak flow are used: annual peak-flow (24-hour average) and mean of the highest 30 days of flow (to incorporate duration). Flow (cfs) was divided by watershed area (square miles) to provide a comparable measure of disturbance for different sized rivers. Equations are derived from Latterell et al. (1998) after unit conversion for a scenario of 100 adult trout per 250 m (adult trout are a second factor in the model, but do not change the gradient of the response).

Minimum flow requirements for trout are well documented using site specific methods, such as IFIM (Raleigh et al. 1986) and empirical models (for a review, see Fausch et al. 1988). Studies of trout in Rocky Mountain streams generally identify low flow as a potentially limiting factor where temperature is otherwise suitable (Binns and Eiserman 1979; Jowett 1992; Nehring and Anderson 1993; Rahel and Nibbelink 1999; Raleigh et al. 1986). Low-flow relationships for trout can be assessed within this context by limiting application of guidelines to streams and rivers that are known to sustain trout or recreational trout fisheries. Two separate issues arise for low flows: habitat during the summer autumn period and ice refuge during winter.

Flows during winter deserve consideration as trout overwinter successfully only in pools that do not freeze to the bottom and where gill abrasion from frazil ice can be avoided (see page 106 in Annear et al. 2004). Hubert et al. (1997) outlined some of the difficulties in setting and applying flow standards that maintain refuges from ice. More recent advances in hydraulic modelling have enabled predictions of the change in habitat with flow under the ice (Waddle 2007) but are still unable to predict the effect of flow on ice formation. Complications arise at multiple scales. For example, pools can develop an even cover of ice compared to fast flowing areas that freeze along the edges to form an open tube (Waddle 2007). At larger scales, a reverse altitude effect can occur, with snow pack providing insulation and reducing ice formation in higher altitude streams (Hubert et al. 1997). In addition to low flows during winter, peak flows throughout the year are important in the formation of deep pools, and these pools subsequently provide over winter refuge areas. Access for fish upstream or downstream to ice refuges (e.g. large pools or beaver dams) will also be important. Despite the potential importance of this issue, quantitative relationships between flow and over winter survival of trout cannot be produced at this time.

The second issue arising from low flows is the amount of habitat available during summer and autumn. An earlier model of trout abundance in Wyoming streams rated the relative suitability of summer low flows as part of a broader Habitat Suitability Index (Binns and Eiserman 1979). The study included Rocky Mountain streams (most >6000 feet altitude, mean annual flow 25 to 500 cfs) and summed the abundance of four trout species (same as those found in Colorado). The authors assigned five categories for suitability of summer low flow (Table 3). The categories appear to be subjective, but they did form the basis of what remains one of the more robust predictive models for trout biomass (Raleigh et al. 1986).

The origins of the Binns and Eiserman (1979) category thresholds include earlier work by both Wesche and Tennant. Publications by Thomas Wesche dating back to 1973 document 25% of mean annual flow as a threshold of physical habitat deterioration in small trout streams in Wyoming (mean annual flow 30 cfs) (http://library.wrds.uwyo.edu/wrs/wrs-37/abstract.html). Hubert et al. (1997) cites Burton and Wesche (1974) as finding six streams where 25% of MAF was met or exceeded 50% of the time (July to September) had good trout fisheries (246-705 fish/acre). This was compared to five streams that did not meet the criterion, where trout populations were small (5 to 190 fish/acre).

Similar categories were developed by Tennant (1976) for Montana, Wyoming and Nebraska streams (see Table 5 in the section on Warm-water fish - Great Plains). This method was reviewed by Mann (2006) for its representation of physical habitat (depth, velocity, width and weighted usable area). Mann concluded that Tennant's categories provide a reasonable representation of Interior Western streams (termed the Temperate Desert Division) and of low gradient streams (<1%) such as the Great Plains area (from Nebraska correlations). In other areas, such as the Rocky Mountains (termed Temperate Steppe Regime Mountains), Mann (2006) recommended that application of the Tennant method be limited to flow standards for initial planning (i.e. should not be used to prescribe flow requirements). By comparison, the categories from Binns and Eiserman (1979) were developed for steep gradient rivers (mean slope 2.2%, range 0.1 to 10%, median 0.95%) and are considered more applicable to Rocky Mountain streams.

The categories are valid for assessing suitability of low flows if applied to temporal comparisons (i.e. changes over time for individual watersheds), or spatial comparisons across one stream type (Rocky Mountain snowmelt hydrograph streams). But spatial comparisons across different stream types may be invalid because a higher proportion of mean annual flow could simply represent a naturally stable flow regime. Its validity also depends on the use of natural mean annual flow as the reference condition for both pre- and post-development (see page 160 in Annear et al. 2004).

One drawback of the flow categories (both Tennant and the Binns and Eiserman approach) is that these may underestimate flows for small streams. The assumption that habitat for both small streams and large rivers can be represented by the same proportion of mean annual flow may not hold true (Jowett 1997). Hatfield and Bruce (2000) predicted the flow providing maximum habitat for large adult trout (modelled using PHABSIM) from mean annual flow (Figure 11). Their results demonstrate the higher flow requirements (proportionately) to maximise habitat in smaller streams. The categories of Binns and Eiserman (1979) were developed from surveys of streams as small as 30 cfs (mean annual flow), so streams too small to be represented by their categories are likely to be too small to support a recreational fishery. Smaller trout can persist in smaller streams, but flow magnitude will ultimately limit the trout biomass that sustains recreational fisheries (Jowett 1992). It is therefore important to limit the application of the categories in Table 3 to existing trout fisheries, and to calculate low flows as a percentage of natural mean annual flows (cf. altered flows).

More recent methods for assessing low flow guidelines of trout at a regional scale would require further work for application to Colorado, hence are beyond the scope of this report. Generalized habitat models were developed for New Zealand and France (Lamouroux and Jowett 2005) and offer a worthwhile avenue of research for Colorado. This method does not produce flow guidelines, but the relationships between habitat and flow that are produced may provide a useful basis for refining guidelines for low flows. Alternatively, generalized flow guidelines could be developed based on existing habitat survey results for individual stream types in Colorado, by adapting the method used by Wilding (2007).

Table 3 Categorical rating of low-flow suitability for trout (cutthroat, brook, brown and rainbow), from (Binns and Eiserman 1979). Summer flows (average for August to mid-September) are expressed as percentage of mean annual flow.

Rating	Summer low flow (% of mean annual flow)	Description
0 (worst)	<10%	Inadequate to support trout.
1	10-15%	Potential for trout support is sporadic.
2	16-25%	May severely limit trout stock every few years.
3	26-55%	Low flow may occasionally limit trout numbers.
4 (best)	>55%	Low flow may very seldom limit trout.

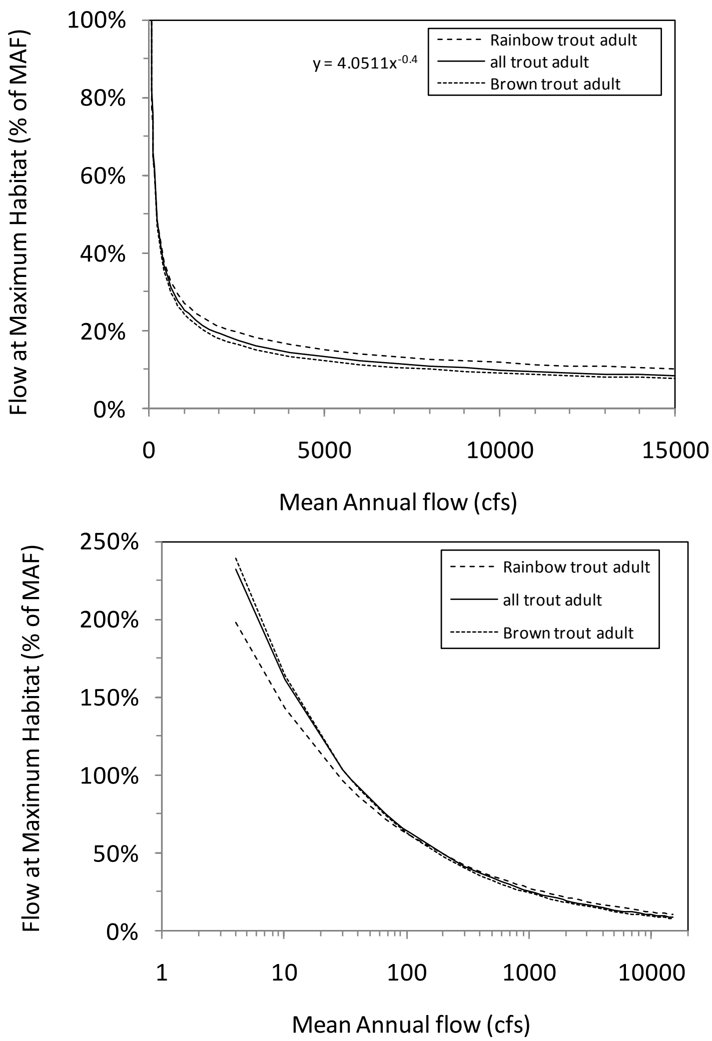


Figure 11 Relationship of flow for maximum trout habitat to mean annual flow (MAF). The same plot is presented on a linear axis (upper plot) and log axis (lower plot) for mean annual flow. Equations were derived from Hatfield and Bruce (2000) for a scenario of latitude 41° (latitude is a second factor in the models for rainbow trout and "all trout"). The equation for "all trout" is presented (see upper-graph), after conversion from m^3/s to cfs.

Warm Water Fishes – Interior Western

Several extensive and long-running monitoring programs have documented fish communities of the Colorado, San Juan, and upper Colorado tributaries. Studies on the San Juan covered too narrow a flow range, documenting a return to a near-natural flow regime (Navaho Dam relicensing investigations). Conversely, studies on the lower Colorado River (below Glen Canyon Dam) lack spatial or temporal reference data for natural conditions (by political decree, see Lovich and Melis 2007). Despite the abundance of data from the lower Colorado River, only investigations from the upper Colorado tributaries provided a wide spectrum of flow conditions, including natural and altered conditions.

Bestgen et al. (2006) present data for a wide range of species over a long period (1962-2006). Spatial coverage is limited (Green River below Flaming Gorge Dam), but this represents one of few studies documenting pre-dam conditions. Reproductive success was reported for fish of the Green River, under various management regimes (temperature and flow manipulation). These data are plotted in response to magnitude of peak flow, low flow and summer temperature (Figure 12). The correlation with both peak flow (positive response) and low flow (negative response) is adequate. However, temperature is the better descriptor of variation in the data (higher R^2), limiting the use of coincidental flow-changes as a causal predictor of fish reproduction.

All 11 species of warm water fish stopped breeding in this reach of the Green River after completion of Flaming Gorge Dam (Bestgen et al. 2006). Outflow was sourced from the cold depths of the reservoir (below the thermocline) which reduced summer temperatures to 6 °C (from 22 °C mid-reach). Seasonal flow variability was also reduced significantly. The installation of variable-depth penstocks in 1978 increased river temperatures to 13 °C (considered optimal for introduced trout), but the flow regime remained stable. The temperature rise alone was adequate for seven species of native fish to start reproducing again, and this period represents the high outlier for the flow response plots in Figure 12. Subsequent operational changes produced a flow regime closer to natural conditions (higher peak flow and reduced low flow), and the number of species reproducing increased to nine (humpback chub and bonytail are yet to recover). But interpreting this latest increase as a response to flow is complicated by the concurrent increase in temperature. Reservoir discharge temperature was increased, and lower flows in summer allow the river to warm more rapidly. Clearly temperature is a critical issue for the persistence of warm water fish in highly regulated rivers, and further investigations were necessary to distinguish the importance of flow.

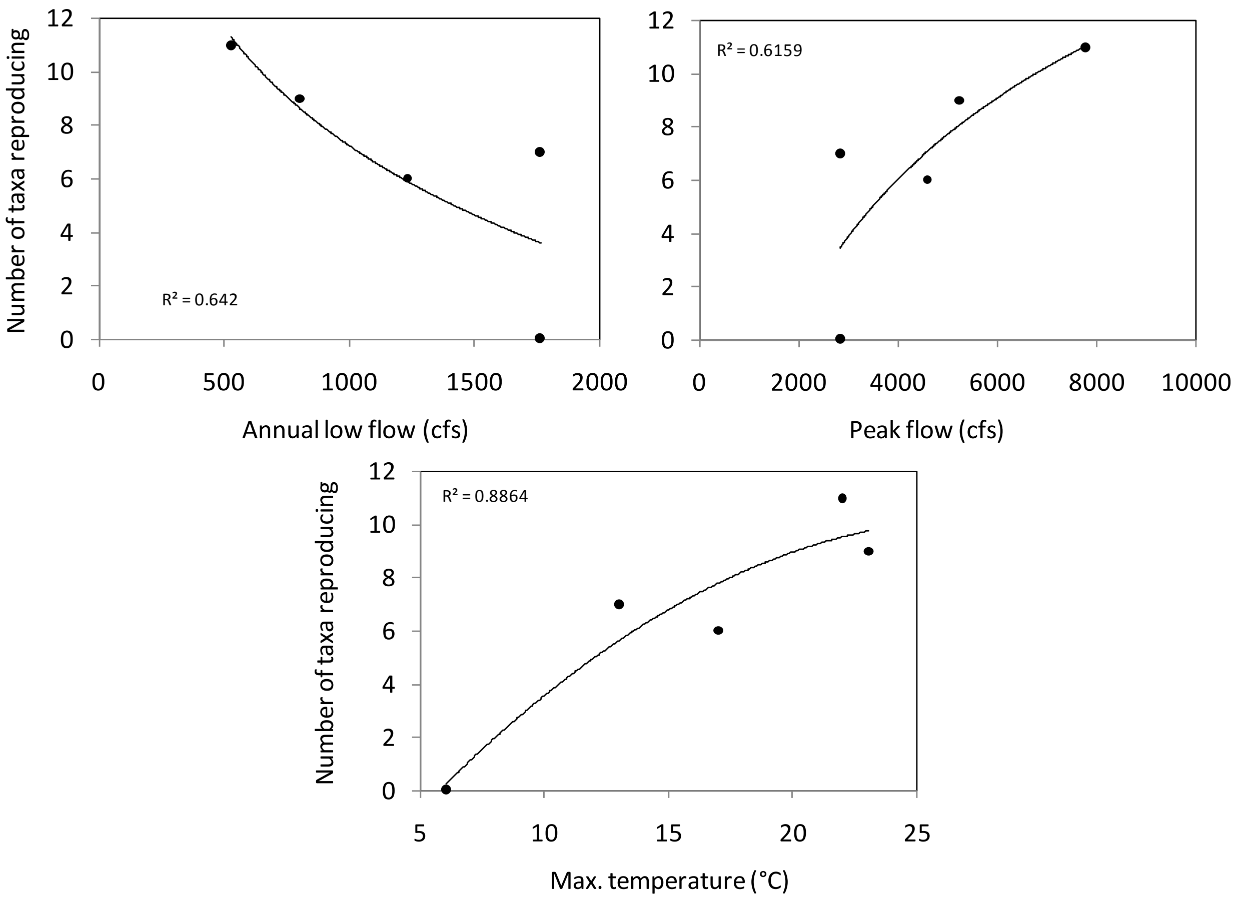


Figure 12 Response of warm water fish to low flow, peak flow and temperature (data from Bestgen et al. 2006). Fish response is measured as the number of taxa reproducing (maximum of 11 taxa including mountain whitefish, humpback chub, bonytail, roundtail chub, Colorado pikeminnow, speckled dace, bluehead sucker, flannelmouth sucker, mountain sucker, razorback sucker and mottled sculpin). Data points represent periods under various dam operations (including pre-dam) on the Green River between Flaming Gorge Dam and Yampa confluence.

By employing data from rivers where temperature is not a major limiting factor, it is possible to distinguish the effects of flow modification. Anderson and Stewart (2007) provide data across a wide range of flow conditions, representing gradients of flow modification, inter-year and site variability, using comparable methods. This study provided recent fish biomass and flow data for the Yampa, upper-Colorado, Gunnison and Dolores Rivers (biomass units are standardized by area fished, which enables comparison between different sized rivers). The four rivers have adequate summer temperatures for warm water fishes, and so provide a better depiction of flow response, when temperature is not an overriding issue. The Gunnison is the most regulated of the four rivers, but the study reaches were far enough downstream of dams for temperatures to exceed 18 °C (daily average) in summer (U.S. Fish and Wildlife data). Anderson and Stewart (2007) provide data for four species of native, large-bodied, warm water fish, including:

- bluehead sucker (*Catostomus discobolus*); feed on benthic algae and invertebrates; rocky riffle habitat (Ptacek et al. 2005).
- flannelmouth sucker (*Catostomus latipinnis*); feed on benthic algae and invertebrates; habitat generalist (Rees et al. 2005a).
- roundtail chub (*Gila robusta*); feed on algae, invertebrates and fish; occupy deep, low-velocity habitats with cover (Rees et al. 2005b); species of special concern.
- Colorado pikeminnow (*Ptychocheilus lucius*); piscivore (fish eater); inhabits deep pools and backwaters, feeding in riffles at night (Modde et al. 1999); federally endangered.

Three species (bluehead sucker, flannelmouth sucker, roundtail chub) demonstrate a positive response to increased low flows (Figures 13 and 14). The logarithmic response represents a steep decline in biomass for flows less than 300 cfs, and a gradual response at higher flows. No zero biomass values were observed above 200 cfs for bluehead sucker, flannelmouth sucker or roundtail chub. Preference for higher flows may reflect improved physical habitat, or increased productivity of food sources (e.g. larger areas of benthic algae). It must be kept in mind that total stream area increases at higher flows, and therefore a constant biomass *per unit area* actually represents a gradual increase in *total* biomass with flow.

The response of Colorado pikeminnow to low flow (summer-autumn) was weak (Figure 14). The biomass of pikeminnow (per unit area) did not appear to benefit from elevated low-flows in regulated rivers, beyond basic persistence. This likely reflects other limiting factors, given that pikeminnow are rare or absent in all three regulated rivers, despite a wide range of low flows. By comparison, the free-flowing Yampa River supported a higher biomass of pikeminnow (per unit area) in years with low flows greater than 30 cfs. Inadequate low flow may have the potential to limit the population, with detailed assessments on the Yampa recommending 93 cfs to maintain habitat for Colorado pikeminnow (Modde et al. 1999) and much higher flows for the Green River (Muth et al. 2000). Low flows that are adequate for bluehead sucker, flannelmouth sucker and roundtail chub may also be adequate for pikeminnow, with no data to suggest otherwise.

Three species (roundtail chub, bluehead and flannelmouth sucker,) show a negative, but weaker, response to specific peak flow compared to the low flow response (Figure 13 and 14). The flow required to disturb or scour a stream bed is a product of, among other things, channel size. This is presumably why specific peak flow (peak flow per unit watershed area) produced a clearer response (higher R^2) for all species, compared to total flow, and is presented here. Specific peak flows that are greater than 2.5 cfs/mile^2 were associated with reduced potential biomass of bluehead sucker, flannelmouth sucker and roundtail chub. The magnitude of low flow is a better predictor of biomass than peak flow for these three species (higher R^2 value and smaller P-value, Figure 13 and 14). Brouder (2001) documented a positive response for juvenile roundtail chub to the magnitude of peak flow, but this did not translate to higher catches of adult chub. Conservation Assessment reports highlight migration barriers and introduced fish as primary threats to these fishes, but research on mechanisms of flow regime effects is limited (Ptacek et al. 2005; Rees et al. 2005a; Rees et al. 2005b).

In contrast to the response of the other three species, Colorado pikeminnow did show a positive correlation with specific peak flow (Figure 14). This federally endangered species was rarely encountered in all rivers but the Yampa, which is the only unregulated river of the four studied. The upper bound (P-value 0.017) therefore describes the response of Yampa River pikeminnow to specific peak flow (all biomass data points >25% are from the “Sevens” site on the Yampa River).

Bestgen et al. (2007a) reported a population decline of Colorado pikeminnow in the Green River basin post-2000 (Yampa sites included in study). The decline was largely attributed to recruitment failure, which has fallen short of adult mortality since the late 1990s. Pikeminnow biomass at the “Sevens” site on the Yampa, which supports the highest biomass of sites monitored by Anderson and Stewart (2007), demonstrated a stronger correlation with peak flow than year ($R^2 = 0.813$ and 0.247 respectively), indicating that peak flow is not a pseudo correlate for temporal population decline. The response of the Green River basin population to flow is likely to be complex and time lagged, compared to the relationships provided here that describe a more immediate flow response. Given the long life span of Colorado pikeminnow (>6 years to maturity) and distant rearing habitat (mid and lower Green River), the year-to-year variation in biomass described by specific peak flow (Figure 14) is more likely a product of mortality rather than variable recruitment (movement of adults between sites may also influence results). For example, predation by northern pike may increase in the absence of flow disturbance to scour its preferred macrophyte habitat (Bestgen et al. 2007b). Detailed assessments of flow requirements for Colorado pikeminnow are presumably available for critical habitat reaches, including rearing habitat. The relationships derived here will go some way to identifying impoverished flow regimes further afield.

It seems likely that prescribing an upper limit on peak-flows based on the weak negative relationship demonstrated by the other three species (smaller R^2 value and higher P-value, Figure 13 and 14) could be unnecessarily detrimental to Colorado pikeminnow. Notably, Muth et al. (2000) placed no upper limit on their peak flow recommendations for the Green River.

Colorado pikeminnow share traits in common with other federally endangered fishes of Interior Western rivers (bonytail, humpback chub, razorback sucker). Olden et al. (2006) class these fish as long-lived, preferring slow to moderate velocities, and place them in the same reproductive guild (non-guarding, open-substrate). Peak flows appear to be a critical issue for these endangered fish. Muth et al. (2000) stated that recovery of razorback sucker require peak flow of sufficient frequency, magnitude, and duration to inundate floodplain habitats (for the growth and survival of juveniles). The same authors noted that spring flows provide spawning cues and prepare spawning habitat for humpback chub. In the absence of flow-ecology relationships for the full range of fish fauna for the Interior Western rivers, it may be reasonable to assume the positive response of adult pikeminnow to peak flow is typical of other federally endangered species that share similar life history strategies and habitat needs.

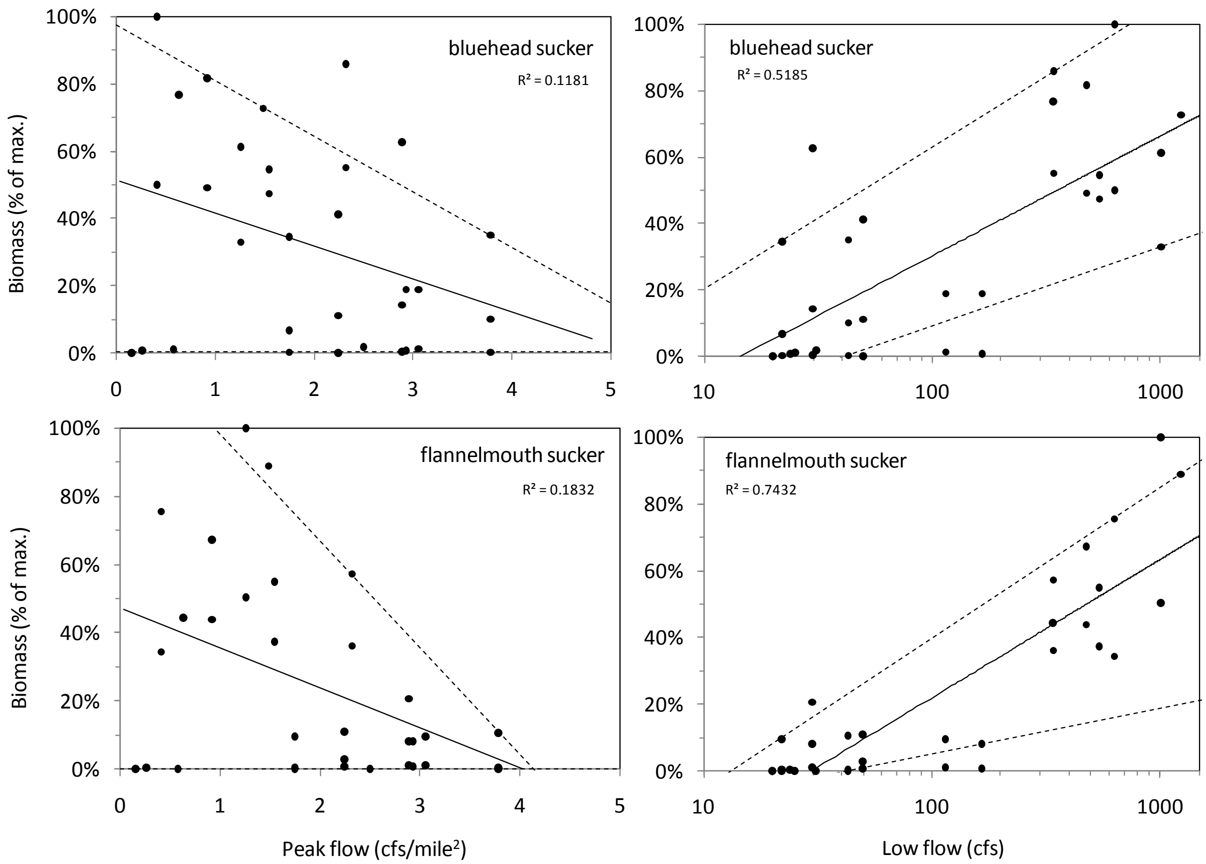


Figure 13 Response of warm water fish (bluehead and flannelmouth suckers) to specific peak flow (left plots) and low flow (right plots, log scale). Data are sourced from Anderson and Stewart (2007). Fish biomass was measured in kilograms per hectare, and is standardized by the observed maximum. Annual peak flow (cubic feet per second, 24-hour average) was divided by watershed area (square miles) to provide a comparable measure of disturbance and inundation for different sized rivers. Low flows are minima for the summer-autumn period (24-hour average), presented on a log scale. Standard regression lines (solid line) and corresponding R^2 values are presented, along with 10% and 90% quantile regression lines (dashed lines). P-values for 90% quantile regressions are, clockwise from top-left, 0.177, 0.054, 0.094 and 0.001.

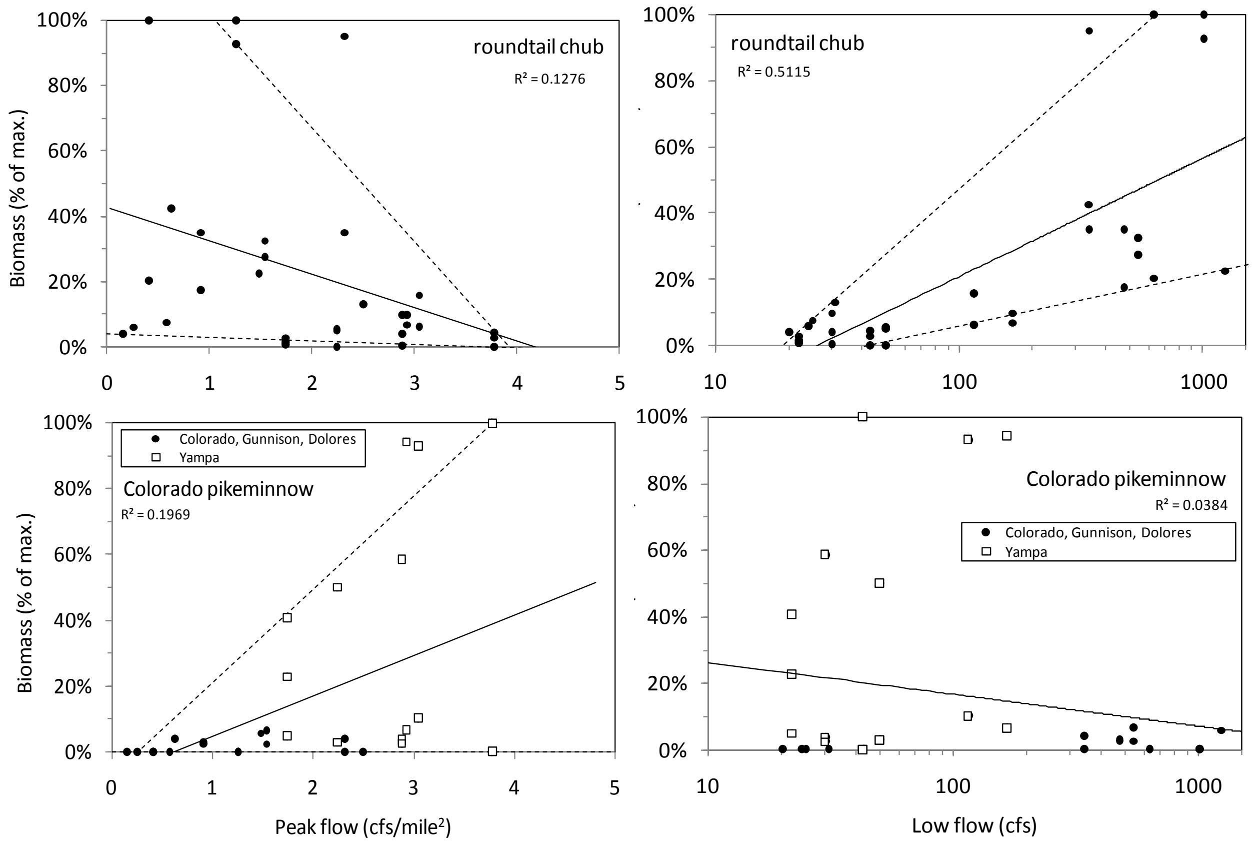


Figure 14 Response of warm water fish (roundtail chub and pikeminnow) to peak flow (left plots) and low flow (right plots). Data are sourced from Anderson and Stewart (2007). Fish biomass was measured in kilograms per hectare, and is standardized by the observed maximum. Annual peak flow (cubic feet per second, 24-hour average) was divided by watershed area (square miles) to provide a comparable measure of disturbance and inundation for different sized rivers. Low flows are for the summer-autumn period (24-hour average), presented on a log scale. Standard regression lines (solid line) and corresponding R^2 values are presented, along with 10% and 90% quantile regression lines (dashed lines). Yampa River results are distinguished for Colorado pikeminnow to highlight their paucity in other rivers (regression based on all 4 rivers). P-values for 90% quantile regressions are, clockwise from top-left, 0.297, 0.008, 0.017 and 0.756 (latter not presented).

The effect of introduced fish is a critical issue for warm water fish of Interior Western rivers. The mechanisms of effect on native fish (e.g. competition, predation, hybridization) potentially have complex interactions with flow and temperature. Generally speaking, the more severe environmental conditions of Interior Western rivers in their natural state (extremes of flow, turbidity and temperature) are expected to favor native fish (Olden et al. 2006). But attempts to restore natural conditions in regulated rivers (excluding sediment regimes) sometimes fail to reduce numbers of introduced fish (Brooks et al. 2000). Flow conditions that provide suitable habitat for native fish are a fundamental starting point for water management in Colorado rivers, and hence are the basis of relationships presented in this report. As the relationships presented here are intended as a screening tool (rather than site-specific flow requirements), we have not attempted to generalize flow provisions that both reduce numbers of introduced fish and provide suitable habitat for native species.

Warm-water fishes - Great Plains

Temporal changes across the Great Plains of Colorado have left half of the fish species (19 out of 38) extirpated (locally extinct), endangered, threatened, or classed as species of special concern (Scheurer et al. 2003a). Altered flow regimes are a critical issue in the decline of these fishes, together with migration barriers that prevent recolonization when flow does return (Fausch and Bestgen 1997). Unfortunately, we lack historical data and reference conditions to evaluate quantitative response to flow for Great Plains fishes.

Lohr and Fausch (1997) identified different fish communities inhabiting mainstem rivers, perennial tributaries and intermittent tributaries of the lower Purgatoire watershed (Table 4). Mainstem rivers that receive snowmelt runoff from Rocky Mountain headwaters (e.g. South Platte, Purgatoire), support different fish communities than smaller tributaries that originate on the plains (Table 4). Tributary streams can be perennial where groundwater levels are adequate, but they are often intermittent. We can define intermittent streams as those with permanent pools that are connected only seasonally by flow. These pools might extend to short flowing sections of stream, revealing the continuum between intermittent and perennial. Habitat preference data from Conklin et al. (1995) at least support the main-river dependence of channel catfish (prefer moderate depths and velocities), and the smaller stream affinity of plains killifish (prefer slow, shallow water). Red shiner and sand shiner do not need particularly fast or deep low flows (Conklin et al. 1995), and their apparent absence from perennial tributaries suggests these are too small to satisfy even modest flow requirements (Table 4). Fausch and Bestgen (1997) observed that larger rivers (e.g. mid- and lower Platte) support more large-bodied fish that live longer than fish characteristic of tributary streams.

Table 4 Fish communities inhabiting different stream types in the Purgatoire River watershed, as observed by Lohr and Fausch (1997). The authors distinguished these communities based on percent occurrence in streams of varying persistence of water (e.g. mainstem river species present at 50% of main river sites, and less frequently elsewhere), and this data is reproduced in the right columns. The lowest flows reported by Lohr and Fausch (1997) or Fausch and Bramblett (1991) are also presented as an approximation for summer low flows. See also Table 6.2 in Fausch and Bestgen (1997) for a broader description of fish communities on the plains.

Community Type	Species	Common name	percent occurrence		
			Mainstem river	Perennial tributary	Intermittent tributary
Mainstem river					
	Cyprinella lutrensis	red shiner	100	0	3
	Platygobio gracilis	flathead chub	100	14	0
	Notropis stramineus	sand shiner	67	0	3
	Rhinichthys cataractae	longnose dace	100	0	0
	Ameiurus melas	black bullhead	92	14	33
	Ictalurus punctatus	channel catfish	92	0	3
Perennial tributary					
	Campostoma anomalum	stoneroller	25	57	27
	Fundulus zebrinus	plains killifish	42	71	17
Generalist (including intermittent)					
	Lepomis cyanellus	green sunfish	42	43	93
	Pimephales promelas	fathead minnow	33	71	40
	Catostomus commersoni	white sucker	83	57	33
	Lowest reported flow	(cfs)	23	0.1	0

Large-bodied species and those with specialized reproductive strategies were often the first to disappear after water resource development on the plains, indicating their sensitivity to flow change. Mean annual flow of the Arikaree River, which originates on the plains, has declined steadily since 1960 and is associated with the loss of five species of fish, including plains minnow, suckermouth minnow, river shiner, stonecat and flathead chub (*pers. comm.* Jeffrey Falke, Colorado State University). Eberle et al. (1993) documented the extirpation of two of the same species (plains minnow and flathead chub) from sections of the Arkansas River, as did Hargett et al. (1999) from the Cimarron River (Kansas). These losses were attributed to the reduced spring/summer peak-flows, which are necessary to carry the neutrally buoyant eggs of plains minnow.

The loss of large river specialists from Great Plains rivers was followed by the decline in small-bodied fish, as flow reductions have continued. Both Arkansas darter and brassy minnow are state threatened, and orangethroat darter is a species of concern. Red shiners and sand shiners were found to benefit from occasional return of seasonal flow by Hargett et al. (1999), and a similar response was observed for Arkansas darter (Labbe and Fausch 2000). The harsh conditions of isolated pools are tolerated by several species, but each depends on flow returning seasonally in order to persist.

Those inhabiting pools of intermittent tributaries are dependent on adequate depths to avoid drying out in summer or freezing to the bottom in winter, as well as depending on wet-season flow to allow reproduction and dispersal (Labbe and Fausch 2000; Lohr and Fausch 1997; Scheurer et al. 2003b). Pool depth depends on groundwater level (Falke and Fausch 2007), and the peak flows that form these channel depressions (Labbe and Fausch 2000). The harsh environment in these pools (high summer temperature, low oxygen, flood disturbance and poor connectivity) is believed to restrict establishment of introduced predators, such as largemouth bass (Lohr and Fausch 1997; Scheurer et al. 2003b).

Adequate data were not found to support a quantitative assessment of relationships with peak flow and low flow. Tennant (1976) developed categories of low flow that provide different levels of habitat maintenance (Table 5). These categories were based on habitat data (wetted width, depth, velocity) for large rivers of the northern Great Plains (Republican, North Platte, Shoshone), several of which had montane headwaters. The categories were intended to represent both cold and warm water fishes, though individual species requirements were not specifically investigated. Only the 10% category is an instantaneous flow, compared to the higher thresholds which Tennant labelled simply as baseflows. This implies the 10% category is tolerable for a shorter duration than the higher thresholds. Application of the higher thresholds to 24-hour mean annual low flow seems appropriate for the purpose of this report, and maintains consistency for application (one could also argue that baseflow refers to a mean monthly flow).

The Tennant method was reviewed by Mann (2006) for its representation of physical habitat (depth, velocity, width and weighted usable area). Mann concluded that Tennant’s categories provide a reasonable representation of low-gradient streams (<1%) such as the Great Plains area (from correlations for Nebraska sites). Tennant’s method is only considered appropriate for mainstem rivers of the Great Plains, given Tennant’s use of large rivers in his study and the underestimation of flow requirements for small streams that is produced by the Tennant method (Jowett 1997; Orth and Leonard 1990).

In addition to low flow categories from Tennant (1976), this method was adapted by Tessmann (1980) to provide month-specific flows for the northern Great Plains (Table 6). The decision criteria effectively place lower and upper limits on the degree of flow modification, and it appears all are based on Tennant’s category for “good habitat” (40%). The original publication was not available for review, and we have no information to interrogate the methods appropriateness for peak flows. But these revised categories may go some way to describe the response of fish habitat to peak flow for mainstem rivers of the Great Plains, in the absence of alternatives.

In addition to mainstem rivers, guidelines are also needed to assess response to flow alteration in tributary streams of the Great Plains. Because of the degree of flow modification, and large proportion of threatened species in remaining habitats, it might be fair to assume that both peak flows and low flows are presently stressed in tributary streams of the Great Plains. The number of extirpations (local extinctions) suggests there is little or no buffer remaining in the system to offset further changes such as global warming or further water abstraction. In the absence of flow ecology relationships, detailed site specific studies may be necessary to determine otherwise.

Table 5 Low flow categories for maintaining various levels of habitat quality, expressed as a percent of mean annual flow. Tennant (1976) developed these categories, which are applicable to mainstem rivers of the Great Plains.

	Low flow (% of mean annual flow)
Optimum habitat	60%-100%
Outstanding habitat	60%
Excellent habitat	50%
Good habitat	40%
Fair or degrading habitat	30%
Poor or minimum habitat	10%
Severe degradation	<10%

Table 6 This expansion of Tennant's categories by Tessmann (1980, as presented in Annear et al. 2004) provides guidelines for minimum monthly flows for maintaining good habitat in mainstem rivers of the Great Plains. MMF = mean monthly flow; MAF = mean annual flow.

	Minimum monthly flow
MMF < 40% of MAF	MMF
MMF > 40% of MAF and, 40% of MMF < 40% of MAF	40% of MAF
40% of MMF > 40% of MAF	40% of MMF

Recreation – Canoeing, Kayaking, Rafting

Rood et al. (2006) investigated flow relationships for recreation involving non-motorized boats. The study focussed on Rocky Mountain rivers of Alberta, Canada, but also assessed rivers further south (including Colorado). Three methods were used to measure recreational flows, including paddler surveys, stage-discharge modelling (for target depths) and expert judgement from guide books. Recreational flow analysis was found to be simpler and less stochastic, compared to instream flow determination for fish or riparian vegetation. They proposed the "Alberta equation" to provide an initial estimate for recreational flows for rivers, especially those draining Rocky Mountain areas (based on mean annual flow). Both the minimum flow and preferred flow for recreation are reproduced in Figure 15. The authors posed two qualifications. First, the equations are believed poorly suited for very large rivers, which seldom have flows that are insufficient for paddling. Second, they considered the equations unsuitable for the most challenging reaches as most paddlers restrict usage of Grade-V white water to low flows.

The equations provided by Rood et al. (2006) provide an excellent basis for desk-top assessments of reaches that are known to have value for recreational paddlers. As with the other guidelines provided in this document, this should not override or replace site-specific investigations where recreational use is likely to be a critical issue.

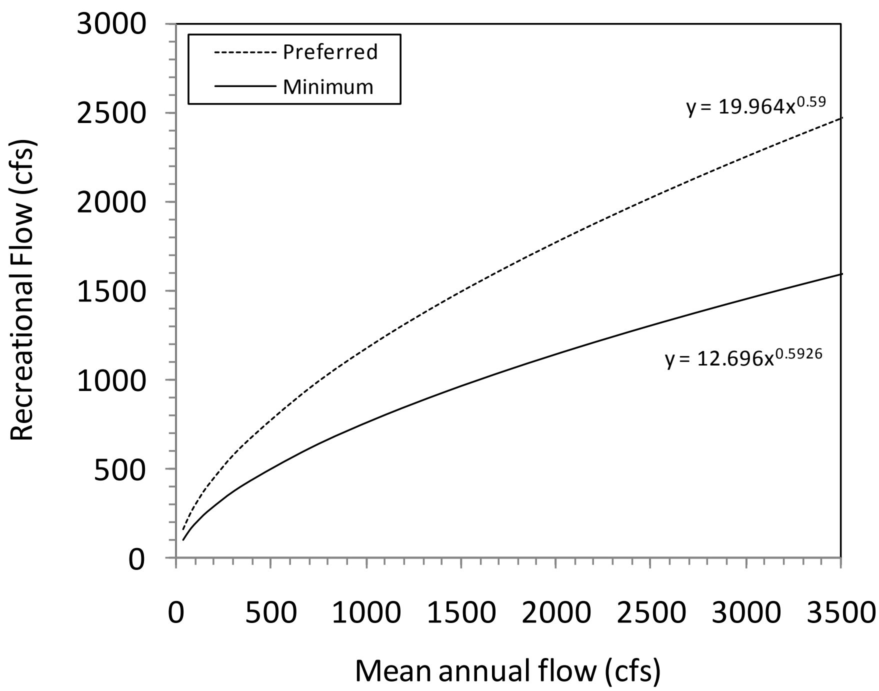


Figure 15 Recreational flows for canoeing, kayaking and rafting (from Rood et al. 2006). Both the minimum flow and preferred flow are presented (converted to cfs from m^3/s units of original publication), and Pearson R^2 values for these regression equations were 0.94 and 0.96 respectively.

4. Summary

This report encompasses an unprecedented range of ecosystems and stream types for the state of Colorado, in an effort to describe their response to flow change. Cottonwoods of the Great Plains, trout of high mountain streams and sucker fish of western canyons are among the plants and animals covered. Drawing on existing scientific research that is intensive and rigorous, but often site-specific, we developed general relationships to improve our understanding of the majority of streams in Colorado.

Complex relationships between ecosystems and their environment are simplified here for the purpose of providing a practical screening tool for water managers. Just as water restrictions have consequences for local economies and our standard of living, basic persistence of stream communities is inextricably linked to flow. The need for food, space to live and successful reproduction often have complex and competing dependence on flow. For example, the same high flow that flushes spawning gravels of silt may wash away newly hatched fish if it occurs at the wrong time of year. The natural flow regime of a river has the best chance of maintaining the plants and animals that naturally occur there. Constructing dams and diversions changes the flow regime and immediately incurs some level of risk that the natural ecosystem will change and species will be lost. But change is not guaranteed, or necessarily bad, because animals and plants can cope with a range of flow conditions. We benefit from water abstraction and regulation of rivers. The question then is how much change can river systems tolerate? Using relationships provided in this report, water managers can evaluate the risk of effects from a given flow change and compare these to aspirations of people in the community.

This report is intended to improve our understanding of the effects of flow change, and is by no means exhaustive. The trade-off between practicality for end users and capturing the complex response of aquatic ecosystems is balanced by limiting the application of the results. Using any one flow-ecology relationship on its own will bias the assessment and omit potentially critical issues from consideration. The relationships are generalizations, and are not intended for prescribing flow requirements (e.g. minimum flows). Instead, they were developed for identifying sites where flow is less likely to be adequate, and for identifying potentially critical issues that warrant site specific investigations. Likewise, this tool alone is unsuitable for the restoration of threatened species, given the wide range of issues, in addition to flow, that require consideration (e.g. water quality, migratory access). The relationships provided here are not a replacement for detailed site-specific studies, but instead are complementary. Relationships developed using intensive site-specific studies should not be rejected in favor of relationships described here for the same issue. For example, relationships between trout and flow are expected to be less accurate than site-specific PHABSIM studies. However, other issues that were not previously evaluated (e.g. riparian vegetation) may warrant evaluation using the relationships provided, to ensure broader consideration of ecosystem response.

Relationships based solely on flow are more robust if applied to sites that are otherwise suitable for the species of interest. Limiting the calculation of flow response to streams that support the species (or supported them prior to flow modification) is therefore recommended. Application will require some knowledge of what aquatic communities are likely to be present at the site of interest. The results section provides more detailed accounts of other critical parameters (other than flow) that commonly constrain response to flow for each stream community (e.g. temperature limitation for Interior Western fish).

This report is not a stand-alone tool. Flow statistics representing both the natural (historic) and the modified condition (e.g. before and after dam construction) are required for site-specific application. Relationships between aquatic ecosystems and flow are the principle tools provided here and they can be used to compare and rank sites. But determining an acceptable level of ecosystem change that triggers further action will be up to end users. Completing an assessment will highlight competing demands among non-consumptive water users (e.g. flow for trout versus riparian vegetation). Developing an understanding among end-users of these competing demands is an important output in its own right. Round tables of interested parties provide an excellent forum for clarifying the specific objectives for flow management in the face of such competing demands.

The user will also need to determine the stream type of the study site in order to select the appropriate relationships (see Stream Types in the Methods section for a description of each). A comprehensive stream classification was beyond the scope of this study, and subsequent development of such a tool would have many advantages for non-consumptive needs assessment in Colorado. We have simplified the diversity of Colorado streams into three classes; Rocky Mountains, Great Plains and Interior Western. These recognizable land forms provide a correlate for major drivers of stream ecosystems (e.g. climate, soil, slope). The rapid transition from mountains to plains simplifies stream classification for Colorado, and flow-ecology relationships are intended to capture variability within each stream type (e.g. moderate to high gradient mountain streams). Exceptions to this are noted in the results (e.g. mainstem versus tributary habitats of the Great Plains). Transition zones do exist between stream types, and the length of these transition zones will vary. Relationships were not developed for transitional reaches, given their implicit variability (transition from one stream type to another over a short distance). Application of relationships intended for both stream types that border the transition zone (assuming each community is present) is expected to provide some appreciation of flow response. For example, sections of Fountain Creek are transitional between the Rocky Mountains and the Great Plains. Here, flow relationships for trout, riparian vegetation and warm-water fish of the Great Plains may all apply. The adequacy of these relationships for transition zones cannot be determined with certainty, so high-value stream communities would warrant detailed assessments.

5. Application

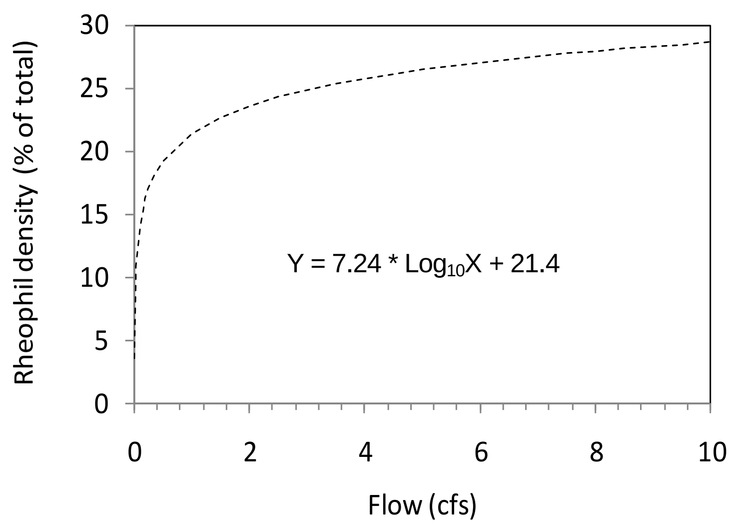
The results section provides details for the derivation of individual flow-ecology relationships. This section summarizes the results to clarify which relationships are most appropriate for use, and to provide a quick reference for implementation. The user must understand the limitations and qualifications of the relationships, as described in the Results and Summary sections. Plots are cross referenced back to the original figure in the Results section, which may appear different because of the change to linear scales here (cf. log scales, etc.). Relationships are presented in turn for each stream type and community.

Rocky Mountain Streams

Invertebrates

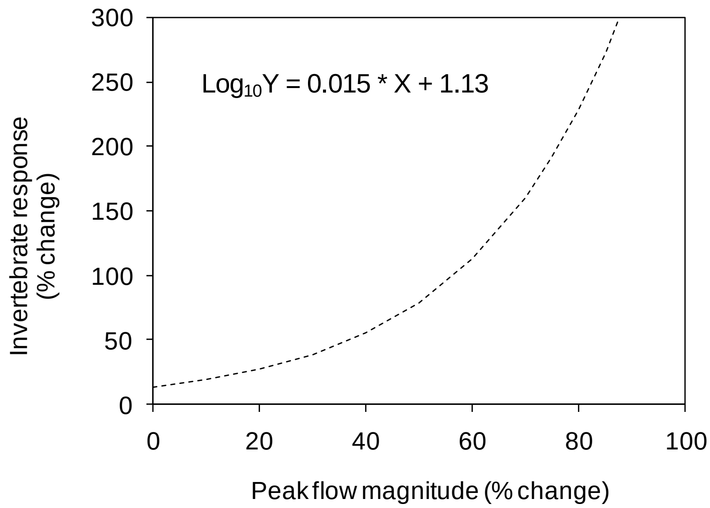
The density of fast-water invertebrates (rheophile species) responds to magnitude of low flow. Method 1 employs the 90% quantile from Figure 6 (Results section). Using the Method 1 equation, calculate a value for the natural flow condition of the site under consideration (24-hour mean annual low flow) and compare this to the value calculated from the existing (altered) flow regime. The response can be presented as a percent change using the two numbers (i.e. [natural – altered] / natural).

Method 1:



Method 2 describes the change of invertebrate populations (diversity and abundance) in response to peak flow alteration. This uses the 75% quantile from Figure 7. Use the percent change in peak flow for the site under consideration (24-hour average annual peak flow) to derive the predicted magnitude of change of invertebrate populations.

Method 2:



Trout

Productive trout fisheries depend on adequate low flow during the summer and autumn. The categories described in Method 3 enable comparison of habitat suitability before and after flow modification, based on summer flows (August-September average) divided by mean annual flow.

Method 3:

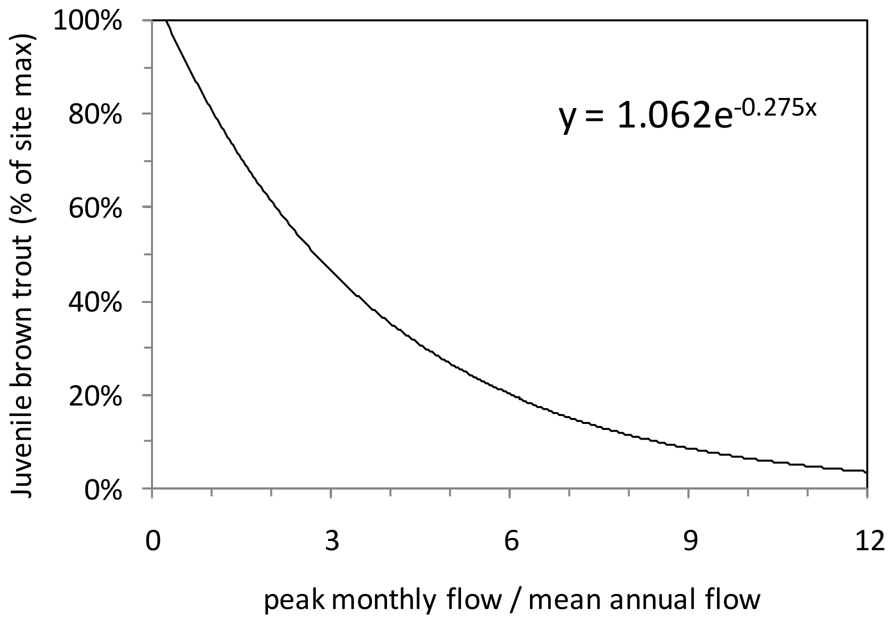
Rating	Summer low flow (% of mean annual flow)	Description
0 (worst)	<10%	Inadequate to support trout.
1	10-15%	Potential for trout support is sporadic.
2	16-25%	May severely limit trout stock every few years.
3	26-55%	Low flow may occasionally limit trout numbers.
4 (best)	>55%	Low flow may very seldom limit trout.

Recruitment of juvenile trout declines in response to peak flow, but elevated peak flows are needed for channel maintenance and excessive trout recruitment can negatively affect the trout fishery (reduced size of adult fish). This effect will be more pronounced for fisheries that presently support high densities of adult trout. The methods provided can be used to evaluate juvenile survival, but not to evaluate overall fishery condition.

Two options are presented for determining recruitment success. As a first option (Method 4), peak monthly mean flows that are <2, <4 and >6 times the mean annual flow indicate high, moderate and poor recruitment of juveniles respectively (derived from Figure 8, Results section). Comparison of peak monthly flows before and after recruitment flow alteration will indicate change in the suitability of peak flows for recruitment. If time series data is available, the inter-year frequency of peak monthly flows for each category will provide a more detailed representation of recruitment success.

Alternatively, the response of trout recruitment to peak monthly flow can be assessed using Method 5. This uses the mean response from Figure 8. Using the Method 5 equation, calculate a recruitment value for the natural flow condition and compare this to the value calculated from the existing (altered) flow regime. The response can be presented as a percent change by dividing the two numbers (i.e. [natural – altered] / natural).

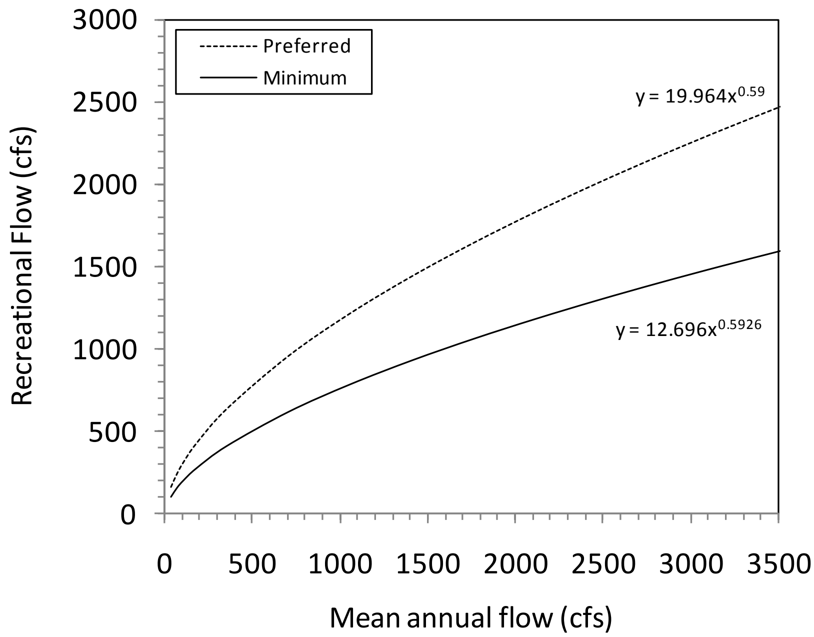
Method 5:



Recreation

Recreational paddlers (rafts, kayaks, etc.) will struggle when flows are too low. Method 6 can be used to estimate a minimum flow and a preferred flow for the site of interest, using the pre-alteration estimate of mean annual flow. Method 6 is reproduced from Figure 15 (Results section). Mean annual low flow for the site of interest can be compared to the minimum flow estimate for paddling, both before and after flow alteration. Preferred flow could be evaluated in the same way or, alternatively, by comparing frequency of days with 24-hour average flows equalling or exceeding the preferred flow before and after flow alteration. The response can be presented as a percent change by dividing the two numbers (i.e. [natural – altered] / natural).

Method 6:



Riparian

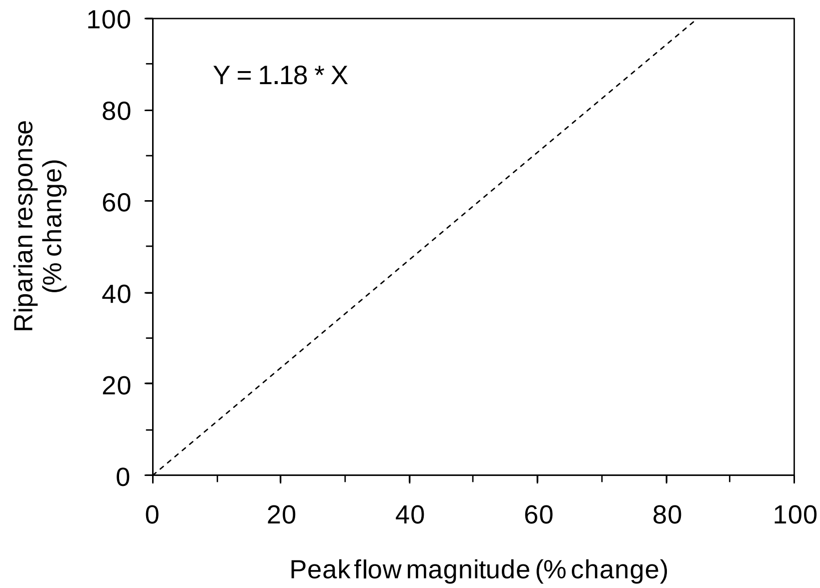
The effects of flow change on riparian communities can be approximated using riparian/peak-flow relationships provided in the Interior Western section (Method 7).

Interior Western Streams

Riparian

Method 7 describes the response of the extent and composition of riparian vegetation to reduced peak-flows. This uses the 90% quantile from Figure 3 (Results section), and can be applied to the site in question using the percent change in peak flow (24-hour mean annual peak flow).

Method 7:



The following table (Method 8) converts the relationship from Method 7 into values for change in peak-flow associated with various levels of change in riparian communities. Such a categorical approach may be useful in some instances (e.g. delineating slight to severe alteration).

Method 8:

Riparian Response	Peak-flow change
10%	8%
25%	21%
50%	42%
75%	64%

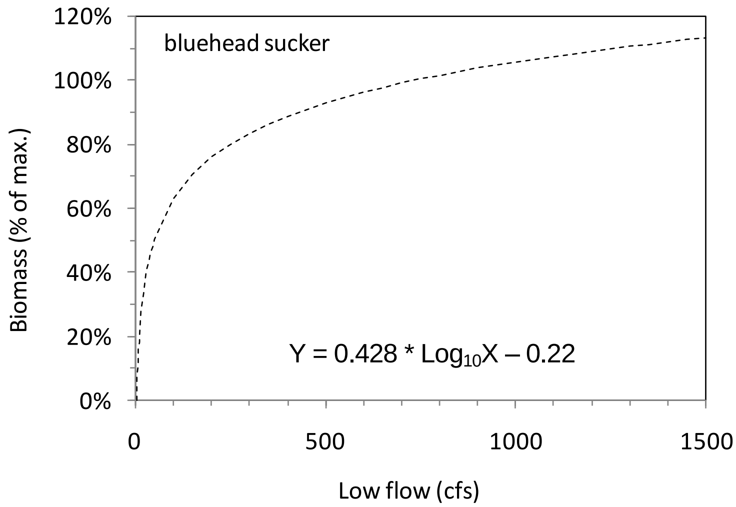
Invertebrates

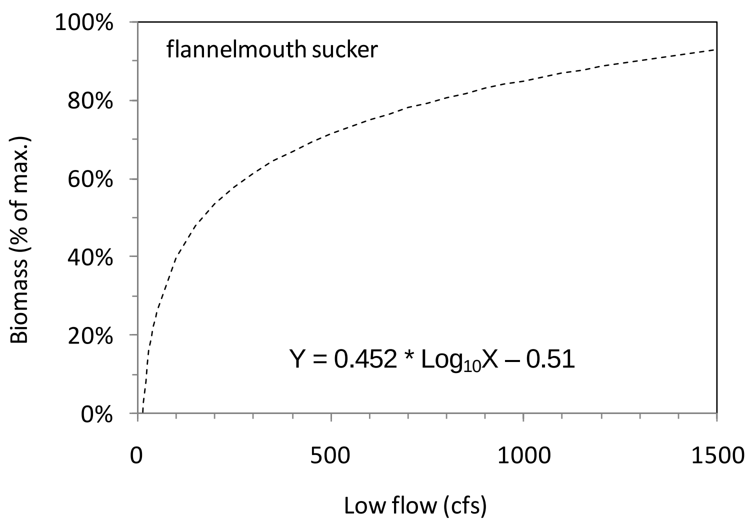
Reduced peak flows affect invertebrate communities, and the responses described for Rocky Mountain streams (Method 2) is also applicable to Interior Western streams. Adequate data were not available for response to change in low flow.

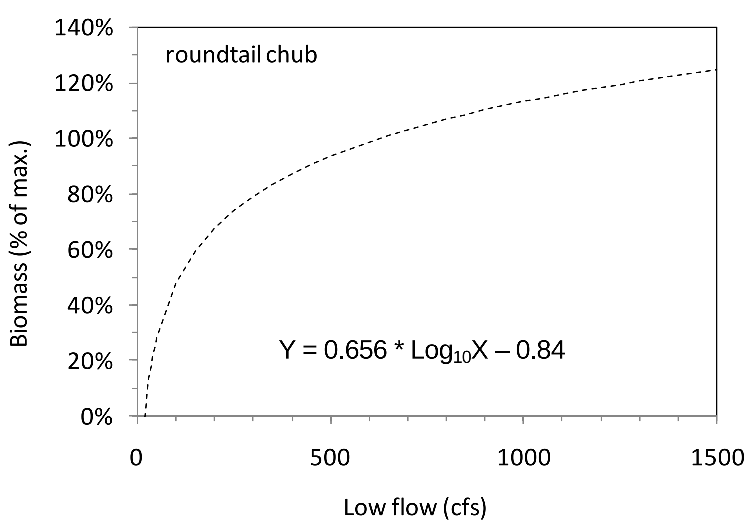
Warm Water Fish

The response of warm water fish to low flow is described in Method 9 for three species inhabiting Interior Western streams. These are based on the 90% quantiles presented in Figures 13 and 14 for low flows. Calculate a value for species relevant to the site under consideration using the 24-hour average low flow for summer autumn. Compare values from flows pre- and post-alteration. The response can be presented as a percent change by dividing the two numbers (i.e. [natural – altered] / natural).

Method 9:

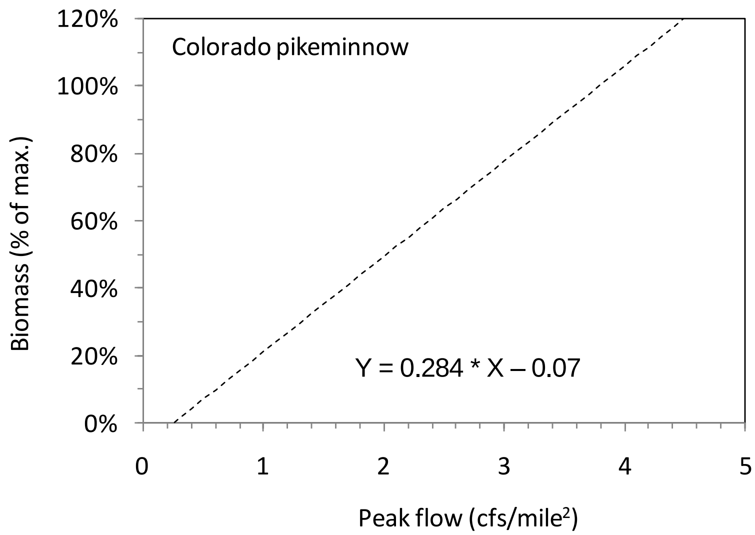

bluehead sucker
Y = 0.428 * Log10X – 0.22
Biomass (% of max.)
120%
100%
80%
60%
40%
20%
0%
0
500
1000
1500
Low flow (cfs)


flannelmouth sucker
Y = 0.452 * Log10X – 0.51
Biomass (% of max.)
100%
80%
60%
40%
20%
0%
0
500
1000
1500
Low flow (cfs)


roundtail chub
Y = 0.656 * Log10X – 0.84
Biomass (% of max.)
140%
120%
100%
80%
60%
40%
20%
0%
0
500
1000
1500
Low flow (cfs)

Method 10 describes the response of Colorado pikeminnow to specific peak flow. This is based on the 90% quantile in Figure 14 for peak flow. Pikeminnow are a federally endangered fish that remain in a few Interior Western rivers of Colorado, and peak flow requirements may have been determined already by site specific investigations. In the absence of such information, use Method 10 to calculate a biomass value for the natural flow condition (24-hour average annual peak flow divided by watershed area) and compare this to the value calculated from the existing (altered) flow regime. The response can be presented as a percent change by dividing the two numbers (i.e. [natural – altered] / natural).

Method 10:



Great Plains Streams

Riparian Vegetation

The response of riparian vegetation to altered peak-flow for streams of the Great Plains is described in the Interior Western section using Method 7.

Warm Water Fish

Flow alteration of many tributary streams (streams without Rocky Mountain headwaters) is severe enough to have already eliminated some fish species. Data was not found to support quantitative relationships with flow for these tributary streams. Likewise, limited information was available to quantify the response of fish to change in peak flow for all rivers of the Great Plains (see Results section for options).

For larger mainstem rivers of the Great Plains that have Rocky Mountain headwaters, Method 11 provides categories of response to low flow for fish habitat. This is reproduced from Table 5 in the Results section (Tennant method). These categories can be compared to 24-hour mean annual low flow prior to and after flow alteration for a given site. This will support conclusions on the degree of fish habitat alteration (e.g. good to poor).

Method 11:

	Low flow (% of mean annual flow)
Optimum habitat	60%-100%
Outstanding habitat	60%
Excellent habitat	50%
Good habitat	40%
Fair or degrading habitat	30%
Poor or minimum habitat	10%
Severe degradation	<10%

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