DISSERTATION

REGIONAL METHODS FOR EVALUATING THE EFFECTS OF FLOW ALTERATION ON STREAM ECOSYSTEMS

Submitted by

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ABSTRACT

REGIONAL METHODS FOR EVALUATING THE EFFECTS OF FLOW ALTERATION ON STREAM ECOSYSTEMS

Three stand-alone chapters explore the development and implementation of regional flow-ecology methods. Ecohydrology is an interdisciplinary field that brings together specialized research in hydrology, hydraulics, geomorphology and ecology. My dissertation reflects the need for interdisciplinary knowledge, tackling issues as diverse as low flows for trout (Chapter 2) to peak flows for cottonwood (Chapter 3). A regional-scale view unifies these investigations, with Chapter 1 establishing the scientific foundation and management objectives for regional flow-ecology methods.

Summary

Chapter 1 - To balance the benefits of dams and water diversions against society's expectations for the natural environment, flow managers require scientific advice on the ecosystem response to flow alteration. The methods selected to investigate the ecosystem effects of flow alteration (e.g., PHABSIM - Physical Habitat Simulation) should reflect the scale of flow management and the information requirements of flow managers. In addition, a hierarchical habitat framework provides an ecological foundation for the development and implementation of flow-ecology methods, because ecosystem response to flow is constrained by large-scale processes. This can be put into practice using hydrogeomorphic classification to define the higher-level physical processes (e.g., sediment transport, disturbance) that dictate the mechanisms of biotic response to flow. Regional flow-ecology methods provide a vehicle for incorporating prior knowledge and hydrogeomorphic processes into flow management at both regional and local scales.

Chapter 2 - Changes in hydraulic habitat (depth and velocity) with flow can be predicted using intensive reach-specific methods, such as PHABSIM. I used existing PHABSIM data to develop GHMs (Generalized Habitat Models) that predict trout habitat-flow curves for unsurveyed streams of the southern Rocky Mountains. Predicted habitat was significantly correlated with the abundance of large brown trout ($P<0.01$), but not smaller trout (using Colorado Division of Wildlife monitoring data). The rapid-survey GHM (from channel width) represents a major reduction in survey effort compared to a full PHABSIM survey, and produced better predictions of observed habitat than the desktop GHM (from mean annual flow).

Chapter 3 - Cottonwood trees are valued members of riparian ecosystems and, in the drier areas of North America, their recruitment depends on high flow events. To help plan for anticipated increased water demand, the ELOHA framework was used to develop flow-ecology relationships for three basins in Colorado (total area 53,000 km^2). Existing data revealed a negative relationship between the abundance of plains cottonwood (*Populus deltoides* Bartram) and reduced peak-flows. The hypothesis that this flow constraint would also apply to a second species, narrowleaf cottonwood (*Populus angustifolia* James), was not supported because four reaches (out of the 39 surveyed) had abundant and reproducing narrowleaf forest, despite pronounced flow alteration (>40% flow reduction). Historic photographs revealed that narrowleaf in the Middle Park area (Colorado) have increased in abundance since dam closure, colonizing previously bare

gravel bars. That narrowleaf appear less sensitive to flow alteration than plains cottonwood could reflect different species traits (e.g., alternative sources of disturbance for root suckering by narrowleaf), together with the many physical transitions from plains to mountains that are associated with the species transition.

Colorado’s flow management – a New Zealand perspective

As an international student, I bring an outside view to Colorado on the application of science to meet societal goals for water. Colorado and New Zealand occupy an equivalent land area (269,837 & 268,021 km^2 respectively) with similar populations (5.1 & 4.4 Ma people respectively) and a relatively short European history (1800’s). Introduced trout provide valued recreational fisheries in both New Zealand and Colorado, and scientists have invested much research in the development of flow-ecology methods that are suited to trout (PHABSIM developed in Fort Collins USA, Bovee, 1982; RHYHABSIM developed in Hamilton NZ, Jowett, 1989). New Zealand and Colorado occupy temperate latitudes (CO 37°N to 41°N; NZ 34°S to 47°S), but the predictable snowmelt flow regime of perennial rivers in Colorado has few analogs in New Zealand, where streams are more often rainfed.

The drier climate of Colorado is reflected in the intensity of water development and in water law. Outside the federal projects and critical habitat for endangered species, water quantity regulation is vested primarily with the State of Colorado and its prior appropriation doctrine (Dawdy, 1992). This doctrine was established in the late 1800's to ensure fair allocation among out-of-stream users, and the water allocated to date remains a permanent (and tradable) property right. The Instream Flow Act of 1972 represented the first step forward for streams, in so much as no legal avenue existed previously to retain flow for aquatic ecosystems. Instream flow rights can only be held by the Colorado Water Conservation Board, which relies on donors because the Board does not purchase existing water rights. The burden of proof lies with the donor of water rights to demonstrate that minimum flows are required to preserve the existing natural environment "to a reasonable degree". Instream flows only impinge on junior water rights (those issued more recently), meaning the instream flow is inconsequential to the operation of senior diversions. The Colorado Division of Wildlife can recommend instream flows using the R2Cross method to estimate minimum depths for fish passage through a riffle (Espegren, 1996). Over 13,400 km of Colorado streams (out of 148,000 km) are afforded some level of protection by instream flow rights, which bears testimony to the efforts of all involved in securing those rights.

New Zealand water law (Resource Management Act, 1991) arguably represents the other extreme, with the burden of proof instead on the *developer* to demonstrate that environmental effects can be avoided, remedied or mitigated. Both Colorado and New Zealand water law seek equity among users, but the Resource Management Act seeks intergenerational equity, that safeguards natural resource options for future generations (Upton, 1995). The legislative differences presumably reflect differences in societal expectations between moist and dry climates. But I would argue the permanent property right means that Colorado water law is permanently bound to societal expectations of the late 1800’s, when the prior appropriation doctrine was formulated. A shift in societal expectations for the natural environment during the 1960’s produced the Instream Flow

Act of 1972, but this legislation could in no way challenge the sanctity of existing private property rights.

Colorado offers a natural laboratory for understanding the consequences of extreme flow alteration for ecosystems. Perhaps this is why Fort Collins scientists have made foundational advances in the development of flow-ecology methods, from IFIM in the 1980’s (Bovee, 1982) to ELOHA in the new millennium (Poff et al., 2010). Research in New Zealand made a significant contribution to the development of PHABSIM (e.g., Jowett, 1992) and I hope this dissertation contributes to the development of ELOHA. I believe New Zealand can also play a role in testing the application of ELOHA to sustain aquatic ecosystems because flow management is regional (Regional Councils implement the Resource Management Act) and this management is receptive to new flow-ecology methods. The potential for collaboration is ongoing.

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Bill Miller and Don Conklin have the foresight to archive the data in a retrievable fashion that studies such as this are possible (three decades separate this chapter from the data collection, in most cases). These people also provided valuable advice, as did Mark Uppendahl, Matt Kondratieff and Vernon Bevan (CDOW). Phil Chapman (Department of Statistics, Colorado State University) provided invaluable advice on the data analysis and provided a better quadratic function that was adapted for this chapter. This chapter was improved from Pamela Kaval’s comments.

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I thank my wife Pam for staying up late to help me study, for raising our son Charlie then working through the night to pay the bills, and for getting me out the house to live life when I needed it most. To Charlie – the best kid in the world.

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INTRODUCTION

Water is a vital resource for both ecosystems and people. Many nations manage flow alteration in an effort to protect ecosystem health and science has an important role to play to inform water management decisions. To fulfill this role, scientists have many tools available for investigating the effects of flow change (Acreman & Dunbar, 2004; Jowett, 1997; Tharme, 2003). Some scientists invest heavily in multiyear studies below one dam (Lancaster & Downes, 2010; Lovich & Melis, 2007), while others develop basin wide methods for several biotic groups on small budgets (Lamouroux & Souchon, 2002; Sanderson et al., 2012). These examples illustrate the divergent scales at which scientists characterize physical processes and biotic patterns.

In this dissertation, three stand-alone chapters explore the development and implementation of regional flow-ecology methods. Ecohydrology is an interdisciplinary field that brings together specialized research in hydrology, hydraulics, geomorphology and ecology. My dissertation reflects the need for interdisciplinary knowledge, tackling issues as diverse as low flows for trout (Chapter 2) to peak flows for cottonwood (Chapter 3). A regional-scale view unifies these investigations, with Chapter 1 establishing the scientific foundation and management objectives for regional flow-ecology methods.

CHAPTER 1: REGIONAL FLOW-ECOLOGY METHODS FOR WATER MANAGEMENT – THE WAY FORWARD

Summary

To balance the benefits of dams and water diversions against society's expectations for the natural environment, flow managers require scientific advice on the ecosystem response to flow alteration. There are many existing methods for investigating the ecosystem effects of flow alteration (*flow-ecology* methods), but little consensus among scientists on which to use. Method selection should reflect the scale of flow management (e.g., large-scale basin planning versus small-scale single diversions) and the information requirements of flow managers. In addition, a hierarchical habitat framework provides an ecological foundation for the development and implementation of flow-ecology methods, because local ecosystem response to flow is constrained by large-scale processes. This can be put into practice using hydrogeomorphic classification to define the higher-level physical processes (e.g., sediment transport, disturbance) that dictate the mechanisms of biotic response to flow. Flow-ecology methods can then assess the likelihood of flow alteration, imposing an over-riding constraint on instream values. These methods should focus on the intersection of species valued by society and flow-dependent species for the specific physical settings where flow dependence arises. Regional flow-ecology methods are an essential tool for applied scientists, providing a vehicle for incorporating prior knowledge and hydrogeomorphic processes into flow management at both regional and local scales. I propose that regional flow-ecology methods should be implemented by

water management agencies as regional guidelines that provide spatially explicit directions for where to focus more intensive flow-ecology methods, in addition to prescribing flow requirements for less contentious flow decisions.

Introduction

Dams and diversions have altered the flow of many streams. For example, Graf (1999) reported some 75,000 dams in the USA over 2 m high and the World Commission on Dams reported over 45,000 dams exceeding 15 m globally (WCD, 2000). The consequences for stream ecosystems have included the collapse of fisheries (Kareiva et al., 2000) and extinction of native fishes (Bestgen et al., 2006b; Falke et al., 2011). Water is a vital resource for both ecosystems and people. Many nations manage flow alteration in an effort to protect ecosystem health (MacDonnell, 2009; McKay, 2005; Memon, 1997; Peters et al., 2011) and science has an important role to play to inform water management decisions.

To fulfill this role, scientists have many tools available for investigating the effects of flow change (Acreman & Dunbar, 2004; Jowett, 1997; Tharme, 2003). Heated debate continues to add uncertainty on which methods to use (Jowett & Biggs, 2009; Lamouroux et al., 2010; Lancaster & Downes, 2010; Williams, 2009). Some scientists invest heavily in multiyear studies below one dam (Lancaster & Downes, 2010; Lovich & Melis, 2007), while others develop basin wide methods for several biotic groups on small budgets (Lamouroux & Souchon, 2002; Sanderson et al., 2012). These examples illustrate the divergent scales at which scientists characterize physical processes and biotic patterns. Rather than promoting one approach as superior to the other, I seek a common, integrative platform that underpins the many flow-ecology methods in order to provide a way forward for science to better inform flow management. Starting with terminology, *flow-ecology methods* relate specific ecological metrics (e.g., abundance, habitat metrics) to flow quantities and variation (e.g., mean flow, ratio of mean to median flow). More specifically, r*egional* flow-ecology methods examine this relationship at a regional scale (see section "Defining the Region").

The objective of this chapter is to establish a common foundation for flow-ecology studies that operate at diverse spatial scales to inform the various needs of flow management. I argue that regional methods are an essential tool for applied scientists, as they provide a vehicle for incorporating prior knowledge and large-scale processes into flow management at both regional and local scales.

Ecological foundation for flow-ecology studies

Habitat is the templet on which the success of evolutionary strategies is determined (Southwood, 1977) and, for streams, physical habitat is defined, constrained or at least influenced by flow (Minshall, 1988; Poff et al., 1997). The habitat templet can be viewed as a hierarchy, with large-scale processes constraining the biotic response to small-scale processes (Allen & Starr, 1982; Frissell et al., 1986; Poff & Ward, 1990; Thorp et al., 2006). The hierarchical filters framework of Poff (1997) provides a useful synthesis of these concepts and an ecological foundation for the application of flow-ecology methods for streams. For example, the flow disturbance regime constrains (or "filters") what species survive to respond to small-scale processes such as substrate size and biotic interactions (Figure 1.1). In this conception, *high*-level constraints that apply across a broad spatial extent are expected to exclude a species (or reduce abundance) over a greater contiguous area or time than are *low*-level constraints, which are more localized in their effects.

Understanding the concept of *scale* is central to understanding the hierarchical framework (Allen & Starr, 1982; Biggs et al., 2005; Dollar et al., 2007; Dunbar et al., 2011; Habersack, 2000), and ecology in general (Connell & Sousa, 1983; Levin, 1992; Wiens, 1989). The spatial area over which physical and biological processes act (or, at least, are observed) are best understood by separating *grain* and *extent* (Guisan & Thuiller, 2005; Wiens, 1989), with grain describing the sampling unit (e.g., 0.1 m^2 quadrat) and extent describing the area over which sampling is completed (e.g., 100 m^2 riffle). These concepts also apply to temporal scaling, with grain defining the sample duration (e.g., time-step) and extent defining the total monitoring period.

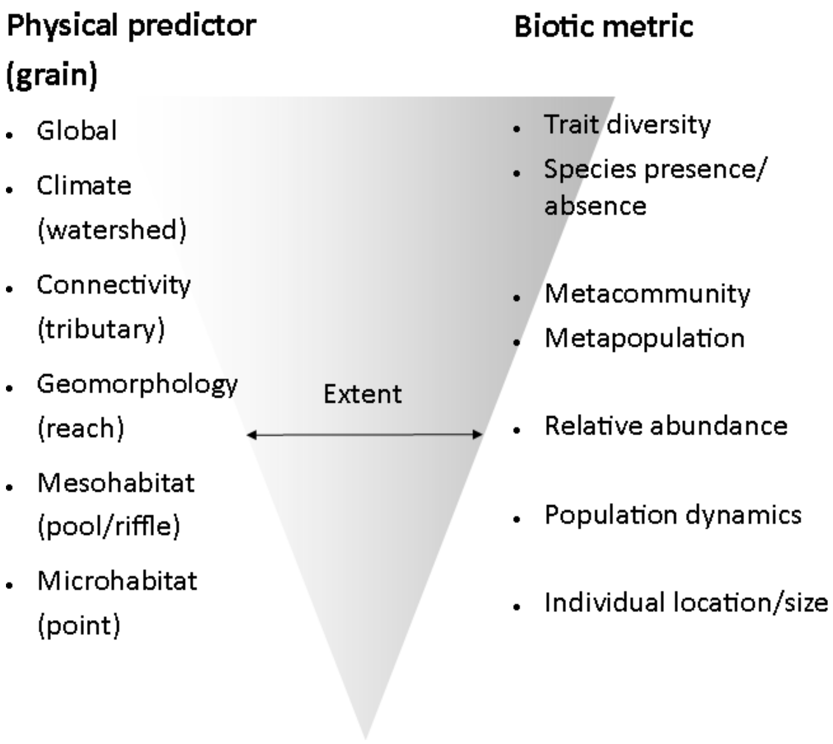


Figure 1.1 The hierarchal framework, showing a stream example with climate delineated at higher levels, which constrains the regional species pool available to respond to geomorphology, and so on. The extent over which each constraint applies decreases at lower levels in the hierarchy, as represented by funnel width, with the grain (sampling unit) named in parentheses. Metrics for biotic response increase in detail for lower-levels, made possible by the smaller grain of investigation.

The hierarchical framework also provides context for individual flow-ecology methods and individual flow management decisions (Figure 1.2). Flow is not the only constraint acting on a population, but models that are constructed to inform flow management must incorporate those flow components that are a potential constraint for the valued species, as a consequence of the altered flow regime. Hydraulic habitat models (e.g., PHABSIM - Physical HABitat SIMulation) describe few mechanisms of constraint (velocity, depth and substrate at baseflows) and fall well short of describing all possible population constraints, including the disturbance regime and other flow-related constraints (Poff et al., 1997; Power et al., 1996). But hydraulic habitat can impose a flow-related constraint on some populations (e.g., drift-feeding trout; Fausch, 1984) and, therefore, PHABSIM is one of several flow-ecology methods worthy of consideration.

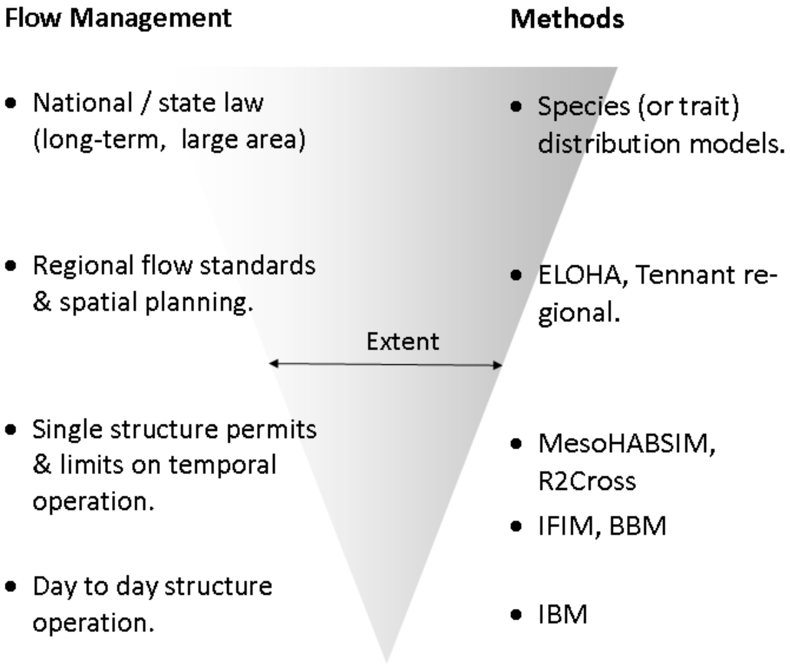


Figure 1.2 Flow-ecology methods and flow-management are both placed within a hierarchical framework, as per Figure 1.1. On the management side, this portrays laws constraining local decisions on individual structures, and so on. The methods used should reflect the scale of management under consideration. For example, prescribed operational limits for a single dam can be informed by more precise flow-ecology methods, such as IFIM. Because of the limited spatial extent of such precise methods, ELOHA (Poff et al. 2010) is the better option for spatial planning (e.g., where to build a dam). Acronyms are described in the following section.

The population size of any species at any point in time/space represents the integrated effect of all constraints, both abiotic and biotic. The flow regime does not completely determine the physical environment and, hence, population dynamics are not completely dictated by flow management. Even if predicting population abundance is the sole purpose of the model, it is rarely possible to consider all necessary physical and biological processes (Pearson et al., 2004). For example, population dynamic models based on detailed demography and dispersal data are often constrained to the small extents ($<10^2$ km^2) over which such metrics can be measured (Grossman et al., 2006; Milhous & Bartholow, 2006), and so are unlikely to be useful in defining both high and low temperature limits for a species (given the expense of replicating the study across temperature extremes). Conversely, species distribution models that describe occurrence over large extents (10^6 km^2) might only consider large-scale physical processes, such as temperature and flood frequency (Fausch et al., 2001; Guisan & Thuiller, 2005) and, thus, miss important local-scale constraints. Furthermore, these species distribution models typically do not attempt to distinguish good years for recruitment from bad. Compiling an adequate sample-size of small-scale population dynamic models (10^2 km^2) as the grain for regional-scale species distribution models (10^6 km^2) is logistically infeasible and financially impractical and, thus, a framework is needed to guide the selection of appropriate methods. Defining the natural flow regime and geomorphic setting in which to develop flow-ecology methods, as recommended by Poff et al. (2010), helps define the large-scale physical processes from the outset (see section “Defining the Region”).

The biotic response that we observe for a given physical process is scale dependent (Allen & Starr, 1982; Wiens, 1989). For example, flow-disturbance can act as a small-scale constraint, with an individual high-flow *event* typically producing a *negative* effect on population abundance (Brooks & Boulton, 1991; Lancaster, 1996; Matthaei et al., 1996; Poff, 1992). But we can also look at the flow disturbance *regime* (sensu Poff et al., 1997) as a large-scale constraint, revealing the importance of disturbance for community structure and for the success of introduced species (Bernardo et al., 2003; Fausch et al., 2001; Marchetti et al., 2004; Riis & Biggs, 2003). Over evolutionary time scales, species may become adapted to certain elements of the flow regime (Lytle & Poff, 2004; Poff, 1992). In ecological time, the decline in abundance with each passing flood (small scale), and subsequent recovery, will propagate over multiple flood events to drive community structure, as revealed by decadal studies (Boulton et al., 1992; Power et al., 2008; Vinson, 2001). But few studies manage to quantify abundance over sufficient time or space to demonstrate the net effect on communities, especially if the net effect is a product of rare events (e.g., Rood et al., 1998). Large-extent studies can demonstrate the integrative effect of the disturbance regime for communities, in part because the variability of coarse biotic metrics (e.g., presence-absence) is not overwhelmed by short-term population fluctuations (e.g., abundance) (Allen & Starr, 1982; Thorp et al., 2006).

There is a trade-off between the grain at which we can quantify abundance and the extent over which this fine a grain can be replicated (Wiens, 1989). Oftentimes, we must choose either small-grain, precise mechanistic studies (e.g., Lancaster & Downes, 2010; Waddle et al., 2000) that have a high uncertainty of net effects at large extents where other factors come into play, or large-extent, observational studies of the net effect of flow (Poff et al., 2010) that have greater uncertainty as to the contribution of the non-flow process to local observations. We must consider this trade-off for each investigation, but the two approaches should be complementary across studies, with scientific literature guiding the development of *mechanistic hypotheses* as a starting point for developing regional flow-ecology methods (Lowe et al., 2006; Poff et al., 2010; Wiens et al., 1993). A mechanistic hypothesis specifies the physical processes that gives rise to the expected biological pattern, which is relevant here for understanding biotic response to flow-driven processes.

I have framed flow-ecology relationships in terms of a hierarchical framework and scale, which are not exclusive of other ecological paradigms. For example, food webs (Power et al., 2008) and the natural flow regime (Poff et al., 1997) can be described as hierarchical constraints, while geomorphic stream units can be described as patches (Thorp et al., 2006; Winemiller et al., 2010). These paradigms are important and flow-ecology studies have much to gain from them.

Management Objectives

Let us define a *flow manager* as a person or group making decisions that limit the quantity and timing of water flow alteration (e.g., a commissioner or board deciding the fate and operating rules for a proposed dam). Decisions affecting flow management are made at many levels, from establishing law, to planning for future water demand, to managing individual dams and diversions. Like stream ecosystems, these roles can be viewed hierarchically (Figure 1.2), with policy makers constraining a flow manager’s decisions on individual dams and diversions. The flow manager’s decision, in turn, determines what subset of all proposed dams and diversions meets regulatory requirements or society’s expectations, and constrains day-to-day reservoir operations. In this chapter, I treat laws or policy prescriptions as fixed, in order to focus on the role of science to inform both regional flow managers and single-structure flow managers who must operate within the confines of existing law.

A flow manager is often tasked with balancing society’s competing expectations for water supply, jobs and the natural environment. The relative weighting afforded to each expectation varies with the socio-political context (MacDonnell, 2009; McKay, 2005; Memon, 1997; Peters et al., 2011), but still requires scientific advice on the consequences of flow alteration for instream values. To contribute effectively to flow management, the scientist must understand the specific information requirements of the flow manager. The following list can provide a useful starting point:

- focus on species valued by society - more specifically, the intersection of valued species and flow dependent species for the specific physical settings where flow dependence arises (e.g., flood dependence by cottonwood (*Populus*) seedlings on point bars in meandering river reaches);
- formulate predictions in terms of the flow components being altered;
- state the predictions at a scale relevant to management/development (e.g., single reach or basin, months or decades);
- complete the study within the permitting timeframes (e.g., <1 year) and budgets;
- communicate results effectively to managers.

Effective communication often clashes with the currency of science – uncertainty (Baron, 2010; Wiens, 2002). When talking to flow managers and stakeholders, the main point can easily be lost in caveats and error bars (error is a mistake to most people). But it would undermine scientific credibility if uncertain outcomes were presented as truth. How far should the scientist go to convey the climatic and land use factors that might overwhelm the response to flow? Scientists can focus on what they do know by describing the scenarios under which a study’s main findings are likely to hold (e.g., a particular season in dry or wet years, or a confined geomorphic setting). Or, as Carpenter (2002) suggests, information should be structured to help flow managers identify management actions that are robust across future scenarios of climate, development, and other aspects of global change.

Any single flow management decision will not *completely* dictate the future physical stream environment. Flow managers are limited in their scope of authority to affect change. With few exceptions, degradation of local streams and rivers is the sum of many small, incremental changes in land and water use that have cumulated over decades. Natural climate will also continue to drive the physical environment, in spite of flow regulation (Lovich & Melis, 2007). Rather than predicting population sizes of species resulting from an individual dam or diversion, a more realistic goal for flow-ecology studies is to assess the likelihood of flow alteration imposing an over-riding constraint on instream values and, ideally, the scenarios under which this constraint could arise.

To further clarify the management objectives, I contrast the role of *flow* management (e.g., dam regulation) with the role of *population* management (e.g., fisheries, endangered species). Models for population management aim to predict population abundance to inform decisions regarding stocking, restrictions on harvest, or whether interventions will help the recovery of endangered species. Flow might be included in population models, but this is secondary to their purpose. For example, Bestgen et al. (2006a) used an Individual Based Model to predict impacts of introduced predators on survival of Colorado pikeminnow larvae (using predator density, temperature, etc.). That flow is absent from this model reflects its use for population management, rather than flow management. In contrast, flow-ecology models must include flow metrics that are relevant to flow management. The flow metrics must also be relevant to the species of interest, but predicting population dynamics is not the primary objective. For example, Thomas & Bovee (1993) used PHABSIM to precisely quantify the spatial and temporal dynamics of depth and velocity, as a function of flow, and relate this to the species of interest using only a yes/no classification of habitat suitability. Each model describes a specific constraint; hence, we should not assume their scope is adequate to inform management. But much of the debate regarding the validity of flow-ecology methods (Lamouroux et al., 2010; Lancaster & Downes, 2010) can be reformulated into a more useful contrast between the competing objectives of flow management versus species population management.

What if the flow management objectives include population targets? This might be expected where large flow developments impinge on highly valued fisheries or endangered species (e.g., Lovich & Melis, 2007). In this case, a more balanced model may be required that uses a flow-dynamic model to generate the predictor variables for a population-dynamic model (e.g., Jager et al., 1993; Van Winkle et al., 1998). Population predictions will require a broader range of predictor variables than flow alone, because flow is unlikely to be the sole determinant of abundance (i.e., flow is not the only hierarchical constraint). For this reason, *balanced models* are a better complement to *balanced management* – management that has control over a broader range of population constraints (e.g., pollution, invasive species, catch rates, flow alteration). Predicting population dynamics is challenging (Carpenter, 2002; Van Winkle et al., 1998); long-term predictions are arguably impossible (e.g., over a 25 year permitting cycle for a dam).

Adaptive management may help, as it enables model flexibility at a temporal scale at which predictions of population dynamics can be revised and improved (see Walters & Holling, 1990). For adaptive management based on population dynamic models, the financial commitment to ongoing monitoring and model revision might only be justified when society as a whole depends on development (see Lee, 1999; McLain & Lee, 1996) and population collapse is not acceptable. Managing multiple developments jointly may facilitate more sophisticated modeling. For example, the Northwest Power and Conservation Council manage hydroelectric dams across the Columbia River basin, including Idaho, Montana, Oregon, and Washington (NPCC, 2010). This facilitates advanced research and monitoring methods that would not likely be possible for each dam in isolation, but it also further complicates implementation (McLain & Lee, 1996).

For large developments, negotiating economic gains against incremental habitat change may be desirable (e.g., IFIM; Bovee et al., 1998), but nobody wants to be drawn into lengthy negotiations for every small-scale development (e.g., small diversion from a large river). At the other end of the method spectrum, *historic flow methods* are developed using only flow data and may be implemented as a non-negotiable standard (e.g., $7Q_{10}$). Such methods tick all the boxes for simplicity and speed, so these may continue to be used as a default standard by flow managers for those many small developments (e.g., ACT, 2011).

Regional methods are needed to bridge the gap between intensive methods (applied to large developments) and historic flow methods (applied to the smallest diversions). I believe this gap is also where direction is most needed, because the scientists performing this task are not likely to be specialist ecohydrologists, insofar as they have to shoulder much broader responsibilities, such as point discharges, wetland vegetation, etc. (Annear et al., 2009). Regional methods have many other applications, including planning for future water use at a large-basin scale (Sanderson et al., 2012) and guiding the selection of intensive reach-specific surveys. Regional methods could ultimately eliminate the need for historic flow methods if the regional methods can be implemented just as easily; this was shown to be possible for the state of Michigan with a user-oriented web tool (Hamilton & Seelbach, 2011).

Defining the Region

Defining the region in which to develop flow-ecology methods helps define the large-scale physical processes that constrain the response to flow alteration. Poff et al. (2010) recommend classifying the flow regime as the higher level constraint (e.g., Poff, 1996), then subdividing this by the geomorphic setting (e.g., Montgomery & Buffington, 1997). A hydrogeomorphic region then defines a population of reaches (connected or not; Thorp et al., 2006) that experience similar physical processes and, therefore, provides a foundation for developing mechanistic hypotheses of biotic response to flow (Montgomery, 1999; Poff et al., 2006; Thorp et al., 2010). Within the region defined, a common mechanism of response to flow (e.g., trout bioenergetics; cottonwood seedling growth on point bars) should improve the predictive success of flow-ecology methods.

Geomorphic frameworks have evolved over time from the River Continuum Concept (Vannote et al., 1980), to Process Domains (Montgomery, 1999) and Functional Process Zones (Thorp et al., 2006). Each strives to represent physical processes, such as regimes of flow disturbance and sediment transport, plus the factors that govern these processes (climate, geology, topography) (Montgomery, 1999; Thorp et al., 2006). These processes dictate the habitat templet for stream biota, including channel morphology (e.g., meandering, riffle/pool), substrate size (e.g., cobble, sand), water depth and velocity. Classifying stream units (e.g., reach) into process zones or domains can be achieved using remotely sensed predictors, such as water runoff models combined with valley form and channel slope (Bledsoe & Carlson, 2010). Defining the hydrogeomorphic unit as a reach also defines the grain of regional flow-ecology methods. It is then a matter characterizing a sample of reaches using existing survey data (e.g., biological surveys in Chapter 3; reach-specific flow-ecology studies in Chapter 2).

There is a trade-off between the extent of the region and reliability of the flow-ecology relationship defined at the reach grain. Reducing the extent of application for a flow-ecology method to only surveyed sites should improve the chance of predictive success, but the diminished extent exacerbates the problem of science not keeping pace with water resources planning and development. The natural landscape will also impose restrictions on the extent of application. For example, changes in physical processes will be more rapid for more heterogeneous riverscapes and, therefore, a smaller region may be required (e.g., North America’s Great Plains are larger than New Zealand’s volcanic plateau).

There are two options for regional definition. One option is to define the region using *a priori* physical thresholds, such as using channel slope to delimit step-pool from pool-riffle streams (Montgomery & Buffington, 1997). Standardized classifications have applications across sub-disciplines of stream science (e.g., flow response of stream invertebrates - Wilding et al., 2011; and riparian vegetation - Chapter 3). The second option for regional definition is to select the thresholds that better discriminate biological response (Leathwick et al., 2011). This should improve the definition of regional boundaries that are specific to a biotic group and/or a flow-ecology method. Biological delineations can then be developed, if and when the need arises, from the more foundational physical attributes (e.g., slope, water balance). A flexible and adaptable regional definition will permit refinement over time as our knowledge of the system improves, including improved remote sensing of areas that experience similar physical processes (Mertes, 2002) and a better understanding of the mechanisms of ecological response to flow.

The rise of regional flow-ecology methods

Excellent reviews are already available describing the many flow-ecology methods (Acreman & Dunbar, 2004; Annear et al., 2004; Jowett, 1997; Karim et al., 1995; Tharme, 2003). This section instead focuses on a select few methods that illustrate method development over the last four decades and that provide contrast in scale of observation and management to better illuminate a way forward.

Tennant Method

Donald Tennant published this foundational method in 1976, which offers both a reach-specific survey method plus a regional method (Tennant, 1976). The reach-specific method uses field surveys that are repeated at several different flows (e.g., wetted perimeter, photos), to inform expert opinion on what flow is required by a multitude of instream values. Tennant (1976) considered a broad range of instream values (cold and warmwater fish, invertebrates, riparian plants and animals, recreation and aesthetics). Expert opinion on these values may have been informed primarily by changes in width, depth and velocity (from the parameters studied in his Table 2, and his Figure 3 plot).

The regional method was developed from the many reach-specific surveys already completed by Donald Tennant. He managed to summarize his extensive knowledge in a simple table of thresholds that were expressed as a percent of mean annual flow (Table

1.1). It is one of the most commonly applied regional methods (Reiser et al., 1989), arguably because it can be applied quickly over multiple streams (only requires mean annual flow) and the output can be conveyed simply to managers. Tennant was satisfied that streams required the same *proportion* of mean flow, regardless of size or stream type, and this is probably his most contentious assertion (Orth & Leonard, 1990; Rosenfeld et al., 2007). Even so, blanket minimum flows of 10% of mean flow represent a very selective interpretation of the Tenant method. The original article stated that flow recommendations should consider “flows that mimic nature” (p. 7) and further pointed out the method’s flexibility for setting “stream flows that are appropriate portions of monthly, quarterly, or annual instream supplies of water” (p. 8).

Table 1.1 Thresholds defined by Tennant (1976) for flows that provide described levels of protection for instream values (left column), expressed as a proportion of mean annual flow. In addition to this regional method, Tennant also describes site-survey methods that were the basis of these thresholds.

	Apr.-Sept.	Oct.-Mar.
Flushing or maximum	200%	200%
Optimum habitat	60%-100%	60%-100%
Outstanding habitat	60%	40%
Excellent habitat	50%	30%
Good habitat	40%	20%
Fair or degrading habitat	30%	10%
Poor or minimum habitat	10%	10%
Severe degradation	<10%	<10%

Waters Method

The reach-specific method developed by Tennant (1976) used data collected at a discrete set of flow magnitudes and lacked a formal method for interpolating between those flows. Likewise, Waters (1976) surveyed a specific reach at a discrete set of flows but, instead of expert opinion, he developed more quantitative methods for describing habitat at each flow. His model used measurements of depth, velocity and cover, with each related to trout habitat criteria that were derived from the literature (e.g., trout resting habitat, spawning and invertebrates as trout food). The output was akin to weighted usable area (Figure 1.3); this approach was inspirational for the developers of PHABSIM (*pers. comm.* R. Milhous). Both the Waters Method and Tennant's site-survey method are somewhat dependent on a large dam to release flows on demand to enable surveys at informative flow increments. Waters (1976) did not provide a regional method, but he did suggest that methods could be developed for applying the results from surveyed streams to other streams of the same type based on a "stream coding system".

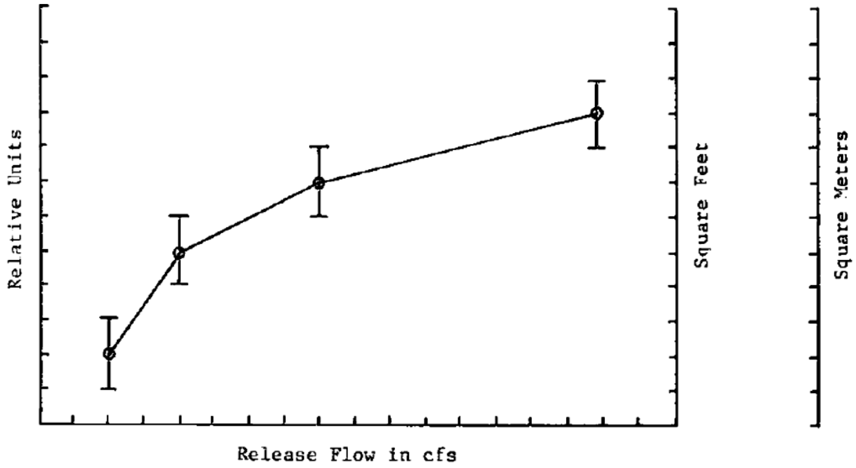


Figure 1.3 Example output from the reach-specific habitat model of Waters (1976). This model quantified trout habitat (y-axis) in terms of depth, velocity and substrate at a discrete set of flows (x-axis), with straight-line interpolations simply connecting the dots. Interestingly, 90% confidence intervals were calculated from the standard-deviation of spatial replicates (reproduced from Waters, 1976). Flow expressed in cfs – cubic feet per second.

R2Cross

This reach-specific survey method was developed in the 1970s (Isaacson, 1976) and is still in use today for justifying instream flows in Colorado (Espegren, 1996). One cross-section can be surveyed to represent the shallowest riffle in a reach, with Manning's equation used to predict change in depth with flow. The practitioner can then estimate the flow that achieves a minimum depth for adult trout to swim through and also consider targets for velocity and wetted perimeter (Table 1.2). The depth criteria, which often dictate the recommended flow (Nehring, 1979), were based on a sliding scale (1% of width) because smaller adult fish were assumed to live in smaller streams. Flow recommendations were typically 25% of mean annual flow (Nehring, 1979), presumably as a result of the sliding scale. R2Cross provided a rapid-survey, reach-specific method, rather than a regional method. Only a single riffle was surveyed, but R2Cross claimed reach extent by requiring the surveyor to traverse the reach in search of the shallowest riffle. Nehring (1979) considered R2Cross less biologically informative than PHABSIM. To understand R2Cross, we must understand that flow management by the State of Colorado does not prescribe a minimum flow, but rather specifies the cubic feet per second allotted to instream use (Dawdy, 1992). Flow-ecology methods are not the limiting factor for improved water management because pre-existing water diversions are permanent property rights that are unaffected by junior (i.e., later) instream flow allocations. The continued use of R2Cross also presents a valuable lesson for scientists in the value of a method that is quick to implement (1 site visit, 1 cross-section) with standardized habitat targets (Table 1.2).

Table 1.2 R2Cross targets for depth, width and velocity used to derive flow recommendations from a riffle cross-section (from Espegren, 1996)

Bankfull width (ft)	Average depth (ft)	Wetted perimeter (% of bankfull)	Average velocity (ft/s)
1-20	0.2	50%	1.0
21-40	0.2-0.4	50%	1.0
41-60	0.4-0.6	50-60%	1.0
61-100	0.6-1.0	≥70%	1.0

IFIM - Instream Flow Incremental Methodology

The IFIM was developed in the late 1970s and early 1980s as a state-of-the-art framework for informing flow management of individual structures (Bovee et al., 1998). Pre-existing methods surveyed a *discrete* number of flows (e.g., Tennant, 1976; Waters, 1976) and therefore presented few flow alternatives. IFIM instead offered a more *continuous* approach that described the incremental change in habitat with flow (Bovee et al., 1998). This could form the basis of negotiations by stakeholders for large water projects (e.g., federally funded dams). The level of protection could then be varied according to the benefits of development (e.g., number of jobs) and the significance of instream values (e.g., endangered species). This framework integrated both social and scientific considerations (p. 6 in Bovee et al., 1998). To this end, the IFIM manual details how to approach stakeholders and develop their concerns into mechanistic hypotheses (pp. 17-32 in Bovee et al., 1998). IFIM was designed to describe change in *habitat* with flow, rather than number of *fish* with flow, because of the difficulty measuring populations and the many other determinants of population success including stochastic processes (p. 30, Bovee et al. 1998).

It is important to distinguish the framework (IFIM) from the component models that include hydraulic habitat (PHABSIM; Waddle, 2001) and temperature (SNTEMP; Bartholow, 2000). That said, PHABSIM is the cornerstone of the IFIM framework. PHABSIM effectively combined the Waters (1976) Method for quantifying hydraulic habitat at surveyed flows with hydraulic methods that interpolate depths and velocities between survey flows (e.g., Water Surface Profiling; Spence, 1976; R2Cross; Isaacson, 1976). PHABSIM has become more sophisticated over time including more options for hydraulic modeling (Ayllón et al., 2008; Maddock, 1999; Waddle, 2001), and is still based on labor intensive measurements at a point-scale, which often limits the spatial extent to a few hundred meters of stream. The method relies on the surveyor to choose a "representative reach" so that the survey can be assumed representative over the extent of interest to flow managers (e.g., all reaches between a dam and major confluence in a particular geomorphic setting).

In contrast to PHABSIM, the SNTEMP model is designed to be used to predict water temperature at a watershed-extent and is calibrated using temperature observations at a reach grain (if temperature is sufficiently uniform over the reach). The IFIM framework also includes a stream network model (Bartholow & Waddle, 1986), which can be used to combine and upscale individual model predictions into units of river miles of suitable habitat (for a given flow scenario) if this better matches the management scale.

IFIM is not a regional method – it is better described as the antithesis of regional methods. Rebelling against the simplifications of one-size-fits-all methods and the subjectivity of expert opinion (e.g., Tennant, 1976), IFIM started a trend of increasing reach-specificity and model complexity. The method is complex, but natural systems are even more complex and hence the simplifications and implicit assumptions of PHABSIM have been extensively debated in the literature (Hudson et al., 2003; Lancaster & Downes, 2010; Orth & Maughan, 1982; Petts, 2009; Railsback et al., 2003; Rosenfeld, 2003; Scott & Shirvell, 1987; Williams, 2009). At the same time, its complexity also presents a cost/time barrier (Armour & Taylor, 1991) which often relegates its use to large water developments (Estes & Orsborn, 1986). Used in the right context (e.g., cool trout streams), PHABSIM is still an informative tool (Jowett, 1992).

MesoHABSIM

MesoHABSIM predicts the change in physical habitat with flow using a larger grain size than PHABSIM, from which this method evolved (Parasiewicz, 2007). The author advocates hierarchical sampling, with basins divided into hydrogeomorphic classes (e.g., based on channel slope), and the class of interest is further divided into pools, riffles, etc. (mesohabitat), with point-scale samples (microhabitat) within each mesohabitat. The change in area of mesohabitat with flow is modeled (or described), which represents a larger grain size than the microhabitat modeled by PHABSIM (point-scale depth and velocity). Like the methods from Waters (1976) and Tennant (1976), MesoHABSIM surveys habitat at a discrete set of flows without a mechanistic model to interpolate between these flows.

The increase in grain size allows increased spatial extent, compared to PHABSIM (Parasiewicz, 2007). An increase in surveyed length is helpful, given flow managers are typically concerned with a greater length of river than can be surveyed in any detail (e.g., between dam and a major confluence). But this is still a labor-intensive method that is justified for large resource developments. MesoHABSIM selects variables for the biological models (habitat use criteria) that better predict spatial variability in species occurrence (e.g., substrate, cover), to the point where velocity and depth can be omitted entirely. The question then arises, do the best static predictors of spatial occurrence (e.g., substrate) also determine the temporal response to flow alteration (e.g., flow required to submerge the substrate)? The potentially heavy emphasis on habitat/cover reveals this method's strength for the many non-salmonid species that are less dependent on drifting food (Parasiewicz & Walker, 2007).

BBM - Building Block Method

Like IFIM, the BBM is a framework targeted at individual projects with the method manual focusing on intensive reach-specific studies (p. 65 in King et al., 2000). The BBM also resembles Tennant's site-survey method, using expert recommendations that are informed by site visits and empirical data. And like the Tennant Method, the BBM promises consideration of a broad range of instream values and how these vary over time (from low flow to flood flow), using point measurements of depth and velocity to relate these values to flow units (p. 60, King et al., 2000). Tennant (1976) mentioned the importance of the flows that mimic nature, compared to the BBM that examines, more formally, the components of the natural flow regime that will maintain natural biota. Each flow regime component is a "building block" defined by flow magnitude, duration, frequency and timing (p. 54, King et al., 2000). The BBM is site specific, using the IFIM approach of defining one or two sections that are representative of a multi-reach geomorphic unit – a spatial extent relevant to the management of a single large dam or diversion. Site replication is a potentially expensive undertaking (p. 72, King et al., 2000), so I do not consider BBM to be a regional method. The BBM can be triggered if proposed flow alterations exceed the instream flows that are predicted by a desktop regional method, and this regional method was apparently developed from previous BBM investigations elsewhere (p. 48, King et al., 2000).

ELOHA – Ecological Limits of Hydrologic Alteration

The ELOHA framework (Poff et al., 2010) has much in common with IFIM and BBM, including some authors (John Henriksen, Rebecca Tharme). Like the earlier frameworks, ELOHA recognizes that the social and scientific processes must be brought together before, rather than after, the model predictions are presented to stakeholders. Both ELOHA and IFIM describe methods for developing mechanistic hypotheses of biotic response to flow.

The main point of distinction is scale. ELOHA provides a framework for developing flow-ecology methods that can be applied at a regional extent to assess many streams and rivers simultaneously, in contrast to IFIM and BBM that are formulated for individual developments with few sites. ELOHA offers scientists an affordable escape from historic flow methods (e.g., $7Q_{10}$) in situations where more intensive methods are not warranted. The flow-ecology relationships can be more flexible in terms of the species assessed, the scale of assessment and the flow regime components incorporated, provided that the necessary biotic and flow data are available. The ELOHA framework can make use of reach-specific methods, the extent of which becomes the grain of the regional flow-ecology methods (e.g., the extent of a PHABSIM study becomes the grain of a generalized habitat model in Chapter 2). ELOHA can also use biological data directly, for which the mechanistic intermediary (e.g., velocity and depth) is only represented in the hypotheses. Users are directed to classify areas with a common flow regime (e.g., snowmelt) and then sub-classify by the geomorphic setting (e.g., wide alluvial valleys) to define reaches that experience similar hydrogeomorphic processes. Within this stratified physical context, biotic response to flow should be more consistent and perhaps predictable. This more quantitative recognition of the broader environmental setting is essential for larger study areas, compared to BBM and IFIM that may traverse fewer stream types and, hence, can rely on expert judgment for classification.

Historic flow methods

Historic flow methods are developed and implemented using only flow data, with at best a theoretical biological basis (e.g., assuming natural drought flows are acceptable minimum flows for aquatic ecosystems). There is continued demand for such methods which have diversified over the years from considering only low-flows (e.g., $7Q_{10}$) to considering the broader flow regime (ACT, 2011; Richter et al., 2011). Historic flow methods can be applied at a regional extent and this is achieved using widely available predictor variables (e.g., mean flow).

I have defined these methods by the absence of biotic data used in their development. But historic flow methods still fulfill a vital need for managing flows in the many streams and rivers where scientific understanding of local flow-ecology relationships is lacking.

Lessons from History

Regional flow-ecology methods are nothing new, nor are they simply a precursor of more advanced reach-specific methods. There is ongoing demand for methods that can be applied rapidly over multiple streams, as seen in the continued use of R2-Cross (Espegren, 1996) and the Tennant Method (Tennant, 1976), plus the recent application of the ELOHA framework in 8 states (Kendy, 2012). Reach-specific methods have gained in complexity over time (e.g., Tennant to BBM), and so too have regional methods ($7Q_{10}$ to ELOHA) that often use the results from reach-specific surveys as the replicate grain to cover a large extent (e.g., PHABSIM surveys are the grain for Generalized Habitat Models; Chapter 2).

The grain and extent of flow-ecology methods should relate to the management scale, as portrayed in Figure 1.2. Regional methods are a good match to large-extent spatial management questions, such as planning for multiple water developments spread over large areas (be they small diversions or large dams). In contrast, the question of how much flow should be released from a single dam location (i.e., flow magnitude and timing) is more of a temporal management question (with both temporal and spatial consequences for the receiving environment). Intensive reach-specific methods provide a better match for managing single-structures (e.g., BBM, IFIM, MesoHABSIM). But the question remains of where to focus the reach-specific methods (i.e., which specific reach(es) and what management issues). Regional methods can offer a way forward in answering this and other questions.

A way forward

Flow-ecology methods range from labor-intensive frameworks for single dams to desktop historic flow methods that can be applied over large areas. In terms of effort, regional flow-ecology methods are intermediate between these two extremes, and go hand-in-hand with reach-specific methods, plus the fundamental research that underpins both. Regional methods are typically less precise than reach-specific methods, but offer many benefits that include:

- enabling faster, cheaper evaluation of likely flow constraints;
- increasing the area of application and therefore supporting spatial decisions (e.g., placement of dams or free-flowing reserves);
- providing an empirical screening tool to trigger intensive reach-specific studies;
- providing a large-scale view to reveal large-scale processes that drive ecosystem pattern;
- providing an empirical method for considering more species and more flow regime components.

People learn by doing, and scientists also learn from each other. The value of incorporating prior knowledge into flow-ecology assessments cannot be overstated. This expands the scale of observation beyond what can be considered in stand-alone investigations and also formalizes a learning-by-doing approach at a broader management level than individual locations. To this end, *regional guidelines* can be used to formalize and disseminate knowledge from experts and other practitioners on what methods to use where (e.g., slope threshold for detailed modeling of dissolved oxygen; Wilding et al., 2012). Regional flow-ecology relationships offer a foundation for flow guidelines, by formalizing expert knowledge into mechanistic hypotheses then testing those hypotheses against existing data (i.e., following the ELOHA framework, Poff et al., 2010). For example, hypotheses for the response of cottonwood (*Populus*) to flow alteration were developed from expert panel discussions then tested using existing cottonwood data (Chapter 3). The flow-ecology relationships can provide predictions that are of direct use for flow prescriptions for less contentious management decisions. They can also provide a trigger for detailed reach-specific studies when flow decisions are contentious (e.g., determine that trout habitat is at risk and prioritize reaches for 2-dimensional habitat modeling). Guidelines can be revised and updated with new knowledge over multi-annual cycles, with the revision process drawing from more recent scientific literature, monitoring and targeted investigations.

Water management agencies, be they national, state or regional government, have a critical role to play in developing these guidelines for flow-ecology studies. For example, New Zealand has proposed national guidelines that specify what flow-ecology methods to use for evaluating the effects of flow alteration (Beca, 2008). The guidelines propose the use of simple methods where the risk of impacts is low and use more complex methods where aquatic values are high or the flow alteration is extreme (Table 1.3). Practitioners then select a subset of these methods that are relevant to each development. These guidelines are intended to be updated as better information comes to hand (MfE, 2008). Certainly the New Zealand guidelines could progress further using GIS data (e.g., Snelder & Hughey, 2005; Snelder et al., 2005) and regional methods to determine the physical setting in which a given method is needed (e.g., hydraulic habitat in moderate-slope cold-water streams - Lamouroux & Jowett, 2005; oxygen in low-slope streams - Wilding et al., 2012).

Table 1.3 New Zealand guidelines for selecting flow-ecology methods based on flow alteration and the significance of instream values (adapted from Beca, 2008). Practitioners can then choose a subset of these models they believe relevant to each flow development.

Flow alteration	Instream values		
	Low significance	Medium significance	High significance
Low	Historical flow method Expert panel	Historical flow method Expert panel	Generalized habitat models 1D hydraulic habitat model Connectivity/fish passage Flow duration analysis
Medium	Historical flow method Expert panel Generalized habitat models	Generalized habitat models 1D hydraulic habitat model Connectivity/fish passage	1D hydraulic habitat model 2D hydraulic habitat model Dissolved oxygen model Temperature models Suspended sediment Fish bioenergetics model Groundwater model Seston flux Connectivity/fish passage Flow variability analysis
High	Generalized habitat models 1D Hydraulic habitat model Connectivity/fish passage Periphyton biomass model	Entrainment model 1D Hydraulic habitat model 2D Hydraulic habitat model Bank stability Dissolved oxygen model Temperature models Suspended sediment Fish bioenergetics model Inundation modeling Groundwater model Seston flux Connectivity/fish passage Periphyton biomass model	Entrainment model 1D Hydraulic habitat model 2D Hydraulic habitat model Bank stability Dissolved oxygen model Temperature models Suspended sediment Fish bioenergetics model Inundation modeling Groundwater model Seston flux Connectivity/fish passage Periphyton biomass model Flow variability analysis

Implementing flow guidelines that are spatially-explicit could be achieved using hydrogeomorphic classification (see section Defining the Region). For Colorado, the Watershed Flow Evaluation Tool (WFET) was developed for water resource planning (Sanderson et al., 2012), and it illustrates the use of geomorphic setting for developing and implementing regional flow-ecology methods. The geomorphic setting was modeled for the entire basin by Bledsoe & Carlson (2010), establishing the higher-level constraints that set the stage for the development of flow-ecology relationships. For example, plains cottonwood (*Populus deltoides*) are expected to respond to flow in unconfined valleys where formation of point bars facilitates recruitment (Chapter 3), and this geomorphic setting is replicated across reaches. Scenarios of future water development can now be run, allowing site-specific studies to be targeted based on the prior knowledge captured by the flow-ecology relationships (e.g., high risk reaches below a proposed dam). The flow-ecology relationships also provide a well formulated hypothesis of biotic response to flow alteration as a starting point for reach-specific studies (defining biotic metric, flow metrics and geomorphic setting).

Hydrogeomorphic classification will not completely isolate the biotic response to flow from the response to other physical drivers. More likely, flow will act as an overriding constraint on species populations in certain places and at certain times (e.g., Milhous & Bartholow, 2006; Power et al., 2008). These times and places are expected to define an upper bound for the response of biota to flow, which can be described using quantile regression (Dunham et al., 2002b; Konrad et al., 2008; Lancaster & Belyea, 2006; Milhous & Bartholow, 2006). In comparison, central tendency methods (e.g., conventional least squares regression) fail to recognize the bounded relationships produced by physical constraints (Lancaster & Belyea, 2006), so these methods increase the risk of rejecting important flow-ecology relationships (i.e., Type II error).

Hydrogeomorphic classification is not the only option for developing flow-ecology relationships. Wiens (2002) argues we should instead consider the continuous nature of physical gradients. A combination of classification methods and continuous relationships can exploit the strengths of both approaches. For example, continuous models were used to predict trout habitat using channel width (Chapter 2), with classification used to constrain the study to one broad physical classification (southern Rocky Mountains). I attribute the success of the desktop models, in part, to the constrained setting over which channel width is a reliable proxy for channel morphology. This classification also set the stage in terms of the higher-level constraints for trout (e.g., temperature, flow regime). Both continuous and classification approaches are dependent on GIS databases that quantify reach and watershed attributes. Such databases provide an indispensable desktop tool for the freshwater scientist, and are worthy of ongoing, nationally-coordinated development (e.g., NHDPlus - Bondelid et al., 2010; REC - Snelder et al., 2005).

In the past, scientific debate regarding flow-ecology methods has been somewhat divided (Lamouroux et al., 2010; Lancaster & Downes, 2010; Williams, 2009). Regional guidelines will hopefully shift the methodology debate from *if*, to *where*, the assumptions of a given method are reasonable. For example, Jowett (1992) demonstrated that hydraulic habitat methods (RHYHABSIM – River HYdraulic HABitat SIMulation) were valid for a drift feeding salmonid (brown trout) in cool, stony streams. Likewise, riffle fishes in warmwater streams were successfully evaluated using PHABSIM (Freeman et al., 1997; Orth & Maughan, 1982). But PHABSIM has produced unreliable results for stillwater species (i.e., stream dwelling species that prefer 0 velocity), including smallmouth bass (Freeman et al., 1997; Groshens & Orth, 1993; Orth & Maughan, 1982; Zorn & Seelbach, 1995). Submergence of cover and feeding habitat is of course important for stillwater species, but the very low flows that are adequate for submergence in pools might be insufficient to meet oxygen requirements (Lancaster & Downes, 2010). Biotic interactions can be important in dryland rivers (e.g., Meffe, 1984; Power et al., 2008), where the long periods between flow disturbance events and shrinking habitat allow populations to reach resource limitation (Boulton et al., 1992).

Conclusions

We can, in part, resolve the diverging opinions on how best to proceed with flow-ecology studies by understanding the contrasting *objectives* of flow management versus species population management, and the *scales* of management and investigation. Flow-ecology methods that fail to account for all hierarchical constraints can still be useful if applied within a defined hydrogeomorphic context, especially if our objective is to examine flow constraints on populations, rather than numerically predict population dynamics.

Incorporating prior knowledge into flow-ecology assessments expands the scale of observation beyond what can be considered in stand-alone investigations and also formalizes a learning-by-doing approach at a broader management level than individual structures. Regional flow-ecology methods are an essential tool for applied scientists that will allow development of spatially-explicit regional guidelines on what flow-ecology methods to use where.

CHAPTER 2: PREDICTING TROUT HABITAT RESPONSE TO FLOW FOR COLORADO ROCKY MOUNTAIN STREAMS

Summary

Dams and the diversion of water can dramatically change stream ecosystems. This chapter focuses on how depth and velocity changes with flow, as one component of habitat for brown trout and rainbow trout. Predicting how depth and velocity changes with flow is possible using hydraulic models, such as PHABSIM (Physical HABitat SIMulation). But hydraulic models are expensive to implement and only describe a short length of stream (10^2 m). If science is to keep pace with development, investigators need more rapid and cost-effective models than PHABSIM. I developed a Generalized Habitat Model (GHM) that offers a demonstrated reduction in survey effort for Colorado Rocky Mountain streams. This model combines the best features of GHMs developed elsewhere, including the options of desktop (no-survey) or rapid-survey models. Further, the habitat-flow curves produced by PHABSIM were simplified to just two site-specific parameters: (1) shape (dimensionless) and (2) Q95h (flow at 95% of maximum habitat). Both parameters were predicted from desktop variables, including mean annual flow, using linear regression. Habitat predicted by the desktop GHM was significantly correlated with the abundance of large brown trout ($P<0.01$), but not smaller trout. The rapid-survey GHM produced better predictions of observed habitat than the desktop GHM (rapid-survey model explained 82%-89% variance for independent validation sites; desktop

68%-85%). The predictive success of these GHMs was similar to other published models, but survey effort to achieve that success was substantially reduced.

Introduction

Reducing baseflows constrains the area of wetted habitat available to support fish and invertebrates (Hart & Finelli, 1999; Jowett, 1992). Beyond baseflows, it is important to consider the broader environmental context for individual flow assessment tools and flow management decisions. The hierarchical filters framework from Poff (1997) provides this context, proposing that large-scale processes (e.g., temperature, flood frequency) constrain the number of species surviving to respond to small-scale processes (e.g., baseflow velocity, biotic interactions). This chapter focuses on *hydraulic habitat* (velocity and depth) of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) and how it changes with flow, recognizing that hydraulic habitat is one of several important constraints on trout populations (Milhous & Bartholow, 2006). The importance of hydraulic-habitat as a physical constraint is well established for trout in flowing waters, from observational and experimental studies at a range of scales (Bachman, 1984; Fausch, 1984; Jowett, 1990; Jowett, 1992).

Hydraulic habitat methods, such as PHABSIM, RHYHABSIM and River2D, predict the change in point velocity and depth with flow, based on intensive site surveys and calibrations (Annear et al., 2004). By comparing depths and velocities predicted by the hydraulic model to the observed depths and velocities used by trout (*HSC* - habitat suitability criteria), these methods can generate *habitat-flow* curves (plots of the change in the weighted usable area with flow). This output is useful in better understanding how a proposed flow change will constrain the hydraulic habitat for trout.

A major hurdle for the implementation of conventional hydraulic habitat methods is the cost (Estes & Orsborn, 1986; Nehring, 1979; Souchon & Capra, 2004). This presents a barrier to carrying out such assessments, other than for large developments (e.g., dams or large diversions). Poff et al. (2010) recognized the pressing need to develop regional-scale methods, based on data from reach-specific surveys, in order for science to keep pace with development.

Generalized habitat models (GHM) can help meet this need for increased spatial coverage, as already demonstrated for some regions (Booker & Acreman, 2007; Lamouroux & Capra, 2002; Lamouroux & Jowett, 2005; Saraeva & Hardy, 2009a). A GHM can reduce the survey effort needed to predict habitat-flow response, compared to PHABSIM or River2D. The GHMs also make better use of prior knowledge of habitat-flow response, compared to rapid-survey methods, such as R2CROSS (Espegren, 1996). The steps in producing a GHM can include:

1. Surveying hydraulic habitat to generate habitat-flow curves for a sample of stream reaches (e.g., using PHABSIM);
2. Fitting a function to the habitat-flow curve and extracting function parameters for each reach;
3. Using the observed sample of reaches to train a statistical model that predicts the parameters from selected predictor variables that can be obtained for many sites across a region with an acceptable level of effort; and
4. Generating habitat-flow curves for new reaches where predictor variables are known.

The GHM developed by Lamouroux & Capra (2002) successfully predicted habitat-flow response (89% explained variance for adult brown trout), but predictions were based on reach attributes calculated from the intensive surveys (e.g., Froude number). The degree to which survey effort is actually reduced in applying the model to new sites remains in question.

More recent research explicitly described the survey effort required for model implementation. For example, models by Booker & Acreman (2007) used watershed descriptors, or single-survey hydraulic data, to predict habitat-flow response. The use of three unknown parameters for the habitat-flow function by Booker & Acreman (2007) produced a less parsimonious GHM that is more susceptible to parameter instability than functions used by Lamouroux & Capra (2002). Saraeva & Hardy (2009a) demonstrated the benefit of hydrogeomorphic classification in reducing the number of intensive studies required to make predictions. Their direct scaling of habitat-flow curves to 21 hydrogeomorphic classes achieved an area of application (3500 km^2 watershed) smaller than was achieved using statistical models elsewhere (e.g., England - Booker & Acreman, 2007; France - Lamouroux & Capra, 2002).

In addition to developing a GHM for an area not covered by previous GHMs (Colorado Rocky Mountains), I combined the best features of previous models into one new model. The resultant Colorado GHM provides a demonstrated reduction in survey effort with a desktop (remote-sensing data) and rapid-survey option (after Booker & Acreman, 2007) that minimizes the number of unknown function parameters (after Lamouroux & Capra, 2002) and exploits the hydrogeomorphic commonalities of the Rocky Mountains to reduce the number of intensive surveys required to train the GHM (after Saraeva &

Hardy, 2009a). In addition, I used a similar approach to Saraeva & Hardy (2009b) for simplifying the PHABSIM predictions by omitting substrate-cover and using percent of maximum habitat, rather than weighted usable area. My intention was not to replicate *exactly* the output from PHABSIM, but to provide a biologically informative model that was developed and tested using the PHABSIM data. The successful interrogation of the habitat-flow predictions against observed trout abundance data therefore represents a vital step forward in demonstrating the validity of GHMs.

The objectives of this chapter are to:

- predict the habitat-flow relationships for brown and rainbow trout;
- maximize the number of stream reaches in Colorado where GHMs can be applied and;
- minimize the data required to predict habitat-flow response.

Success of the models was judged by two criteria: first, by better correlations with trout abundance than the Tennant Method (Tennant, 1976) which provides thresholds based on percent of MAF (mean annual flow) and, second, by demonstrating less survey effort than PHABSIM and River2D methods.

Methods

The flowchart in Figure 2.1 summarizes the steps used to construct the GHMs for Rocky Mountain streams, with more detailed methods following.

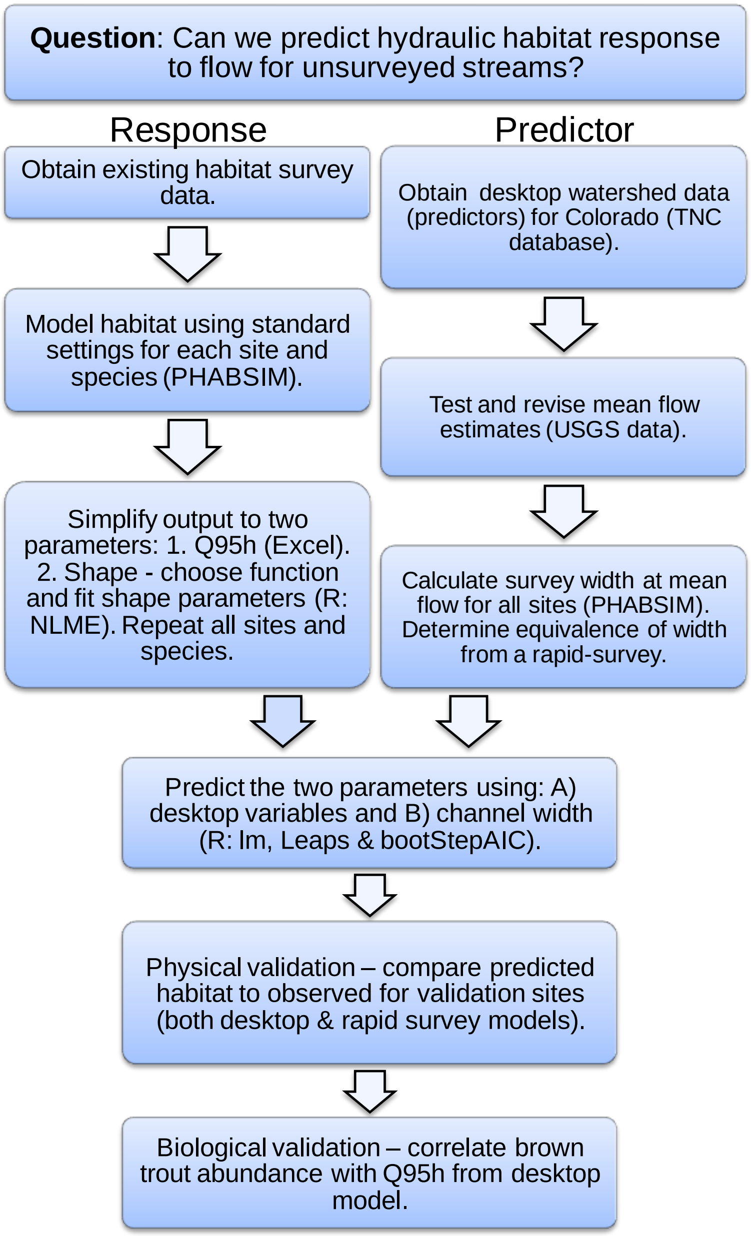


Figure 2.1 Flow chart summarizing the methods used. The name of data analysis software is given in parentheses, including the name of packages implemented using R-Project software.

Study Sites

Data were obtained for 24 PHABSIM surveys in the Rocky Mountains to train the GHM (Table S2.1 – "S" denoting supplemental material at end of chapter). Survey data were obtained from the Colorado Division of Wildlife (Nehring & Anderson, 1993), HabiTech, GEI Consultants, Miller Ecological Consultants, Inc. and Stantec (Fleece, 2011). All but the Stantec survey were completed in the 1980s. Survey methods varied between sites, to some extent, and differences included the number of cross-sections and the range of calibration flows (Table S2.1). Dams and diversions may be the impetus for a PHABSIM study, but the surveys were actually conducted closer to those trout fisheries likely to be affected (e.g., Gold Medal fisheries).

To place the study sites in a broader physical context of regional-scale constraints (sensu Poff, 1997), site distribution was compared to all Colorado reaches (using data from NHDPlus). The temperature distribution for the PHABSIM study sites included cooler streams (most 6-13 °C annual average watershed air temperature). The PHABSIM sites also have a strong bias for larger streams within the Rocky Mountains - reaches with a MAF (mean annual flow) between 1.8 and 14 m^3/s were more likely to be surveyed (the smallest site was 0.2 m^3/s). There was some bias to lower reach slopes within the Rocky Mountains, but considering only large streams (MAF >1.8 m^3/s) produces a similar bias (i.e., larger streams have lower slopes; see Flores et al., 2006). Box 1 portrays the predicted bias in site selection across the entire Colorado riverscape.

Desktop Predictor Variables

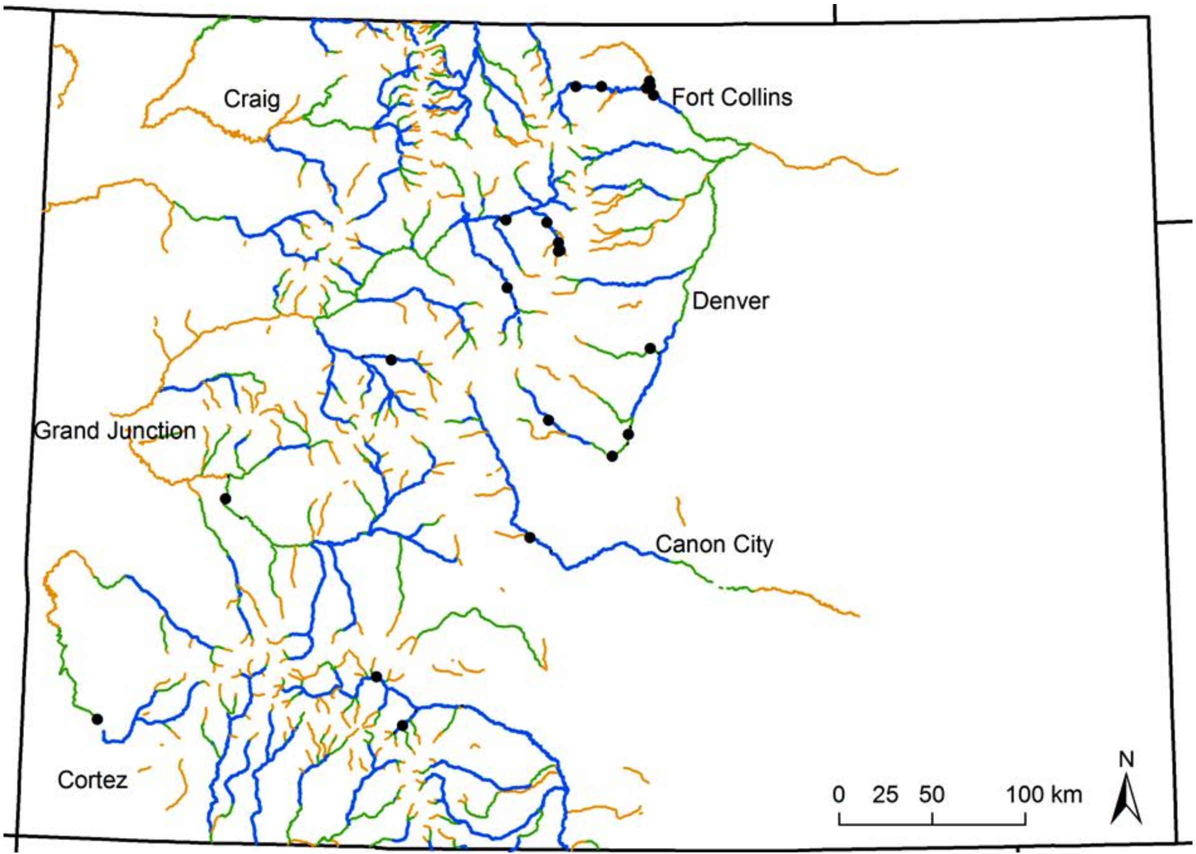
An initial set of desktop variables were retrieved from a GIS database provided by TNC (The Nature Conservancy) for Colorado streams. Most attributes were sourced from NHDPlus (www.horizon-systems.com). The database describes individual reaches that were delineated by tributary confluences, each with a unique identifier (COMID) and attributes. I selected a subset of attributes with expected mechanistic links to hydraulic habitat (Table 2.1).

For snowmelt streams of the Rocky Mountains, MAF is a useful metric of relative stream size that also represents flow magnitude during the warmest months. For example, flows for the Arkansas River (at USGS 07091200, 1989-2006) averaged 108% of MAF for August-September when temperatures averaged 92% of the annual maximum (of monthly means). Values of MAF for Rocky Mountain streams were estimated for NHDplus using the equations from Vogel et al. (1999). This set of models uses watershed average precipitation and temperature calculated from PRISM data (Daly et al., 1997), in addition to watershed area (i.e., the watershed upstream of each reach). Estimates of MAF were validated for my study using USGS gage data (described in Appendix 1). Estimates were generally close to the observed data; the exceptions being the Arkansas River and Cache la Poudre River, for which I developed revised water-balance models (described in Appendix 1).

Table 2.1 Description of selected desktop variables developed by The Nature Conservancy (*) and NHDPlus (+) for Colorado streams (see Table *S*2.2 for site values). Transformations for subsequent analysis are also detailed, with addition of values smaller than 1 (as in Ln[x+**1**]) necessary to normalize data with small non-zero values.

MAF$^+$	Mean annual flow (m^3/s) natural estimate. Ln(X+1) transformed.
MAF Alt.*	Percent flow alteration from transbasin diversions (quantified in HydroBase at http://cdss.state.co.us) plus predicted agriculture consumptive use (acre feet calculated as irrigated acres times 1.85 (Arkansas), 1.54 (Colorado), 1.45 (Dolores), 1.79(Gunnison), 0.83 (North Platte), 1.75(Rio Grande), 1.75 (South Platte), or 1.17 (Yampa).
Elevation$^+$	Reach average elevation of blue line (m).
Reach slope$^+$	Slope of blue line over the reach (% slope = 100 x m/m). Ln(X) transformed.
Watershed slope$^+$	Slope of blue line averaged over the watershed (% slope).
Dam storage density*	Reservoir storage volume / total annual runoff (m^3/m^3). Ln(X+0.1) transformed. Reservoir volume data from the National Inventory of Dams was manually checked against alternative sources.
Riparian width *	Modeled width of flood influence (km). Ln(X+0.001) transformed.

Box 1: How does the bias in site selection translate across the riverscape of Colorado? This map was produced based on temperature and mean annual flow. The probability of site occurrence was calculated using Maxent statistical software (Dudik et al., 2010; Phillips & Dudík, 2008) with re-sampling from 20,875 Colorado reaches as background data (model AUC=0.907). Site selection was biased to large, cool streams of Colorado, as depicted in this map. The coincidence of popular coldwater fishing sites (State Wildlife Areas) with high probability reaches (>0.5) suggests that site bias reflects trout fishery bias – arguably a good thing. Three probability classes are displayed (blue 0.5-0.75, green 0.35-0.5, and red 0.2-0.35). PHABSIM sites are illustrated as black dots. Some cities are labeled.



Rapid Survey Width

The wetted width at MAF was modeled using PHABSIM from survey data for use as a predictor variable when constructing rapid-survey GHMs. Rapid-survey estimates of width can provide an intermediate level of assessment between desktop analysis and a full survey, so correlates of width at MAF were investigated in a pilot study using 117 cross-sections from 17 reaches (pilot detailed in Appendix 2). The inflection point was estimated visually from plots of wetted width versus average depth, providing a close approximation of wetted width at MAF (Y = 0.983*X, R^2 = 0.975). The number of rapid-survey cross-sections necessary to estimate the reach-average width at MAF was also investigated in this pilot study: five cross-sections are recommended (achieved a 95% confidence interval within 7% of the PHABSIM survey estimate).

Estimating the inflection width only requires one site visit with no velocity measurements, and this represents a reduction in survey effort compared to PHABSIM. For physical-validation sites lacking cross-sectional data, the rapid-survey width was measured as the visibly wet or unvegetated channel from aerial photographs in Google Earth (10-20 cross-sections randomly selected over the reach).

Hydraulic Modeling

I remodeled all 24 of the existing PHABSIM surveys using PHABSIM software (Windows Version 1.20; Waddle, 2001) in pursuit of consistent model settings across sites. Some deviations were necessary for sites where different survey methods were used. Water surface levels were modeled using stage-discharge relationships (STGQ model using log-log linear regression) if calibration data were available and adequate (water surface profile models were necessary only for the Dolores River and Fraser River Site #1). The smallest sites (Little Vasquez and Vasquez) were removed at this point, because the calibration of ratings was not adequate at higher flows, leaving 22 PHABSIM surveys to train the GHM. In PHABSIM, velocity was predicted using Manning’s n values for each survey point at each flow increment (VELSIM in PHABSIM). Velocity adjustment factors (VAF IOC 11) were used to adjust observed Manning’s n values for reduced roughness as depth increases.

Selection of HSC (Habitat Suitability Criteria)

PHABSIM uses HSC to convert predicted depths and velocities to hydraulic habitat. Separate GHMs were produced for each individual HSC selected for this study to represent brown and rainbow trout (Figure 2.2). A full description of testing and derivation of all HSC is provided in Appendix 3. The "Cheesman" HSC (Shuler & Nehring, 1994; Thomas & Bovee, 1993) for adult brown and rainbow trout (BT2 and RT2) were modified by increasing the suitability of deep water to 1 (at deeper than optimum), because my re-analysis indicated that low catch rates in deeper water were an artifact of the rarity of deeper pools. This re-analysis used Maxent (Dudik et al., 2010; Phillips & Dudík, 2008) to better contrast the occupied habitat (presence) with the sampled habitat (target-group background) and avoid interpreting absences as avoidance. Maxent was also used to develop new HSC for this investigation, with trout separated only by size-guild (juvenile T1 or adult T2), rather than by species. The new HSC were based on the same trout observations that were used to develop the Cheesman HSC plus data from the Cache la Poudre River (both described in Thomas & Bovee, 1993). Juvenile trout were 7-17 cm (assumed age of 1 year) and adult trout ≥17 cm (assumed age of 2+ years) (Thomas & Bovee, 1993).

In an effort to simplify and improve the GHM, substrate and cover were not included as components of habitat suitability. A pilot study using data from Gard (2005) (107 cross-sections from the Cache la Poudre River) supported omitting substrate/cover, as it had little effect on the habitat-flow response curves after standardizing hydraulic habitat by the maximum weighted usable area (mean absolute deviation 2.8% of habitat between substrate off and substrate on for juvenile rainbow trout, paired t-test P=0.28, n=26). This is consistent with Ayllón et al. (2011), who reported substrate/cover had more effect on habitat magnitude (weighted usable area) than on the shape of the habitat-flow curves. Note that the 11 PHABSIM surveys used for physical validation of the GHM retain substrate/cover in the HSC. Therefore, the reported GHM prediction error includes any real change in substrate suitability with flow. Several species and life-stages were not included in the Colorado GHM, including substrate-dependent spawning habitat, because the GHM is not intended to comprehensively portray the ecosystem response.

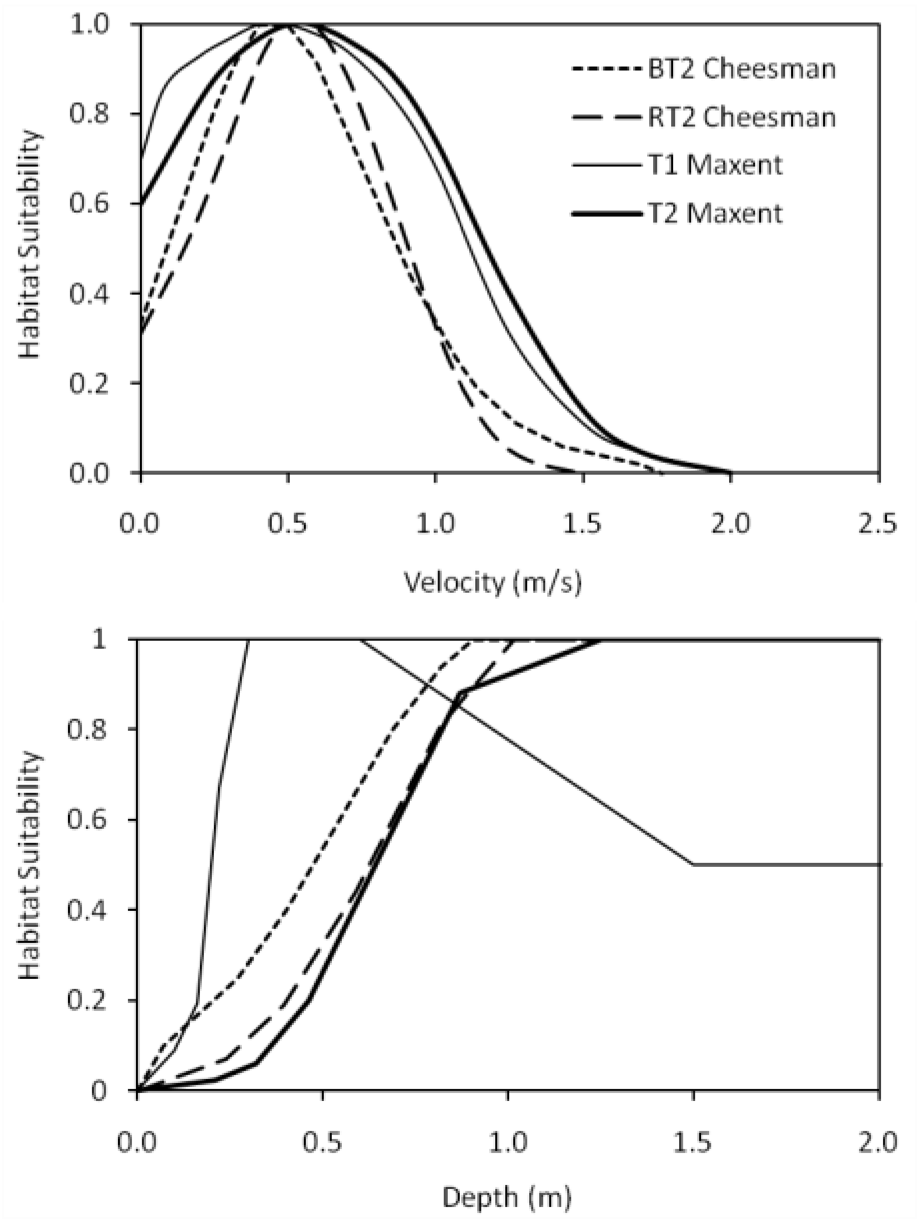


Figure 2.2 Habitat suitability criteria for velocity and depth (y-axis standardized to maximum suitability of 1). The Cheesman HSC for adult brown and rainbow trout (BT2 and RT2) were modified from Shuler & Nehring (1994). The size-guild HSC were developed for this investigation, with trout separated only by lifestage (juvenile T1 and adult T2), rather than species (as described in Appendix 3).

Modeling Generalized Habitat

With the aim of generating habitat-flow response curves for unsurveyed streams of the Rocky Mountains, I decomposed the habitat-flow curves produced by PHABSIM into three components:

- Shape - the shape of the dimensionless habitat-flow response curve. Habitat was converted to a percent of Maximum Habitat and flow was converted to a percent of the Q95h;
- Q95h - flow providing 95% of maximum habitat;
- Maximum Habitat - maximum WUA (weighted usable area).

The first two components, Shape and Q95h, are expected to be most useful for flow management, when used together. By omitting Maximum Habitat (third component), the modeling burden is reduced while still producing informative relationships for flow management. For Q95h, I chose the flow at 95% of maximum habitat as the flow metric, because it was less variable than the logical alternative of 100%. This choice was based on another pilot study (Cache la Poudre River data from Gard, 2005), comparing 50 sub-samples of 6 cross-sections randomly selected from the “population” of 107 cross-sections. The standard deviation of these replicates was nearly halved by using the flow at 95% instead of 100% (standard deviation 1.17 m^3/s for 100% and 0.60 m^3/s for 95%, ANOVA $P<0.001$, $F=250$, $n=50$).

A dimensionless shape function was selected for each reach using the better fitting of two functions - Quadratic or Exponential. A modified version of the standard quadratic ($Y = AX^2 + BX + C$) is applied to make use of y-max having a known value (95% of maximum habitat). In theory, this function can be further reduced to 1 parameter using x-max of 1 (100% of Q95h = -B/2A). But, in practice, a better fit to the data was achieved by allowing B to vary across the reaches, together with a fixed value of A.

Quadratic Function: $$HV_{ij} = A(Q_{ij} - {}^{B_i}/_{(2A)})^2 + 0.95 + \varepsilon_{ij}$$

where subscript ***i*** denotes the individual reach and subscript ***j*** denotes the individual flow increments for each reach. The dimensionless response variable *HV* is the hydraulic habitat value, expressed as a percent of maximum habitat. The independent variable Q is a dimensionless flow, expressed as a percent of Q95h.

The second function is a modified version of the exponential function from Lamouroux & Jowett (2005) (their Model 2).

Exponential Function: $$HV_{ij} = 1 + C_i . \exp{(KQ_{ij})} + \varepsilon_{ij}$$

Each function uses one fixed parameter (*A* for quadratic, *K* for exponential) fitted across all reaches in the hydrogeomorphic region and one reach-specific parameter (*B* or *C*). The parameters for each function were fitted simultaneously using an NLME package (Non-Linear Mixed-Effects model; Pinheiro et al. 2009; implemented using R, Version 2.11.1). The NLME method estimates parameters that maximize the log-likelihood (see Lindstrom & Bates, 1990, for NLME model formulation and computational methods). Having just one reach-specific parameter (the “random” parameter in NLME) provides a more parsimonious GHM, avoids parameter instability, and isolates the response of shape to morphological drivers.

The *AIC* statistic (Akaike's Information Criterion, Akaike, 1974) was used to determine which of the two functions provided a better fit to the data for each species and life-stage (i.e., model with the lowest AIC score), in addition to reviewing plots of predicted versus observed values.

We therefore require two parameters to produce a habitat-flow response function for each site: Q95h and shape (*B* or *C* for shape, depending on which function is selected for each HSC). The next step was to predict the two parameters using the desktop and rapid-survey variables. The parameters and predictor variables were transformed, if this improved normality, with appropriate transformations judged using histograms, Shapiro's statistic and Normal-QQ plots (width was square-root transformed; see Table 2.1 for other transformations). The two parameters were modeled using a multiple linear regression ("lm" function from the "stats" package, implemented in R). The best model for each was judged based on the best subsets analysis, which determined one combination of variables (from all possible) that produced the highest adjusted-R^2 for each number of variables (calculated in R using the "leaps" package; Lumley, 2009). The *BIC* (Bayesian Information Criterion, Schwarz, 1978) was then used to determine *how many* variables should be included in the model (i.e., model with the lowest BIC score), comparing only the best subset models between each number of variables.

A bootstrap stepwise regression was then used to evaluate the stability of the variables, under re-sampling of the dataset, as this helps identify multicollinearity and strong outlier influences (calculated in R using the "bootStepAIC" package; Rizopoulos, 2009), to optimize BIC from 500 replicates). Variable selection was reconsidered if selected in less than 70% of the replicate models. Residuals were also examined for the satisfaction of assumptions (Neter et al., 1996), such as QQ plots for normally distributed residuals, and the F-statistics were checked (using the "summary" function from the "stats" package in R). In most cases, there was an obvious best model that was supported by all statistics. Some level of judgment comes into play when the various methods provide conflicting results, in which case, I selected the model that could be best explained mechanistically.

Two models were produced for each HSC. The first was a desktop model based on the variables available for all stream reaches in Colorado (Table 2.1). The second was a rapid-survey model using stream width plus the desktop variables (excluding MAF as a correlate of width), providing the option of more precise habitat predictions, where needed.

Validation

Both physical and biological validation were completed for the GHMs. The physical validation used independent PHABSIM studies (11 total) for which only technical reports were available. These provided habitat-flow response curves, but not any survey data that could be remodeled using standardized PHABSIM settings and HSC. Most studies were completed by TetraTech for Grand County (8 out of 11, accessed at http://co.grand.co.us/GCHome/April-2008/Reach_Summaries/). The other three studies were carried out by Miller Ecological Consultants (Roaring Fork - Miller, 2009; Willow Creek - TetraTech reports, and Colorado River - Miller, 2008).

This comparison introduced new sources of error, including the HSC selected to represent trout. Of the HSC that I used, the Cheesman HSC are likely to be more comparable to those used in the technical reports than the new size-guild HSC. Several decades also separate most surveys for the training dataset (median year 1985) from the validation surveys (median year 2007). The validation focused on the Q95h parameter, as it is more critical than the shape parameter in determining prediction success (coefficient of variation 55-63%, versus 2-17% for shape).

The biological validation compared predictions from the desktop models to trout abundance data obtained from the Colorado Division of Wildlife (wildlife.state.co.us/Fishing/Reports/FisherySurveySummaries accessed July 2010). This provided data for trout at 24 sites on 12 streams in Colorado (sites likely biased to popular fisheries, access and suitability for fishing methods). This analysis focused on the number of fish per stream kilometer, because the alternative metric of fish per unit area effectively factors out the variable we are interested in – stream size. Data were available for two size classes of fish (>127 mm or > 356 mm). Brown trout were assumed to be better indicators of abiotic habitat, because rainbow trout populations have been decimated by whirling disease (Nehring & Walker, 1996). Annual fish monitoring results were averaged for 2008 and 2009. The predicted Q95h for each reach was divided by MAF, providing a measure of how close the mean flow is to optimal hydraulic habitat. Quantile regression (Cade & Noon, 2003; Cade & Richards, 2007) was used for the biological validation because I expect hydraulic habitat to act as a constraint on trout abundance, rather than the sole determinant of abundance (Dunham et al., 2002b; Milhous & Bartholow, 2006).

To compare performance with the desktop models, correlation of trout abundance with the Tennant Method (Tennant, 1976) was also analyzed. The Tennant Method recommended thresholds for summer flow expressed as a proportion of mean annual flow. In order to test the correlation of this method with trout abundance, the observed summer flows were divided by mean annual flow for each site. I specified summer baseflows as the August-September mean (after Binns & Eiserman, 1979), and calculated the August-September mean over the trout monitoring period plus the five years prior (assuming 5-years since conception of large trout). Summer flow data were obtained from nearby gages (USGS and Colorado Division of Water Resources), with some adjustments needed for differences in location (MAF was used to scale observed flows; Vogel et al., 1999).

Results

I achieved the objective of predicting habitat-flow response for unsurveyed streams, with the rapid-survey model achieving 82%-89% explained variance, and the desktop model 68%-85%. The desktop models employed variables that are readily available for all Rocky Mountain streams to achieve better correlations with trout abundance than the Tennant Method. I achieved this by simplifying the PHABSIM output to just two unknown parameters – shape and Q95h. The results describe which shape parameters were selected, then the prediction of shape and Q95h from the desktop and rapid-survey variables. The validity of the models is then described in terms of physical habitat predictions and correlations with trout abundance.

Shape Parameter

Of the two functions evaluated, the quadratic function provided a better fit to the data for the adult trout (RT2, BT2 and T2), producing smaller AIC values (Quadratic AIC < -1000, Exponential AIC > -1000), higher R^2 values (observed versus predicted R^2 >0.996) and a visually better fit to the data (Table S2.3a). In contrast, the exponential function provided a better fit for juvenile trout (BT1 Quadratic AIC -564, Exponential AIC -604; T1 Quadratic AIC -933, Exponential AIC -988).

The shape parameter was then predicted for each HSC (species/life-stage) from the selected desktop and rapid-survey variables using multiple linear regression (Table S2.3b). The shape parameters did not vary markedly between the sites (coefficient of variation ranged from 2% to 17% for each HSC), so it is perhaps not surprising that only two HSC (T2 and T1) produced significant models (at $\alpha=0.05$), of which one was judged reliable for implementation (T2). Channel slope was the most commonly selected predictor for shape, with watershed slope included in models more often than reach slope (correlation between reach and channel slope $R^2=0.01$).

Q95h Parameter

In addition to predicting the shape of the habitat-flow response curve, models were also developed to predict the Q95h (flow at 95% of maximum habitat). Of the desktop variables, MAF was included in all desktop models (best of all subsets) and stood up to bootstrap re-sampling (selected in >95% of replicate models; Table S2.3c). The MAF-alteration was the only variable to reliably explain the residuals from MAF (reducing BIC for 3 out of 4 HSC). MAF-alteration provides a measure of how flow and/or channel size may have changed from the natural condition to what is observed at present. The North Fork of the South Platte River was a major driver of this variables selection, with the largest flow increase and the largest outlier from the MAF predictions (increase in channel width is visible from aerial photographs at the discharge point: Lat. 39.461, Long. -105.676). The inclusion of MAF-alteration in each model therefore depended on including the North Fork. For this reason, MAF-alteration was selected in less than 70%

of replicate models for the 3 HSC, under bootstrap re-sampling of sites (Table S2.3c). But including the North Fork reinforced a subtle relationship that was visually apparent for the less altered sites, and the mechanism is clear behind this relationship with bigger flows increasing channel size.

The rapid-survey models outperformed the desktop models (BIC average -74 for rapid-survey, cf. -57 for desktop models, Tables S3c and S3d). Width at MAF (mean annual flow) was the first variable selected for all four rapid-survey models and was the only variable selected for three of the models (BIC statistic increased with additional variables). Width provides a direct measure of channel size, and hence, MAF alteration did not feature as prominently in the width based models (only included in the T1 model, Table S2.3d).

Physical Validation

Predictions of the GHMs were compared to 11 PHABSIM studies that were only available as technical reports. Plots of predicted versus observed Q95h indicate general agreement for the two HSC that were compared (R^2 from 0.84 to 0.96, Figure 2.3).

The rapid-survey models gave predictions that were closer to the observed values than the desktop models (median absolute difference for BT2 of 31% for rapid-survey, versus 47% for desktop; and for RT2 14% for rapid-survey versus 40% for desktop). The desktop model consistently overestimated Q95h for the validation sites (Figure 2.3). Therefore, the rapid-survey model offers a worthwhile improvement over the desktop predictions. The width estimates used for most validation sites were actually measured from aerial photographs, rather than the survey data. This was necessary because most technical reports only presented one cross-section (exceptions - Roaring Fork and

Colorado River CR7), and a sample of one is insufficient to calculate a reach-average inflection width.

The full model prediction (shape and Q95h) was compared to the observed values for four randomly selected sites (Figure 2.4). This displays prediction success in a more familiar format of hydraulic habitat versus flow (akin to PHABSIM output). The predictions for Williams Fork BT2 had the largest departure from the observed Q95h (of all the validation sites and HSC), and therefore represents the worst case-scenario. Note that the full-surveys offer alternative reach estimates - not truth (Ayllón et al., 2011; Gard, 2005; Payne et al., 2004; Williams, 2009). Roaring Fork predictions improved drastically using the rapid-survey model, instead of the desktop model (Figure 2.4), indicating that the channel width is narrower than would be expected from MAF. Model predictions for the CR5 reach of the Colorado River compare favorably to both the PHABSIM survey at the lower end of the reach and the River2D survey at the upper end of the reach (Figure 2.4).

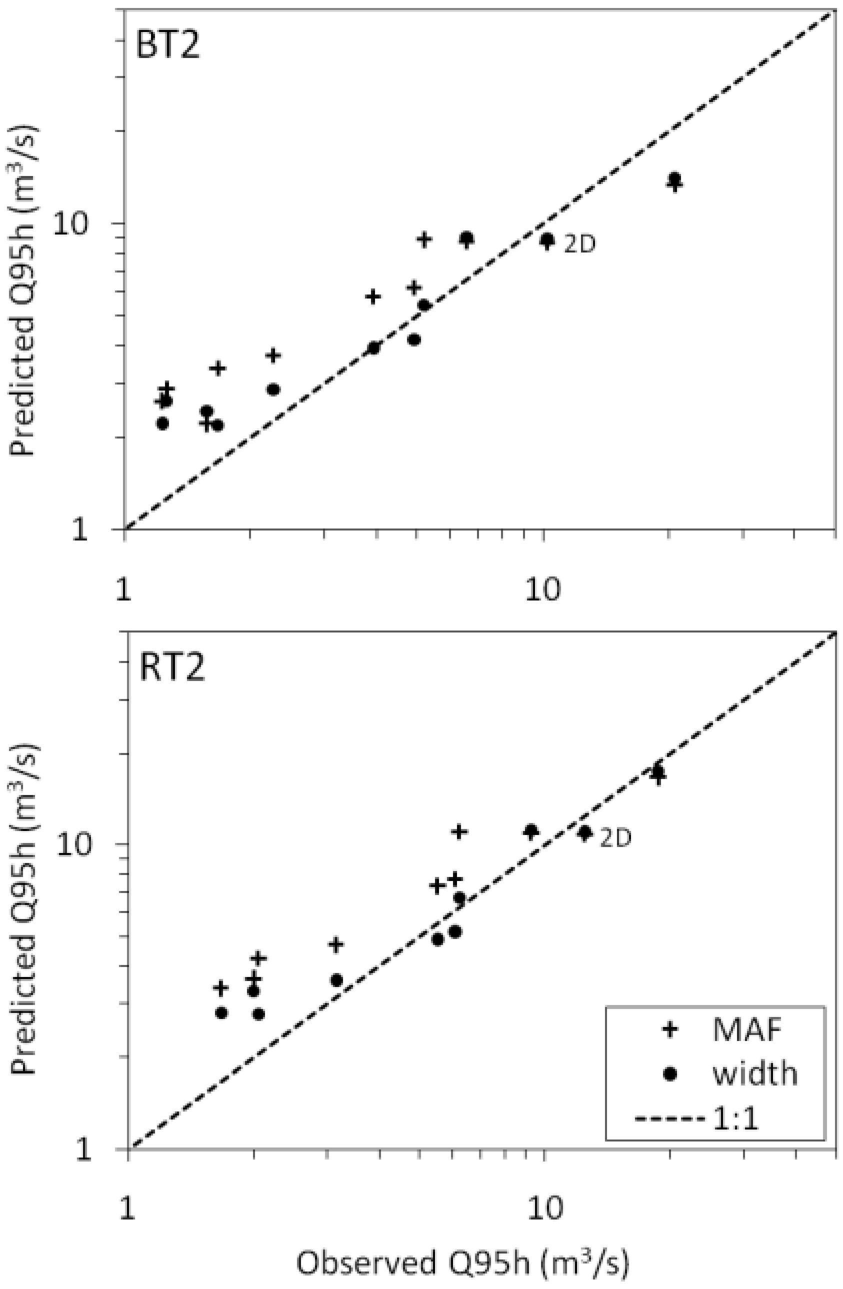


Figure 2.3 Predictions of Q95h (flow providing 95% of maximum habitat), comparing predictions from the Colorado GHMs to the observed values from the independent PHABSIM studies. Results for both the desktop model ("MAF") and rapid-survey model ("width") are presented for brown trout adult (BT2) and rainbow adult (RT2). Points would fall on the 1:1 line if the predicted values matched the observed. The R^2 for BT2 was 0.84 for desktop, 0.92 for rapid-survey; R^2 for RT2 was 0.90 for desktop, 0.96 for rapid-survey.

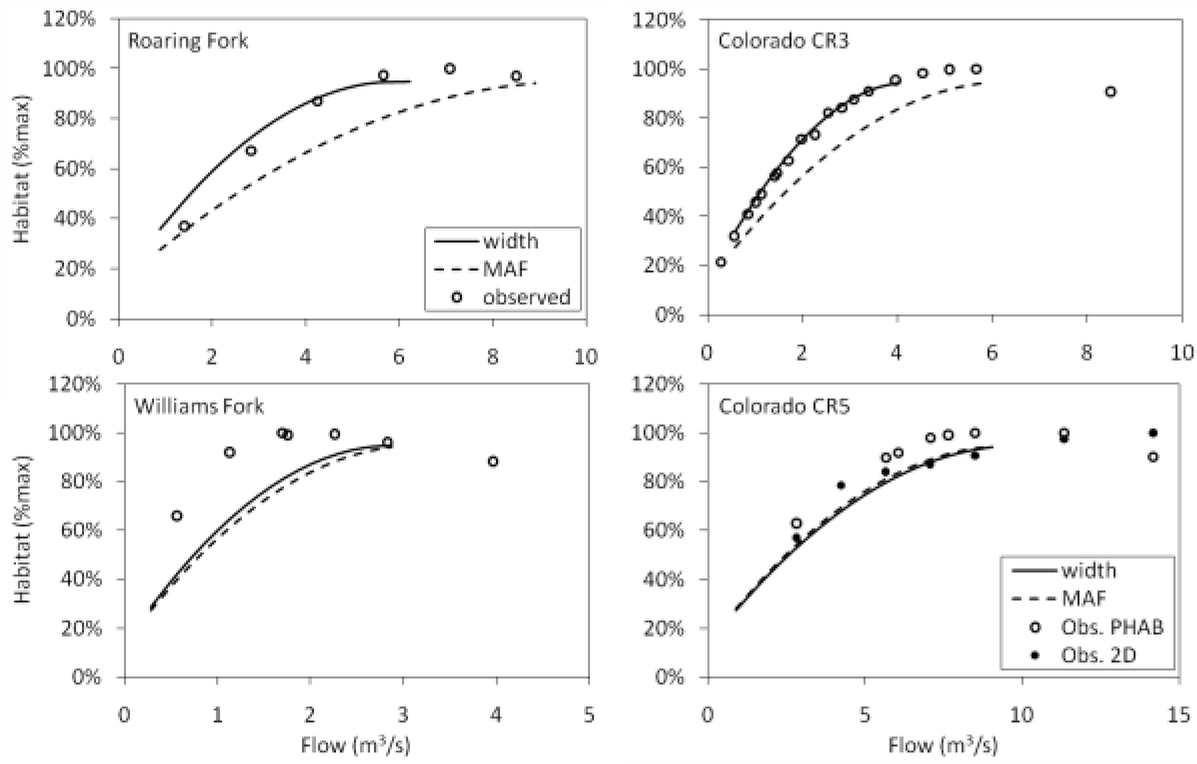


Figure 2.4 Habitat-flow response curves for adult brown trout (BT2), comparing curves predicted from the desktop model ("MAF") and the rapid-survey model ("width") to the observed results from four surveys not included in the training dataset (compare the predicted lines with the observed points). For Colorado River site CR5, the observed results are presented from both a PHABSIM survey and a River2D survey.

Biological Validation

The abundance of all trout caught (>127 mm) was poorly correlated with both the BT2 and T2 predictions (Figure 2.5). This indicates that there are unmeasured population constraints. Some of these constraints might be revealed using hydraulic habitat at flow extremes (e.g., annual low flows, floods). At least we can say the sites that supported the highest abundances of trout (>2000 trout/km) offered near-optimal habitat at the mean annual flow (Figure 2.5).

In contrast, the abundance of large brown trout (>356 mm) was significantly correlated with the predicted habitat (Figure 2.6). High-value fisheries are distinguished by the abundance of large trout, so this is an important population metric. Both of the HSC (BT2 and T2) were correlated with trout abundance, but the results do not reveal which of the two is a better representation of trout habitat.

How does the GHM compare to existing regional methods? The Tennant Method (Tennant, 1976) is still commonly used (Reiser et al., 1989) and arguably offers the only alternative regional method for trout in the southern Rocky Mountains. The observed Tennant flow metric (Aug.-Sept. flow/MAF) was unable to explain much variation in the abundance of small or large brown trout (Figure 2.7). There may be an upper bound response for trout >127 mm, but only if the largest streams are excluded. The need to prune data indicates the limitations of the method, which incorrectly assumes that both small and large streams benefit equally from more flow. Note that calculating August-September flows to test the Tennant Method required more effort to implement (sourcing and analyzing gage records) than the Colorado desktop GHM.

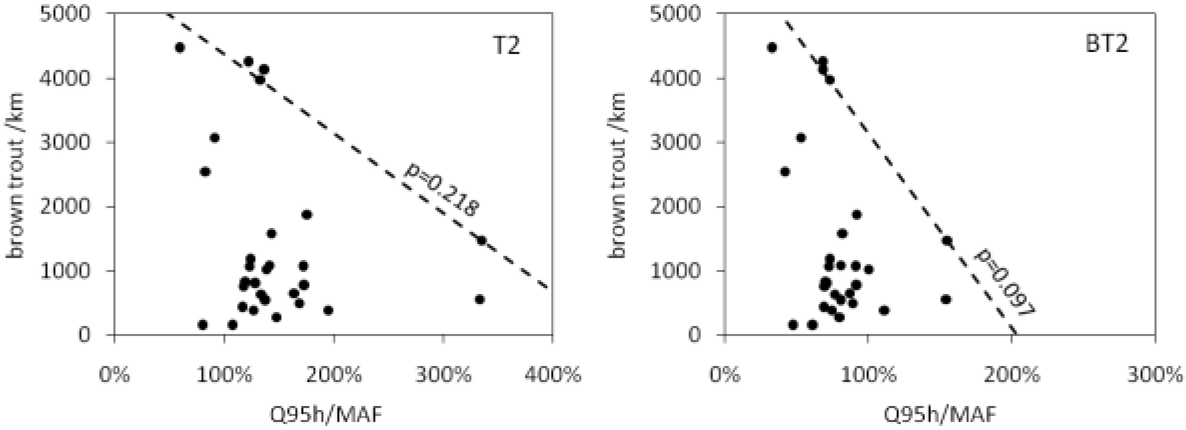


Figure 2.5 Number of brown trout >127 mm per kilometer versus Q95h (standardized by MAF) predicted using the desktop GHM for size-guild adult trout (T2, left plot) and adult brown trout (BT2). Quantile regression was used to describe an upper bound (90%ile and P-Value of asymptotic rank-score statistic calculated using Blossom Software, Cade & Richards, 2007).

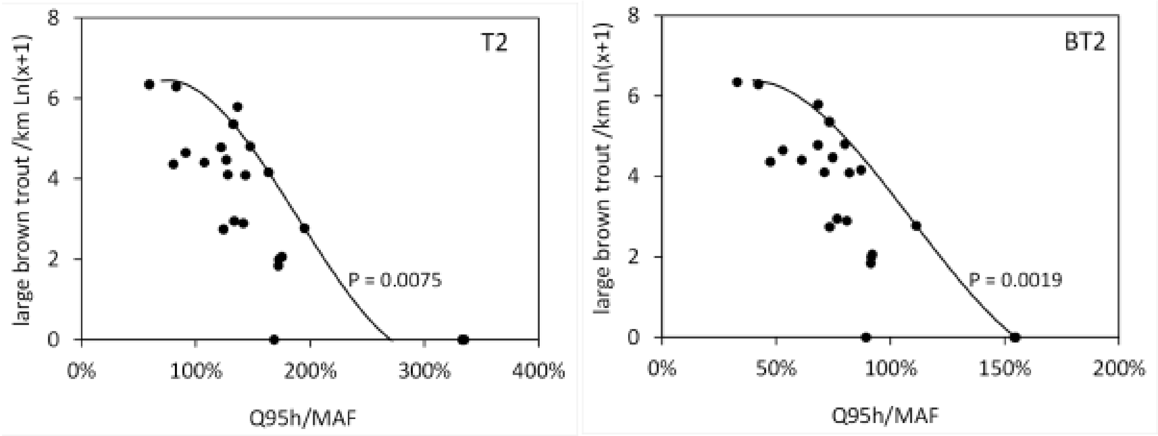


Figure 2.6 The abundance of **large** brown trout (>356 mm per km with log transformation) versus Q95h predicted using the desktop GHM (standardized by MAF). Quantile regression was used to describe an upper bound (90%ile and P-Value of asymptotic rank-score statistic calculated using Blossom Software).

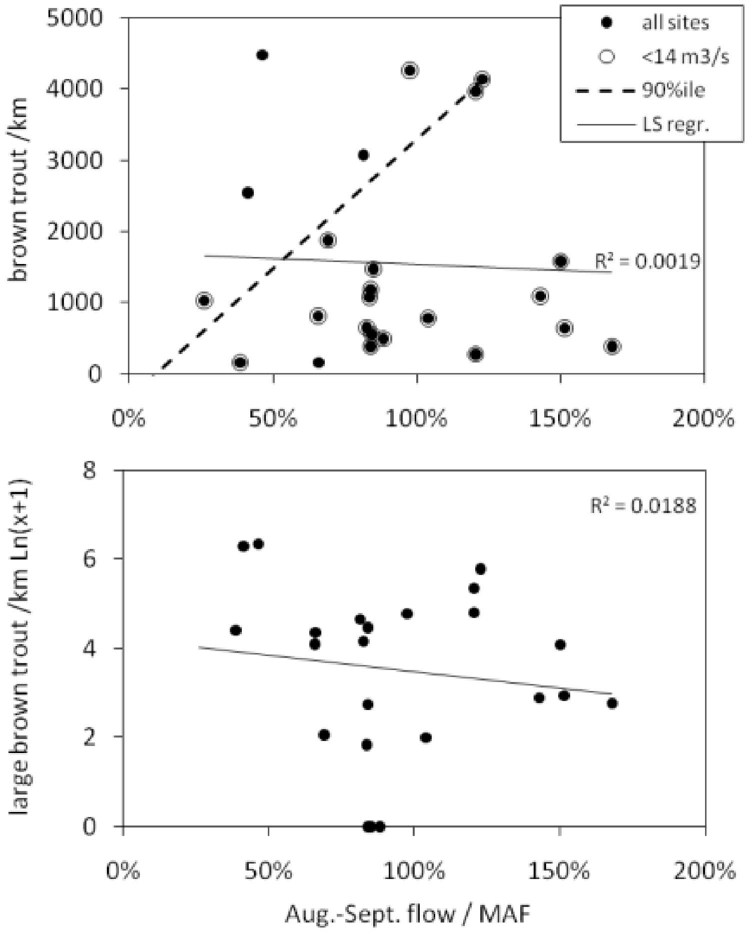


Figure 2.7 Brown trout abundance response to summer flow for all trout caught >127 mm (upper plot) and large trout >355 mm (lower plot). This is intended to compare the validity of the Tennant Method using the measured August-September mean flow divided by Vogel MAF. A quantile regression (90%ile dashed line) was performed excluding large streams (>14 m^3/s) and excluding sites >125% of MAF (P-Value of Asymptotic RS Stat: 0.041). The least-squares regression (solid lines) were fit to all data.

Discussion

My objective was to predict the response function between hydraulic habitat and flow and, more specifically, to maximize the number of reaches in Colorado where the models could be applied, and minimize the required data inputs. The stated objectives were achieved. The Colorado GHMs explained substantially more variation in trout abundance than did the Tennant Method (Tennant, 1976). In addition, the Colorado GHMs required less survey effort than PHABSIM.

An important step in achieving these objectives was reducing the standard PHABSIM output to just two site-specific parameters: shape parameter for a dimensionless function and Q95h (flow at 95% of maximum habitat). There was little variability in the shape parameter and, hence, defaulting to the average value worked in the absence of an adequate predictor (only 1 of the 4 HSC models predicted shape).

Room remains for improvement in the shape predictions, but this is less critical for the model's success than predicting Q95h (the observed coefficient of variation for Q95h was at least 3x greater than that of the shape parameter). In desktop models, the natural MAF (mean annual flow) was an adequate predictor of Q95h, with small improvements achieved for most models by using the percent alteration of MAF as a second predictor.

From the pilot studies, I observed that this combination of natural MAF and MAF-alteration performed better than models that instead used existing flow. This result is surprising, given that the existing flow was calculated directly from natural MAF and MAF alteration. The better predictions using natural MAF imply that channel morphology has not fully adjusted to match the alteration of MAF, retaining a form closer to natural. This perhaps agrees with Williams & Wolman (1984), whose best model for bankfull width used both pre-dam (annual 1-day maximum) and post-dam (MAF) flow metrics. Three explanations for the inclusion of natural flow are considered. First, some channels show little response to flow change, such as steep channels that are armored by colluvial boulders (Ryan, 1997). This seems an unlikely explanation as most of my study sites are pool-riffle streams (slope <1.5%) for which Ryan (1997) did observe a change in width. Furthermore, channel armoring does not explain why Williams & Wolman (1984) found that natural flow was a significant predictor for the width of erodible sand-bed rivers.

Second, if channel forming flows were less altered than MAF, then existing channel morphology would not reflect the existing MAF. These channel forming flows are typically much larger than MAF in cobble streams (e.g., Hey & Thorne, 1986, used bankfull discharge). Ryan (1997) demonstrated that large reductions in MAF (20% to 60% reduction in annual yield) translated to small reductions in bankfull width, where the large floods remained intact (~12 year recurrence).

Third, the selected sites could be in various states of transition. There is a time lag in channel response to flow alteration (Petts, 1987), but this seems less likely given that several decades separated the start of flow alteration from the survey date in most cases (Table S2.1). Therefore, the parameters for MAF-alteration should represent the autocorrelation between the alteration of MAF and the alteration of channel forming flows (minus any temporal lag in channel adjustment).

The rapid-survey model provided better predictions of Q95h than the desktop model. Measured width represents the realized channel size, integrating the consequences of transport capacity (flow regime, slope), sediment supply and bank stability (Anderson et al., 2004; Flores et al., 2006). Width was not considered a desktop variable, as survey estimates of width at MAF (from PHABSIM) were used to train the model. The demonstrated reduction in survey effort comes from the strong correlation between width at MAF (full survey) and inflection width (rapid survey) that approached a 1:1 relationship. Rapid survey width is estimated from plots of wetted width versus average depth, so does not require velocity measurements or return visits. In addition, the success of rapid-survey models in predicting Q95h for validation sites was achieved using rapid-survey estimates of width (i.e., not using width at MAF from PHABSIM surveys). Surprisingly, the validation analysis indicated that the estimates of channel width from aerial photographs produced worthwhile gains, compared to the desktop model. The use of aerial photographs introduces error at a cross-section scale, but this error is offset at a reach scale with more cross-section replicates, unlimited reach access and the ability to measure change in width over time from historical aerial photographs (see (Marcus & Fonstad, 2008). Therefore, aerial photographs can alleviate some of the sampling and scale issues discussed by Dunbar et al. (2011) and Petts (2009). Better predictions are dependent on adequate aerial photographs for the stream of interest and are less useful for small streams where bank vegetation conceals the channel (see Bird et al., 2010).

The desktop model overestimated Q95h for most validation sites. Given that several decades separate most of the training site surveys from the validation site survey (median year 1985 and 2007, respectively), perhaps this overestimation reflects a change in the relationship between a static estimate of MAF and a varying channel size (sensu Milly et al., 2008). There is evidence that larger floods preceded the earlier surveys of training sites, increasing channel sizes. For example, the Yampa River (at USGS09251000) produced the highest 5-year mean flow on record for the period 1982-1986, compared to 2000-2004 that recorded the second lowest flow. The rapid-survey models are therefore expected to be more robust to global change than the desktop models.

In addition to the dynamic predictions of the GHM (habitat response to changing flow), the rapid-survey predictor (width) can also be dynamic (e.g., model change in width with change in peak flow using historical aerial photographs). This presents an opportunity for evaluating the habitat response to flow under some future scenarios of channel width (sensu Carpenter, 2002), which is not offered by PHABSIM (Petts, 2009). We can then take a step forward in our understanding, but must add the uncertainty in how channel shape changes with width to the long list of uncertainties for the streams of tomorrow (see Brandt, 2000, and "Channel dynamics and stability" section in Bovee et al., 1998). Neither the desktop, nor the rapid-survey models, assume static ecosystems. It is up to the investigator to decide if sustaining trout populations is a reasonable expectation for a given site (see Wenger et al., 2011), as dictated by broader environmental constraints (Poff, 1997).

The predictive success that I achieved using the chosen methods compares favorably with the results of similar studies outside Colorado (Booker & Acreman, 2007; Lamouroux & Jowett, 2005; Lamouroux & Souchon, 2002; Saraeva & Hardy, 2009a). The New Zealand GHM by Lamouroux & Jowett (2005) achieved an explained variance of 73% for adult brown and 76% for rainbow trout. For France, Lamouroux & Capra (2002) achieved explained variance of 89% for adult brown trout and 86% for juveniles.

The variance explained by the Colorado models (rapid-survey 82%-89%, desktop 68%-85%) approached the results achieved by Lamouroux & Capra (2002) and exceeded the results achieved by Lamouroux & Jowett (2005). But note that the explained variance from the Colorado model represents the end-product, compared to Lamouroux & Capra (2002) and Lamouroux & Jowett (2005), whose values for explained-variance exclude the added uncertainty of estimating wetted width (i.e., they predicted habitat versus unit-width flow, not versus stream flow). It appears that a similar level of success was achieved here using less training data and a demonstrated reduction in survey effort. I achieved a similar level of prediction success for the validation sites (mean 82% explained variance), despite estimating stream width from aerial photographs (as surveyed width data were unavailable).

The predictive success of GHMs for the Nooksack basin (Washington, USA) by Saraeva & Hardy (2009a) was evaluated using the root mean square error, for which they achieved values often less than 15% (evaluated against the training data). The equivalent root-mean-square-error calculated from all the Colorado validation-sites was 15% for BT2 and 18% for RT2. I attribute this success to focusing on just one region (southern Rocky Mountains), using dimensionless habitat (% of maximum), omitting substrate/cover, and focusing on sub-maximal flows.

Biological validation demonstrated the strength of the Colorado GHM in explaining the number of large brown trout (>356 mm) supported by a reach. The inclusion of small trout (127-356 mm) introduced substantial variability that the models could not explain. This suggests that hydraulic habitat is a primary constraint on a river's carrying capacity for large trout, but numbers of smaller trout are constrained by additional variables, such as flood effects on recruitment (Latterell et al., 1998; Nehring & Anderson, 1993). The poor prediction for small trout might also reflect the more fundamental problem raised by Railsback et al. (2003), where HSC developed for juvenile trout falsely interpreted habitat *use* as habitat *preference* – false because juveniles were forced into sub-optimal habitats by larger trout. Problems with juvenile HSC are further supported by the inferior fit of my Maxent HSC models for juvenile trout compared to adult trout (AUC values 0.73 and 0.90 respectively, Appendix 3). The obvious way around this problem is to base the flow recommendations on adults, rather than juveniles. This is a useful outcome, given that flow managers must ultimately choose a single flow value to apply at any point in time.

There are several important caveats worth mentioning. The GHMs were developed for Rocky Mountain streams of Colorado. There are many important differences to the neighboring Great Plains that could invalidate the GHM (e.g., width:depth ratio, fish community). Within the Rocky Mountains, small steep streams were poorly represented in the dataset, so the models may produce misleading results for streams with a MAF less than 0.6 m^3/s and reach slopes greater than 10%. The quadratic function for shape will under-estimate habitat at flows greater than Q95h. Most caveats that apply to PHABSIM (see Annear et al., 2004) also apply to this GHM. For example, hydraulic habitat is just one of several potential physical constraints (e.g., flood disturbance, temperature) that operate at different scales to determine population performance.

Frameworks such as ELOHA (Poff et al., 2010) provide the context for the development and implementation of individual methods, such as this GHM. Furthermore, New Zealand’s proposed national standards for ecological flows spell out when GHMs can be used in place of intensive surveys, depending on instream values and flow alteration (Appendix 4 in MfE, 2008). In the absence of such specific guidelines for Colorado, the GHM itself could be useful for deciding when to use intensive surveys (e.g., if the GHM predicts substantial reductions in habitat). The potential for developing more biologically relevant metrics from existing remote-sensing data using the Colorado GHM could also advance regional-scale niche modeling.

Table S2.1 Site location, survey details and notable flow alterations for the study sites.

River	Site	Dates Surveyed	No. of XS	No. of Calibr.	Lat, Long	Notable Flow Alteration
Arkansas	Gold Medal Area	July 1985 to Jan 1986	8	3	38.510, -105.965	Receives transbasin water via Twin Lakes and Fry-Ark Project (1975)
Blue	Eagles Nest State Wildlife Area	Summer 1983	5	3	39.722, -106.125	Dillon Res. transbasin diverts out via Robert's Tunnel (1963)
Cache la Poudre	1.Lower wild trout water	Feb to Aug 1983	6	3	40.694, -105.255	Receives transbasin from Laramie Tunnel (1921), Grand (<1934), Michigan (1905) & Wilson (1900) ditches. North Poudre Tunnel diverts out (1952).
Cache la Poudre	2.Below North Fork confluence	Aug & Nov 1986	6	2	40.698, -105.246	Receives transbasin from Laramie Tunnel (1921), Grand (<1934), Michigan (1905) & Wilson (1900) ditches. North Poudre Tunnel diverts out (1952).
Cache la Poudre	3.Below canyon mouth	Aug & Nov 1986	5	2	40.660, -105.209	Receives transbasin from Laramie Tunnel (1921), Grand (<1934), Michigan (1905), Wilson (1900) ditches. North Poudre Tunnel (1952) and Poudre Valley Canal diverts out (1952). Upstream of CBT input (1957).
Cache la Poudre	4.Indian Meadows	Summer 1987	5	2	40.700, -105.541	Receives transbasin from Laramie Tunnel (1921), Grand (<1934) & Michigan (1905) ditches.
Cache la Poudre	5.Below CDOW Poudre Rearing Unit	Summer 1987	6	2	40.699, -105.705	Receives transbasin from Laramie Tunnel (1921), Grand (<1934) & Michigan (1905) ditches.
Colorado	Lone Buck	Apr May 1983	6	3	40.048, -106.139	Lake Granby (1949), Willow Creek Dam (1953), Windy Gap (1985) & Moffat Tunnel (1936) all with transbasin diversions out.
Dolores	below McPhee Dam	July 1986	7	1	37.577, -108.587	McPhee Res. transbasin diversion out (1986); run-of-river diversion prior (1800's)
Fraser	1.Winter Park	1985	9	1	40.039, -105.881	Moffat transbasin diverts out (1936)
Fraser	2.Canyon	1985	6	2	39.942, -105.806	Moffat transbasin diverts out (1936)
Fryingpan	Old Faithful Station	Aug 1984 to Nov 1985	6	3	39.361, -106.841	Ruedi Res. (1968)
Gunnison	Black Canyon	Nov 1982	6	3	38.669,	Uncompahgre Tunnel diverts out (1911); Blue Mesa

River	Site	Dates Surveyed	No. of XS	No. of Calibr.	Lat, Long	Notable Flow Alteration
	(Duncan-Ute Trail)				-107.848	Res. (1967), Crystal Res., Morrow Pt. Res.
Lake Fork	Below Turquoise Lake	June 2010	5	4	39.219, -106.377	Receives transbasin from Busk-Ivanhoe tunnel (1925), Homestake tunnel (1968), Bousted tunnel (1972). Turquoise Reservoir 120 kAF (1968),Mount Elbert Conduit diverts out (1981).
Little Vasquez	980 ft d/s GrdCnty diversion	1985	7	2	39.903, -105.795	Moffat transbasin diverts out (1936)
Middle Fork Sth Platte	Tomahawk Property	May to Aug 1983	6	3	39.080, -105.859	Receives transbasin from Arkansas River (1980?)
North Fork Cache la Poudre	upstream of Seaman Reservoir	July to Aug 1986	6	2	40.728, -105.236	Halligan Reservoir (1910)
North Fork Cache la Poudre	downstream from Seaman Reservoir	July to Sept 1986	6	2	40.703, -105.232	Halligan Reservoir (1910) & Seaman Reservoir (1943).
North Fork Sth Platte	below Foxton	Summer 1983	7	3	39.433, -105.227	Receives transbasin from Blue River via Roberts Tunnel (1963/6)
Rio Grande	Wason Ranch	July to Oct 1985	6	3	37.824, -106.894	Rio Grande Reservoir 54 kAF, (1914).
South Fork Rio Grande		May to July 1981	6	4	37.590, -106.729	Two small reservoirs.
South Platte	11 Mile Canyon	Fall 1984	7	3	38.909, -105.461	Receives transbasin from Arkansas (1980?); 11 Mile Res., Spinney Mtn Res.
South Platte	Happy Meadow Campground	Summer 1983	9	3	39.014, -105.362	Receives transbasin from Arkansas (1980?); 11 Mile Res.; Spinney Mtn Res.
Vasquez	1/4 mile d/s DC diversion	1985	8	2	39.901, -105.804	Moffat transbasin diverts out (1936)

Table S2.1 continued.

Table S2.2 Desktop variables for the study sites derived from the TNC database (variables are described in Table 2.1).

River	MAF (m^3/s)	%Flow Alt.	Elevation (m)	Reach Slope	Watershed Slope	Dam Storage Density	Reach Temp. (^{o}C)	Watershed Temp. (^{o}C)	Watershed Area (km^2)	Riparian Width (m)
Arkansas	17.7	22%	2122	0.34%	4.40%	78%	16.0	9.7	3677	126
Blue	8.3	-35%	2578	0.82%	4.90%	150%	11.4	8.4	994	309
Cache la Poudre 1	9.7	15%	1643	0.82%	4.62%	22%	15.6	9.6	1251	66
Cache la Poudre 2	10.9	14%	1624	0.39%	3.43%	42%	15.8	11.2	2738	78
Cache la Poudre 3	10.8	14%	1586	0.09%	3.43%	42%	16.4	11.3	2746	142
Cache la Poudre 4	7.7	19%	2152	0.86%	4.70%	10%	13.1	7.7	607	114
Cache la Poudre 5	7.4	20%	2335	0.55%	4.47%	9%	10.6	7.1	506	193
Colorado	17.5	-61%	2300	0.37%	4.13%	152%	12.1	8.8	2227	95
Dolores	14.1	-41%	2026	0.48%	4.04%	116%	15.4	12.4	2124	189
Fraser 1	2.1	-44%	2622	0.99%	6.26%	0.54%	10.9	7.6	162	342
Fraser 2	5.2	-41%	2499	0.65%	4.14%	6%	10.8	8.9	601	90
Fryingpan	6.2	-30%	2246	1.02%	4.12%	77%	12.1	8.9	638	84
Gunnison	46.7	-34%	1615	0.90%	3.68%	81%	17.4	10.3	10446	40
Lake Fork	0.64	0%	2905	1.00%	4.09%	813%	9.4	7.2	94	825
Little Vasquez	0.2	-43%	2817	5.18%	6.20%	0.00%	9.1	7.8	14	48
Middle Fork Sth Platte	2.3	16%	2745	0.46%	3.32%	17%	11.5	7.7	433	369
North Fork CLP1	1.8	3%	1681	0.67%	2.55%	52%	15.7	12.3	1463	51
North Fork CLP2	1.8	3%	1642	0.87%	2.57%	66%	15.8	12.4	1483	76
North Fork Sth Platte	2.3	107%	1923	1.26%	4.00%	20%	16.3	11.0	1213	61
Rio Grande	13.3	1%	2606	0.35%	3.53%	65%	12.6	9.4	1765	214
South Fork Rio Grande	2.9	0%	2624	1.49%	5.06%	17%	10.5	8.8	184	136
South Platte 11	2.9	30%	2574	1.47%	1.72%	172%	12.0	10.5	2475	78
South Platte HMC	3.2	28%	2399	0.38%	1.76%	163%	13.8	11.0	2907	77
Vasquez	0.9	-41%	2860	1.89%	5.54%	0.46%	7.5	5.7	58	82

Table S2.3a Function parameters fitted for the Quadratic Function (left table) and Exponential Function (right table) using NLME (Non-Linear Mixed Effects) model. The AIC statistic of the better fitting function is highlighted in bold (smaller AIC is better), together with other goodness of fit statistics. Fixed parameters (A and K) are given in the top rows.

QUADRATIC	BT2+	RT2+	T2+	T1+	BT1+		**EXPONENTIAL**	BT2+	RT2+	T2+	T1+	BT1+
fixed **A**	-0.674	-0.697	-0.693	-0.635	-0.652		fixed **K**	-2.492	-2.347	-2.349	-2.612	-2.615
AIC	**-1188**	**-1043**	**-1223**	-933	-564		AIC	-999	-747	-885	**-988**	**-604**
BIC	-1174	-1030	-1209	-920	-553		BIC	-986	-733	-871	-975	-592
logLik	598	526	615	471	286		logLik	503	377	446	498	306
R^2 (obs vs. pred)	0.9972	0.9966	0.9968	0.9884	0.9900		R^2 (obs vs. pred)	0.9928	0.9827	0.9859	0.9914	0.9930

Table S2.3b Model selection summary to predict the **shape parameter** for each species and life-stage across the riverscape. The BIC values for the best subset models are compared for each number of variables, up to 4 (lower BIC is better). The percent of models that included each variable (under bootstrap re-sampling of the dataset) are given; in addition to statistics for each model and the final selected model itself. Most variables and their transformations are detailed in Table 2.1, except width (m), which was square root transformed.

Species/life-stage:	BT2+		RT2+		T2+		T1+	
Parameter:	Quadratic B		Quadratic B		Quadratic B		Exponential C	
All subsets models:	BIC:		BIC:		BIC:		BIC:	
1 var	-153.0	ln.gradR	-134.2	ln.gradR	-107.8	gradWS	-84.7	gradWS
2 var	-151.8	elevtn +ln.gradR	-133.1	ln.gradR + gradWS	-108.8	gradWS+sqrt .width	-86.1	gradWS+ln.dam_stor
3 var	-149.0		-131.2		-108.0		-83.8	0.0
4 var	-146.0		-128.4		-106.7		-81.6	
Bootstrap stepwise		% select		% select		% select		% select
variable selection	ln.gradR	60	ln.gradR	63.2	gradWS	80	gradWS	88.6
	ln.maf1	46.8	ln.rip_width.001	50.4	sqrt.width	63.4	ln.dam_stor0.1	79.2
	elevtn	44.6	gradWS	49.2	ln.gradR	58.4	ln.maf1	60.4
	gradWS	40.6	sqrt.width	47.4	ln.dam_stor0.1	57.4	sqrt.width	43.4
	ln.rip_width.001	40.6	ln.maf1	44.8	ln.rip_width.001	55	ln.rip_width.001	36.2
	sqrt.width	39.8	ln.dam_stor0.1	39.8	elevtn	53.2	maf_alt	33.4
	ln.dam_stor0.1	37.2	elevtn	39.2	ln.maf1	52.4	ln.gradR	33.2
	maf_alt	30.8	maf_alt	34.4	maf_alt	44.6	elevtn	31.6
	Null	1	Null	1.6	Null	0.8		
Final models:	*quadratic B = -1.485*		*quadraticB = -1.627881*		*quadraticB = -0.11739*gradWS - 1.44013*		*expC = -0.8619854*	
Model statistics: MSE (MS resid.)	0.0310		0.0465		0.0062		0.1454	
F-statistic:					4.727			
degr. freedom					1 & 20			
p-value, Pr(>F):					0.0419			

Table S2.3c Model selection summary to predict the **Q95h** parameter for each species and life-stage across the riverscape using **desktop predictors**. Otherwise, as per Table S2.3b.

Species/life-stage:	BT2+		RT2+		T2+		T1+	
Parameter:	Q95h		Q95h		Q95h		Q95h	
All subsets models:	BIC:		BIC:		BIC:		BIC:	
1 var	-64.0	ln.maf1	-64.7	ln.maf1	-55.2	ln.maf1	-51.1	ln.maf1
2 var	-64.9	ln.maf1+maf_alt	-64.9	ln.maf1+maf_alt	-54.6	ln.maf1+maf_alt	-54.6	ln.maf1+maf_alt
3 var	-63.0		-62.5		-52.2		-53.7	
4 var	-60.2		-59.7		-49.7		-51.6	
Bootstrap stepwise variable selection		%select		%select		%select		%select
	ln.maf1	100	ln.maf1	99.6	ln.maf1	97.8	ln.maf1	95.2
	maf_alt	62.2	maf_alt	57.6	elevtn	54	maf_alt	71
	ln.dam_stor0.1	45.2	ln.dam_stor0.1	38	maf_alt	52	ln.gradR	64.4
	gradWS	37	gradWS	37.2	gradWS	47.4	elevtn	53.2
	elevtn	34.8	ln.rip_width.001	35.2	ln.rip_width.001	45.2	ln.rip_width.001	51
	ln.rip_width.001	32.4	elevtn	32.8	ln.gradR	44.2	gradWS	48.8
	ln.gradR	28.2	ln.gradR	26.6	ln.dam_stor0.1	42.2	ln.dam_stor0.1	40.2
Final model	*Ln(BT2.Q95h+1) ~ 0.6093*ln.maf1 + 0.2480*maf_alt + 0.5289*		*Ln(RT2.Q95h+1) ~0.62001*ln.maf1 + 0.22297*maf_alt + 0.6860*		*Ln(T2.Q95h+1) ~ 0.5886*ln.maf1 + 1.0853*		*Ln(T1.Q95h+1) ~ 0.51676*ln.maf1 + 0.41369*maf_alt + 0.60635*	
Model statistics:								
MSE (MS resid)	0.0397		0.0397		0.0674		0.0634	
F-statistic:	60.67		63.15		72.77		26.69	
degr. freedom	2 & 19		2 & 19		1 & 20		2 & 19	
p-value, Pr(>F):	5.62E-09		4.042E-09		4.264E-08		3.034E-06	

Table S2.3d Model selection summary to predict the **Q95h** parameter for each species and life-stage across the riverscape using **rapid survey width** and desktop predictors (excluding MAF). Otherwise, as per Table S2.3b.

Species/life-stage:	BT2+		RT2+		T2+		T1+	
Parameter:	Q95h		Q95h		Q95h		Q95h	
All subsets models:	BIC:		BIC:		BIC:		BIC:	
1 var	-71.6	sqrt.width	-73.1	sqrt.width	-76.6	sqrt.width	-73.5	sqrt.width
2 var	-72.1	sqrt.width+ln.rip_width	-72.4	sqrt.width+ln.rip_width	-76.0	sqrt.width + ln.rip_width	-75.0	sqrt.width + maf_alt
3 var	-69.5		-69.5		-73.3		-74.6	
4 var	-66.8		-66.7		-70.5		-73.0	
Bootstrap stepwise variable selection		%select		%select		%select		%select
	sqrt.width	99.6	sqrt.width	100	sqrt.width	100	sqrt.width	98.6
	ln.rip_width.001	61.4	ln.rip_width.001	40	ln.rip_width.001	47	maf_alt	80.6
	ln.dam_stor0.1	44	ln.dam_stor0.1	33.6	gradWS	44	ln.gradR	53.6
	gradWS	40.8	gradWS	32.4	ln.dam_stor0.1	39.8	ln.rip_width.001	48.6
	maf_alt	35.6	maf_alt	25.2	elevtn	30.4	elevtn	41
	elevtn	19.8	ln.gradR	20.8	ln.gradR	30.2	gradWS	38.2
	ln.gradR	17.6	elevtn	15.6	maf_alt	30	ln.dam_stor0.1	32
Final model	*Ln(BT2.Q95h+1) ~ 0.43295*sqrt.width - 0.34712*		*Ln(RT2.Q95h+1) ~ 0.44369*sqrt.width - 0.22051*		*Ln(T2.Q95h+1) ~ 0.467423*sqrt.width +0.003519*		*Ln(T1.Q95h+1) ~ 0.39915*sqrt.width + 0.20230*maf_alt - 0.28918*	
Model statistics:								
MSE (MS resid)	0.032		0.03		0.0256		0.0251	
F-statistic:	154		172.6		224.5		81.81	
degr. freedom	1 & 20		1 & 20		1 & 20		2 & 19	
p-value, Pr(>F):	7.508E-11		2.695E-11		2.454E-12		4.609E-10	

CHAPTER 3: COTTONWOOD RESPONSE TO REDUCED FLOOD FLOWS – COMPARING NARROWLEAF AND PLAINS COTTONWOOD

Summary

Cottonwood trees are valued members of riparian ecosystems, and their recruitment depends on high flow events in the drier areas of North America. Understanding the consequences of flow alteration for cottonwood is therefore important, especially in Colorado where water use is already high and projected to increase. To help plan for this increase, the ELOHA framework was used to develop flow-ecology relationships for three basins in Colorado (Yampa, White and upper Colorado River, total area 53,000 km^2). Using existing data, I successfully quantified a relationship between the abundance of plains cottonwood (*Populus deltoides* Bartram) and reduced peak-flows for 64 stream sections from the south-western USA (adult %abundance vs. wet-year 90-day maximum flow, rank score p-value = 0.015). The hypothesis that this flow constraint would also apply to a second species, narrowleaf cottonwood (*Populus angustifolia* James), was not supported because four reaches (out of the 39 surveyed) had abundant and reproducing narrowleaf forest, despite pronounced flow alteration (>40% flow reduction). Historic photographs revealed that narrowleaf in the Middle Park area increased in abundance since dam closure, colonizing previously bare gravel bars. That narrowleaf appear less sensitive to flow alteration than plains cottonwood could reflect different species traits (e.g., alternative sources of disturbance for root suckering by narrowleaf), together with

the many physical transitions from plains to mountains that are associated with the species transition.

Introduction

The modification of river flow regimes has, in many cases, altered riparian vegetation, including plant species richness (Jansson et al., 2000; Nilsson & Svedmark, 2002), plant growth (Stromberg & Patten, 1990), community composition (Merritt & Cooper, 2000; Merritt & Wohl, 2006) and loss of riparian forests (Rood & Mahoney, 1990; Swift, 1984). Riparian vegetation is important, providing shade, habitat and food for both terrestrial and aquatic animals, plus bank stabilization and interception of contaminants (Davies-Colley & Quinn, 1998; Gregory et al., 1991; Naiman & Décamps, 1997; Patten, 1998; Pusey & Arthington, 2003; Scott et al., 2003). In the western USA, cottonwood (*Populus* spp.) are especially dependent on the flow regime and flow-mediated fluvial processes (Friedman & Lee, 2002; Merritt et al., 2010; Patten, 1998; Rood & Mahoney, 1990), so they might serve as indicators of the physical processes that drive the broader ecosystem (Poff et al., 1997). Cottonwood are also directly valued by people (Bark et al., 2009), providing visual relief and shade in dry, treeless landscapes.

It is therefore critical that we understand the consequences of flow alteration for cottonwood, especially in Colorado where water demand is high. Of the 19.2 km^3 (=15.6 million acre-feet) of river water that would naturally reach the state borders annually (average 1998-2007), approximately 13.7 km^3 is diverted out of streams in Colorado for agricultural, municipal and industrial uses (calculated from State Engineer data). Adding to this demand, the population of Colorado is projected to double between 2008 and 2050 (CDM & HE, 2010). The state government has responded by taking a more proactive role in water management (Colorado-General-Assembly, 2005). This state planning process looked broadly at present and future demand across multiple basins (e.g., Yampa, White, upper Colorado), and the consequences for ecosystems (Sanderson et al., 2012). The challenge is predicting biotic response to flow alteration at such a large scale. Site-specific methods exist for investigating tree growth (Stromberg & Patten, 1990), population cohorts (Baker, 1990) and point bar migration (Richter & Richter, 2000), but these are not practical at a basin extent. Methods based solely on historical flow can be applied basin wide (e.g., Richter et al., 1996), but the relevance to cottonwood is not quantified.

The ELOHA framework (Poff et al., 2010) can help fill the gap between site-specific methods and historical flow methods, offering best practices for developing flow-ecology relationships across multiple streams. Setting aside the extensive social process (see Sanderson et al., 2012), the scientific components of the ELOHA framework adopted for cottonwood species in northwest Colorado included:

- Estimating flow alteration for a network of locations throughout the basins (StateMod; CDWR & CWCB, 2009);
- Geomorphic classification (Bledsoe & Carlson, 2010) to investigate the geomorphic setting in which cottonwood respond to flow alteration;
- Formulating hypotheses of the response of cottonwood to flow alteration, with input from an expert panel;
- Developing flow-ecology relationships using existing data for plains cottonwood (*Populus deltoides* Bartram); and,

- Examining the transferability of flow-ecology relationships for plains cottonwood to narrowleaf cottonwood (*Populus angustifolia* James) in northwest Colorado.

An important step in the ELOHA framework is formulating mechanistic hypotheses of the expected ecological response to flow alteration. Fortunately, the mechanisms by which cottonwood depend on flow are well established – at least for recruitment of plains cottonwood from seed in wide alluvial valleys (Cooper et al., 1999; Friedman et al., 1995; Karrenberg et al., 2002; Mahoney & Rood, 1998; Scott et al., 1996; Shafroth et al., 2002; Stromberg et al., 2007). Floods remove competing plants and deposit fresh alluvium on expanding point bars, providing moist, sandy and unshaded conditions for seed germination. The short-lived seeds travel to these surfaces by air or water and their timing must coincide with receding flows to avoid inundation (Fenner et al., 1984; Mahoney & Rood, 1998). In semi-arid and arid areas, flow recession must be gradual enough for the roots of seedlings to keep pace with dropping water levels. It may take three years of growth before plant roots achieve reliable access to groundwater, assuming they are not eaten, burned or washed away (Auble & Scott, 1998; Cooper et al., 1999; Polzin & Rood, 2006; Rood et al., 2007). Given the rarity of this combination of conditions arising, successful recruitment might only occur every 3-5 years in wide alluvial valleys (Rood et al., 2007; Scott et al., 1996).

Do these mechanisms hold true for my study area in Colorado? This is a safe assumption for meandering reaches that support plains cottonwood, because the studies by Merritt & Poff (2010) and Cooper et al. (1999) included sites in northwest Colorado below 1750 m in elevation. But most rivers in northwest Colorado (the upper Colorado, Yampa and White River basins) are at higher elevations and support a different species – narrowleaf cottonwood. Narrowleaf produce large quantities of seed each year, but root suckering (sprout from existing roots) is the more common recruitment strategy for narrowleaf, and other Section *Tacamahaca* cottonwoods (Section is a taxonomic classification below genus level and above species level), compared to seedling recruitment for plains cottonwood (Polzin & Rood, 2006; Roberts, 1999; Rood et al., 1994). Scour at high flows can stimulate suckering by scarifying tree roots, resulting in regeneration patterns in meandering rivers that resemble reproduction from seed (Gom & Rood, 1999; Polzin & Rood, 2006; Richter & Richter, 2000; Roberts, 1999). If root suckering is dependent on peak flows, then narrowleaf recruitment in meandering rivers might show a response to peak flow alteration similar to that observed for plains cottonwood.

My objective was to predict the constraint on cottonwood from flow alteration for StateMod nodes across northwest Colorado. Specifically, I hypothesize that reduced peak flows of a 3-5 year recurrence interval will constrain the abundance of plains cottonwood. In addition, I tested the hypothesis that the response to flow alteration by narrowleaf cottonwood is equivalent to plains cottonwood. To test these hypotheses, I followed these two steps: (1) developed flow-ecology models for plains cottonwood using data from Merritt & Poff (2010) that employed standardized field methods to survey plains cottonwood across the south-western USA; and (2) assessed whether the flow-ecology relationship for plains cottonwood were transferable to narrowleaf cottonwood using methods equivalent to Merritt & Poff (2010) to survey sites across the intended application area (Yampa, White and upper Colorado basins).

Study Area

The study area for plains cottonwood included sites across Arizona, New Mexico, Nevada and Colorado, as described by Merritt & Poff (2010). All sites are arid or semi-arid, receiving 100-425 mm precipitation per year across an elevation range of 79–1989 m (<1750 m in Colorado). Snowmelt from mountainous headwaters feed these rivers, with flows for the southernmost sites also influenced by monsoonal rains in summer.

The application area for narrowleaf extends to higher elevations (<2650 m) across three basins in Colorado, including the Yampa, White and upper Colorado (above the Gunnison confluence), with basin area totaling 53,000 km^2. Precipitation ranged from 280-880 mm/year and mean temperature ranged from 9.2-17.9 °C across the surveyed sites. More than half the sites surveyed in Colorado could be classed semi-arid, and the rest moist (zero water balance threshold between 346-492 mm precipitation/year, depending on temperature, using Equation 2 from Appendix 1). The snowmelt flow regime of these rivers produces predictable timing of peak flows, typically between late April and early July (class SN1 of Poff, 1996). It is important to note that introduced salt cedar (*Tamarix* spp.) were largely absent from the study area in Colorado (co-occurrence with narrowleaf at only 1 of 68 sites), in contrast to its extensive overlap of salt cedar with plains cottonwood in the study by Merritt & Poff (2010).

Methods

Re-analysis of existing data for plains cottonwood

Flow-ecology relationships were developed for plains cottonwood from a pre-existing dataset described by Merritt & Poff (2010). Riparian vegetation was assessed during 1999-2003 at 64 sections on 13 perennial rivers. Reaches were chosen to represent varying degrees of flow alteration and, therefore, selection depended on adequate flow records. This study extended into the state of Colorado (San Miguel, Dolores, Colorado and Yampa Rivers), and all sites were within the elevation range of plains cottonwood (sites at 79-1989 m elevation).

To assess abundance of adult cottonwood (adults: >5 yr), a 200 m long section of river was randomly selected and, at every meter increment, adult cottonwood occurrence (presence/absence) was observed for a perpendicular transect that ran across the entire floodplain Merritt & Poff (2010). This provided frequency of occurrence across 200x1 m wide transects from which to calculate %abundance. Therefore:

% abundance = the proportion of 1m wide transects containing 1 or more adult cottonwood.

The 200 m sections were replicated by spacing additional sections every 0.5 km over the reach of interest. For recruitment, the presence of 2-5 year old saplings was recorded for each 200 m long section. Plants less than 2 years of age were not included because mortality of young trees is high and does not yet indicate successful regeneration.

To relate plains cottonwood to flow, Merritt & Poff (2010) used a multivariate indicator of hydrologic alteration, termed the IFM (index of flow modification). This index was calculated using principal components analysis of 8 flow metrics (alteration of 2 yr, 10 yr & 25 yr return flood, seasonal mean flow, absolute days difference in timing of annual min. and max. flow), from which the axes scores were used to calculate Euclidean distance of each site from the centroid of unregulated rivers. The index performed well in representing flow alteration (accounting for 74% of variation in flow data), while dealing with collinearity among the various flow metrics. The problem is that the IFM is not directly interpretable by stakeholders in terms of flow units and is not compatible with StateMod (CDWR & CWCB, 2009), the hydrologic foundation of the Colorado study (because the IFM uses instantaneous flow maxima whereas StateMod uses a daily time-step).

Consequently, I derived alternative flow metrics for the Merritt & Poff (2010) sites using compatible daily time-step data from USGS gages. Some refinements were made to the dates dividing periods of pre- and post-flow alteration (Table S3.1), most notably for the Rio Grande, where I followed Wesche et al. (2005) (1942-70 for pre-Cochiti Dam, and 1975-2003 for post).

Merritt & Poff (2010) have already established the statistical significance of the relationship between this cottonwood dataset and flow alteration, and accounted for collinearity between flow metrics using principal components analysis. My analysis built on this by disentangling which StateMod compatible flow metric is the best proxy for the complex flow dynamics that actually explain cottonwood success. Candidate flow metrics were selected that are mechanistically linked to plains cottonwood recruitment (daily series 5 and 10 year return flood; 1, 7, 30 and 90-day maximum moving average flow; wet year 1, 7, 30 and 90-day maximum), following an Expert Panel Riparian Workshop (Box 3.1). Wet-year metrics were averaged across years exceeding the 70%ile MAF (threshold calculated separately for pre-and post-alteration) to better reflect the observed frequency of cottonwood recruitment (see Bradley & Smith, 1986; Mahoney & Rood, 1998; Rood et al., 2007; Scott et al., 1996). I focused exclusively on high flows because the sensitivity of cottonwood to low flow magnitude appears limited to intermittent flows and groundwater pumping (Lite & Stromberg, 2005; Stromberg et al., 2007). The flow metrics were calculated using IHA software (Indicators of Hydrologic Alteration, Version 7.1, Richter et al., 1996), and converted to percent alteration during post processing with Microsoft Excel 2007 (%alteration = [existing flow – natural flow] / natural flow).

Quantile regression was used to describe the upper bound for plains cottonwood response to flow, using Blossom statistical software (Cade & Richards, 2007). Quantile regression minimizes the sum of absolute deviations (“least absolute deviation”), which are asymmetrically weighted by the quantile (0.9 in this case) for positive residuals and one minus the quantile for negative residuals (i.e., 1-0.9=0.1). I expect the upper bound (90%ile) will better represent the constraint imposed by flow alteration, when other factors outside the flow managers control can also limit cottonwood abundance, such as grazing or fire (see Cade & Noon, 2003; Dunham et al., 2002a). The significance of the relationships was tested (null hypothesis: slope = 0) using a permutation rank score statistic (Cade et al., 2006) calculated from 5,000 permutations.

The candidate flow metrics were also compared in their ability to explain *recruitment* of plains cottonwood (presence-absence data) using a logistic Generalized Linear Model in R (Version 2.11; “stats” package; function “glm”; binomial family). The best flow metric was judged using AIC (Akaike’s Information Criterion), with P-values also generated from chi-square statistics (using “anova” function in R).

Box 3.1

An Expert Panel Riparian Workshop was convened on 25 February 2010 to provide guidance on flow-ecology relationships for *Populus deltoides*. Seven experts (all based in Fort Collins) attended the 4 hour meeting, from the United States Forest Service, United States Geological Survey and Colorado State University. More than an hour was spent introducing the ELOHA framework (N. L. Poff), the geomorphic foundation (B. B. Bledsoe) and intended use of the relationships (J. Sanderson). I also developed preliminary flow-ecology relationships prior to the meeting, and presented these to stimulate discussion. Questions were then posed to attendees by the moderator (N.L. Poff), including:

- What flow metrics should be used in flow-ecology relationships?
- How do flow-ecology relationships vary with hydrogeomorphic setting?
- What form are flow-ecology relationships likely to take?
- What additional data exist to inform flow-ecology relationships?

Achieving consensus amongst participants on flow-ecology response was less important than refining mechanistic hypotheses as a foundation of subsequent research. Literature research by the conveners prior to the meeting was beneficial in accelerating the discussion beyond fundamental concepts to processes driving cottonwood response to flow.

Survey of narrowleaf cottonwood in the northwest Colorado

Having developed flow-ecology relationships for plains cottonwood based on the Merritt & Poff (2010) dataset, I investigated the transferability of these relationships to narrowleaf in northwest Colorado by surveying riparian vegetation at 68 sections on 39 reaches of 21 streams during July-August 2011 (for locations, see Table S3.2). The higher elevations that I surveyed (1,550-2,650 m) largely excluded plains cottonwood, which were only observed at three sections up to 1,670 m (narrowleaf were at or above 1,670 m). Site selection started with the 223 StateMod points for which I had flow data (Figure 3.1) within the intended area of application (Yampa, White, upper Colorado). The StateMod sites were first partitioned by the geoclimatic setting where cottonwood were expected to respond to flow (unconfined and confined settings, elevation <2,650 m, no canyons, gorges or reach slope >4% to avoid streams coupled to hillslopes). Qualifying sites were subsequently screened for survey access. Reaches were selected this way in the Yampa-White basin and for the Colorado basin between the Eagle River confluence and Gunnison River confluence. Select few sites were added from the Colorado basin above the Eagle confluence only to provide reaches with more altered flows. Favoring public lands introduced limited bias because 74% of the study area is federal or state owned land (calculated using data from NREL CoMap Version 9). At least one section of stream was surveyed (200 m) at each reach (reach delimited by major changes in flow or geomorphology). The location of the first section was randomly selected within the accessible reach (Microsoft Excel RANBETWEEN function used to generate a distance from the downstream end of the reach), and subsequent sections were spaced every 500 m, for up to 4 sections (accessible reach length permitting). Start points were printed on aerial photographs to enable location in the field.

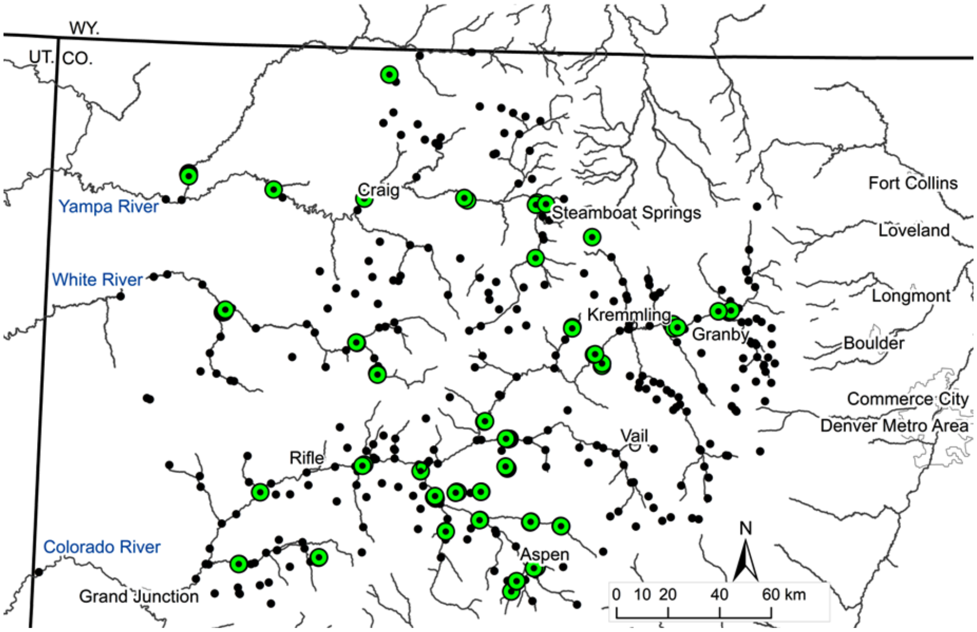


Figure 3.1 Map of sites surveyed in northwest Colorado for testing transferability of flow-ecology curves to a different species of cottonwood (circled points). The black dots represent all StateMod nodes across the Yampa, White and upper-Colorado basins.

Riparian vegetation was surveyed along each 200 m section, mostly adhering to the methods of Merritt & Poff (2010). Points of difference included recording the number of visible narrowleaf saplings (2-5 year old) for each 200 m section, up to a maximum of 50 plants (cf. presence/absence of Merritt & Poff, 2010). To determine the age class, I relied primarily on stem diameter (10-30 mm at ground level for 2-5 years old), having confirmed these size-age thresholds from growth-ring counts at both high and low elevation sites. Willow (*Salix* spp. excluding *S. exigua*) abundance was estimated from aerial photographs, supported by site photos, observations and field notes.[1]

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[1] Though not reported here, the presence/absence of select native species were recorded over each 200 m section, including sandbar willow (*Salix exigua*), *Salix* spp. (excluding peach leaf, crack and sandbar willow), dogwood (*Cornus sericea*), box elder (*Acer negundo*), alder (*Alnus incana*) and spruce (*Picea* spp.).

The metric used in the flow-ecology relationship for plains cottonwood (wet-year 90-day maximum) was calculated using IHA software (Richter et al., 1996) for Colorado survey sites. Daily-series flow data were generated by StateMod - the State of Colorado's Stream Simulation Model (CDWR & CWCB, 2009). In addition to existing flow for 1975-2005, StateMod provided an estimate of natural flows reconstructed for 1975-2005 using, for example, diversion records, simulated reservoir operation and return flows (see CDWR & CWCB, 2009). Strengths of StateMod include the many sites represented (Figure 3.1), long record (31 years) that is sufficient to capture inter-decadal variability (see Kennard et al., 2009), and estimation of natural flows concurrently to help isolate direct flow alteration from climate-driven changes. Monthly time-step metrics were more reliable because some diversion records were recorded at a monthly time-step, and StateMod used disaggregation methods to synthesize a daily record (e.g., using unaltered pattern gages or interpolated demand).

For the purpose of comparison, the Index of Flow Modification was also calculated for northwest Colorado sites using principle components analysis of the same flow metrics used by Merritt & Poff (2010). Instantaneous flood metrics were calculated for sites with adequate USGS flow records, but had to be synthesized for the remainder of the sites (instantaneous peak flows estimated from daily peak flows using equations developed from USGS sites with both instantaneous and daily peak flow data).

Relative abundance of salt cedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*) was also surveyed.

Physical data were sourced from the Geomorphic Valley Classification (Bledsoe & Carlson, 2010) for the Colorado and Yampa watersheds; NHDPlus data compiled and revised by The Nature Conservancy; in addition to remotely sensed (aerial photograph) measurements of channel width (Appendix 4). Valley width was the median of three estimates, including: 1 - valley width estimated from a digital elevation model (Bledsoe & Carlson, 2010); 2 - site sketches of riparian width; and 3 - site sketches of break points in bank slope. Only the latter two estimates were available for the White watershed, as it was not yet classified for the Geomorphic Valley Classification. Water balance was predicted for the riparian study reaches using Equation 2 from Appendix 1, after omitting area from the equation (unit runoff (m^3/year*m^2) = precip/1000 – $0.1395*e^{temperature*0.09182}$).

Temporal response of narrowleaf to flow alteration

Surveys revealed that rivers in the Middle Park area (Colorado) supported extensive narrowleaf forest, despite large dams and, hence, I sought to better understand how riparian vegetation had changed over time. I compared aerial photographs taken pre-dams (October 1938) with photographs post-dams (2005-2010) over a 39 km length of the Colorado River between Windy Gap Reservoir and the entrance to Gore Canyon (longitude -105.98° to -106.43°, latitude 40.1°; major dams constructed 1949-1994). The 1938 images were sourced from the University of Colorado aerial photograph collection (http://libcudl.colorado.edu:8180/luna/servlet) and rectified visually to landmarks in Google Earth for comparison with recent aerial photographs. Unvegetated bars (contiguous point bars or islands) were counted from 1938 aerial photographs. For each 1938 bar, I categorized the existing vegetation cover from recent aerial photographs (2005-2011) as cottonwood, willow dominated, other vegetation, partially vegetated or bare (no vegetation). Long shadows were useful in distinguishing tall cottonwood from other vegetation, as were overlapping site surveys and "Google Street View" imagery (2007). Aerial photographs from 1947 were also inspected for a subset of locations (reflecting availability), and provided confirmation that the 1938 images were representative of pre-dam prevailing conditions. This process was repeated for a 2.2 km reach of the Fraser River upstream of the Colorado River confluence – a tributary with large trans-basin flow diversions (losing), but lacking large dams.

Changes in water level and bed level were investigated for one site where the datum has remained unchanged (USGS 09019500, Colorado River downstream of Granby Dam). Stage was recorded for stream flow measurements for 1934-1949 (pre-dam) and 1983-2011 (post-dam), together with width and mean depth. Ice affected measurements were omitted from the pre-dam dataset (typically December-March) and measurements were only taken from April to October during the post-dam period. This reduced the dataset to 115 measurements pre-dam and 189 post-dam.

Results

Plains cottonwood - Finding a metric of flow alteration compatible with StateMod

To describe the response of plains cottonwood to flow alteration (existing data from Merritt & Poff, 2010), I compared several flow metrics that are compatible with StateMod (daily time series flow). Percent alteration of the wet-year 90-day maximum flow produced the best correlation with adult plains cottonwood (Table 3.1). Quantile regression identified an upper bound (90th percentile, p=0.015, n=41), that is interpreted as describing the constraint imposed by flow alteration (Figure 3.2). For example, a 50%

reduction in the wet-year 90-day maximum flow is expected to reduce the *potential* abundance of cottonwood by 53%. Sites with positive flow alteration (i.e., flow augmentation) were excluded from this analysis to improve the adequacy of a linear equation, and because we are primarily concerned with flow reduction for streams west of the continental divide. The relationship was insensitive to the function used (linear or quadratic), averaging across replicates, or bootstrap section selection (linear coefficient between 1.03 and 1.20, Figure 3.2 inset). The wet-year 90-day maximum flow was correlated with the multivariate IFM metric that it is intended to replace, and other peak flow metrics (Table S3.3).

Table 3.1. Comparing flow alteration metrics based on their correlation with abundance of adult plains cottonwood (data from Merritt & Poff, 2010), but excluding sites with augmented flow (alteration >0) to ensure adequacy of a linear equation. The coefficients and constants describe a 90th percentile boundary calculated using quantile regression (abundance = constant + coefficient x flow alteration). The wet year 90-day maximum flow produced the best correlation, judged using permutation rank score test. The multi-metric IFM from Merritt & Poff (2010) is also tabulated for comparison.

Flow alteration metric	Constant	Coefficient	N	p-value (rank score)
5-yr return	0.8550	-0.3013	45	0.564
10-yr return	1.0008	0.0320	46	0.459
90-day max	1.0485	1.2062	44	0.027
30-day max	1.0347	1.0405	44	0.095
7-day max	0.9997	0.4779	49	0.032
1-day max	1.0895	1.0541	45	0.041
wet yr 90-day max	1.0051	1.0379	41	0.015
wet yr 30-day max	1.1323	1.0725	43	0.184
wet yr 7-day max	1.0000	0.0000	46	0.782
wet yr 1-day max	1.2153	0.9687	41	0.950
IFM LN(Y+1)	0.7756	-1.2723	64	0.001

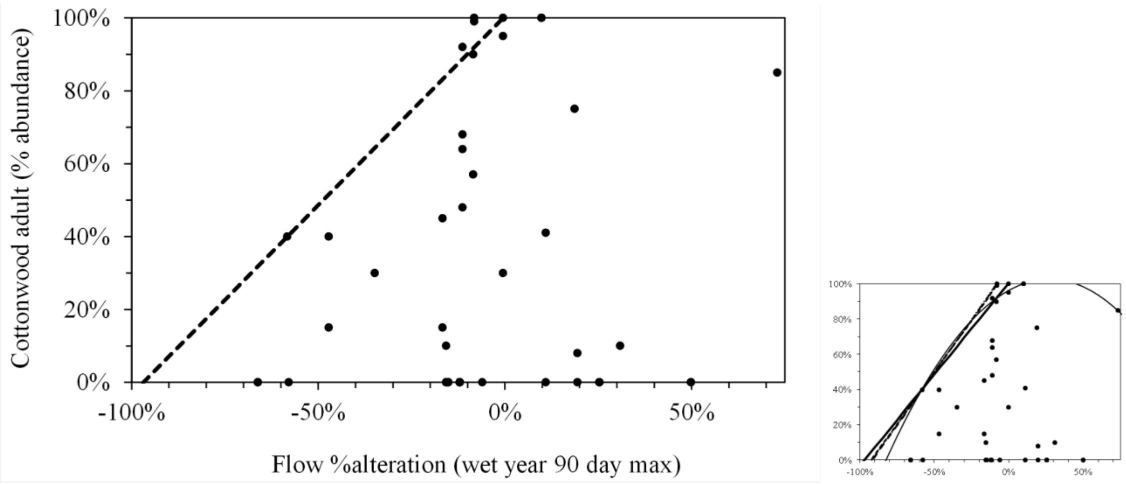

Figure 3.2. The constraint of flow alteration on abundance of adult plains cottonwood is described here using the 90th percentile relationship with the wet-year 90-day maximum flow (% abundance = 1.038 x % flow alteration + 1.005; rank score p-value = 0.015). This flow metric provided the best correlation, compared to other StateMod compatible flow metrics (Table 3.1). The inset plot (right) demonstrates the function is not an artifact of model selection, with similar responses produced using reach means (linear function), bootstrap of single-sections that were randomly selected for each reach (linear function), and a quadratic function fitted to all sections.

I also investigated the occurrence of juvenile plains cottonwood, as a measure of recruitment, to discern the best correlate among the candidate flow metrics. This used a logistic generalized linear model, instead of quantile regression, because juvenile cottonwood were recorded as presence-absence by Merritt & Poff (2010). Once again, the wet year 90-day maximum flow was the best predictor variable and was closest to the IFM in explanatory power (Table 3.2). Recruitment was not observed at any sites where flow was reduced more than 11% (wet year 90-day max) and, consequently, the probability of recruitment was expected to decline steeply with reduced flow.

Table 3.2. For recruitment of plains cottonwood, I used logistic Generalized Linear Models to identify the best alternative to the multi-metric IFM from Merritt & Poff (2010). Of the alternatives considered, the best predictor was the wet year 90 day maximum (lowest AIC value).

	AIC (smaller better)	P-value Pr(>Chi), d.f. 114
5 yr return flow (daily)	105.7	0.0009
90 day max	113.0	0.0562
wet year 7 day max	109.6	0.0077
wet year 1 day max	106.1	0.0012
wet year 90 day max	103.6	0.0003
IFM	93.6	<0.0001

Narrowleaf cottonwood – Transferability of the flow-ecology relationship

Having established a univariate flow-ecology relationship for plains cottonwood data from Merritt & Poff (2010), I then examined the transferability of this relationship to narrowleaf in northwest Colorado. The narrowleaf survey results are presented together with the flow-ecology relationship (dashed line) derived from the plains cottonwood study (Figure 3.3). Most points lie below the 90th percentile line, but there are 4 reaches well above the line - meaning that narrowleaf were abundant, despite the pronounced flow alteration. We cannot dismiss these outliers as relict forests (i.e., formed by pre-dam flows) because recruitment was observed in 2011 for 3 of the 4 reaches. Flow alteration of the 4 reaches is a consequence of large dams upstream and associated transbasin diversions (e.g., Colorado-Big Thompson Project). The hollow circles represent sites where there are large reservoirs upstream with the capacity to hold at least 90% of annual runoff (Figure 3.4).

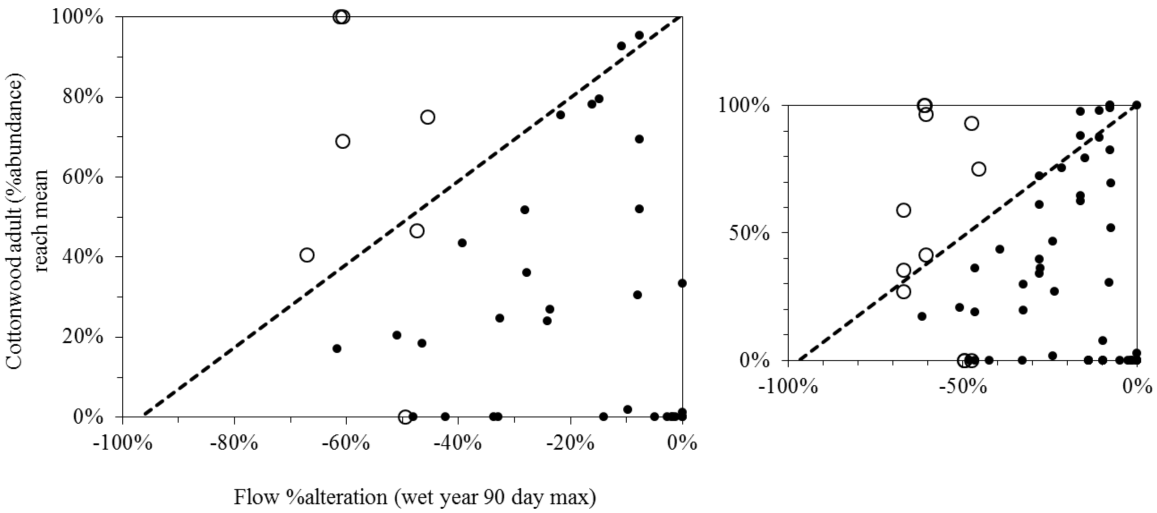

Figure 3.3. Narrowleaf cottonwood abundance versus flow alteration, together with the flow-ecology relationship (dashed line) derived from the plains cottonwood study (from Figure 3.2). Open circles represent sections where upstream reservoir capacity is 90% or more of annual runoff, and black dots less than 90%. The smaller plot (right) uses the same data, but presents individual section results instead of reach means.

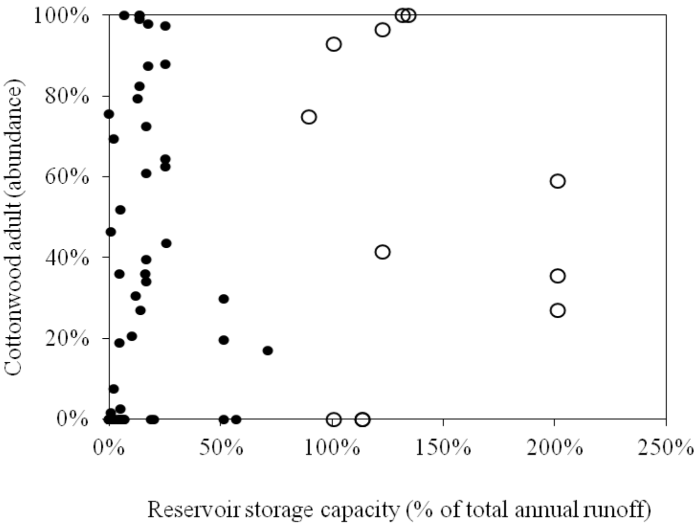

Figure 3.4. Narrowleaf cottonwood abundance plotted against upstream reservoir storage capacity expressed as a percent of annual runoff. Sections with 90% or more storage are distinguished by open circles in this plot, and this marker style is carried through the other plots based on this storage threshold.

My survey sites traversed the elevation/temperature range of narrowleaf (observed range 1650-2500 m; 11.3-16.5 °C annual mean), but it appears the cold limit of narrowleaf was specific to the geomorphic settings surveyed. Stands of narrowleaf were observed above 2500 m, but only in steep, confined settings (e.g., 45% narrowleaf at 2630 m, slope 12%, precipitation 665 mm/yr, annual temperature 10.3 °C). Willow, in contrast, were often dominant in unconfined valleys at high elevations (>2100 m elevation, water balance > 0, for *Salix* spp. excluding *S. exigua*). From site surveys, I observed wetter soils by unconfined streams at higher-elevations where willow were dominant (most streams were flowing near bankfull at the time of survey). In the absence of detailed groundwater data, the interaction between valley confinement and water balance goes some way to capturing this moisture gradient (Figure 3.5), with willow more abundant than narrowleaf in unconfined valleys with positive water balance.

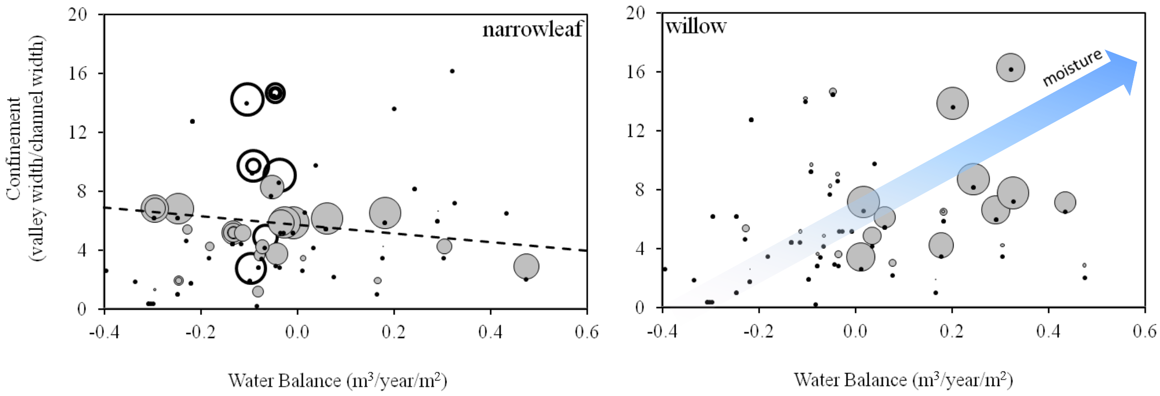

Figure 3.5. Confinement versus water balance, with the size of each data point representing narrowleaf abundance (left plot) and willow abundance (right plot). The smallest data points are 0% and the largest 100% abundance. I examined a possible soil-moisture gradient (depicted by arrow), from low moisture for confined streams (smaller confinement values) with negative water balance, to high moisture for unconfined streams with a positive water balance. Sections with 90% or more reservoir storage upstream are distinguished by open circles. Weighted least-squares regression (dashed line) was used to weight the confinement-water balance relationship by narrowleaf abundance (F-statistic: 0.80 on 1 and 40 DF, p-value: 0.38, R version 2.14, function LM).

Temporal response of narrowleaf to flow alteration

The reaches that supported extensive narrowleaf forests, despite severe flow alteration, were examined more closely to determine the changes in riparian vegetation over time. These reaches are in the Middle Park area below large dams that divert water across the continental divide. Comparing aerial photographs taken pre- and post-dam construction indicates that narrowleaf have increased in extent by colonizing 36 of the 61 bars that were unvegetated in 1938 (all 61 bars are now vegetated) (Figure 3.6). This narrowleaf colonization was more pronounced upstream of sediment inputs from Troublesome Creek, a tributary that lacks major dams (narrowleaf colonized 32 out of the 36 bars upstream of Troublesome). Conversely, most colonization by willow occurred downstream of Troublesome Creek (of the 17 bars dominated by willow, 13 were downstream). The Fraser River, also in Middle Park, provides a temporal reference over the same period (1938-2011), with no major dams used for its transbasin diversions (Windy Gap Reservoir captures sediment from the Fraser where it meets the Colorado). Willow remain dominant for the Fraser reach upstream of the Colorado confluence, with scattered narrowleaf trees only colonizing 2 bars. Unlike the Colorado River, unvegetated bars are still present today on the Fraser River (10 bars in 1938 and 10 bars in 2011, over the same 2.4 km reach). The location of the bars had changed for all but 1 bar, reflecting active meandering of the Fraser River channel.

Reduced flows have lowered water levels of the Colorado River downstream of Granby Dam (USGS 09019500), where the 75th percentile water-level was 0.35 m lower than pre-dam (compare 1934-1949 to 1983-2011). The water level reduction may have translated to a similar reduction in groundwater level for bars colonized by cottonwood. It certainly translated into reduced frequency of riparian flooding, as demonstrated by Figure 3.7, which shows that wetted width more often exceeded 15 m before Granby Dam was built (black points). The change in unvegetated channel width at this site was pronounced, narrowing by 63% (comparing aerial photograph 10/25/1938 to 8/20/2007) while the channel held to the same path. Degradation of the stream bed appears to be minimal, and was likely only responsible for about 0.05-0.1 m of the water-level reduction at this site (from plots of mean depth versus stage, and plots of stage versus width). The cobble substrate of Middle Park would limit the potential for channel incision, with a small proportion of erodible fines (D_{50} = 87 mm; Ward & Eckhardt, 1981).

Figure 3.6 Aerial photographs of the Colorado River above Troublesome Creek (Lat. 40.055, Long. -106.29), comparing pre-dam (23 October 1938) to post-dam (17 June 2005). Point bars and islands have been colonized by narrowleaf cottonwood. The 2005 image was sourced from Google Earth (USDA Farm Service Agency image) and the 1938 image from the University of Colorado (U.S. Forest Service image, BOW 5-54, Copyright, 2007, Regents of the University of Colorado, http://libcudl.colorado.edu:8180/luna/servlet/UCBOULDERCB1~17~17). Photograph width 1.5 km, with river flowing right to left.

Note that the Grand Ditch was constructed before Granby Dam (ditch extended from 1890-1936), so the aerial photograph comparison does not incorporate the flow reduction attributable to Grand Ditch (flow reduction about 7% of natural wet year 90-day max at USGS 09019500).

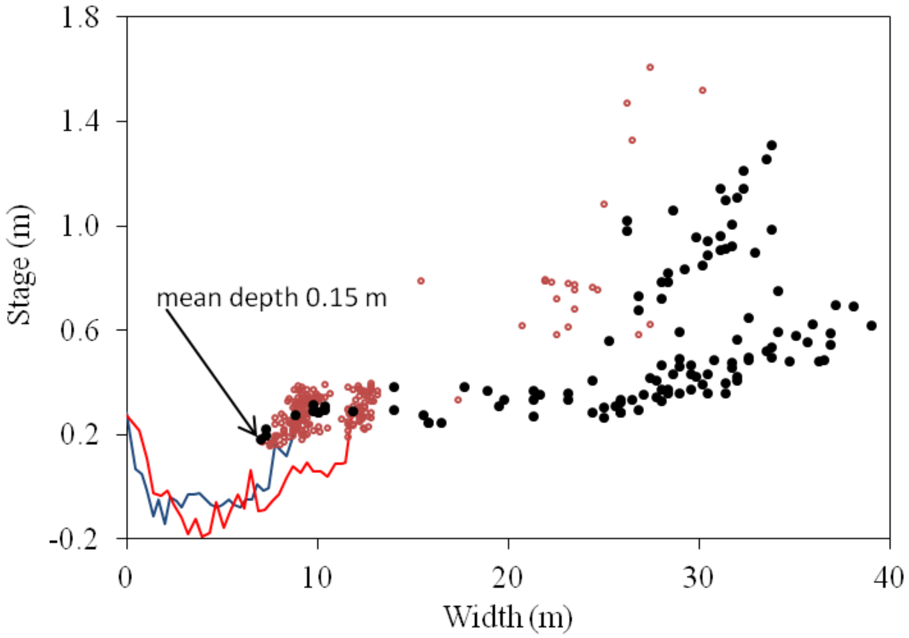

Figure 3.7 Multiple measurements of stage (water surface elevation) and wetted width build up a picture of channel form for the Colorado River below Granby Dam (USGS 09019500). This plot shows the similarity in bank form post-dam (red points 1984 to 2011) to pre-dam (black points 1934 to 1949). Three locations were used for flow measurements post-dam (narrower bank within 10 m of recorder, wider bank 30-60 m from recorder, widest bank at bridge), and cross-sections for two of these locations are plotted as lines to portray channel form below water level (location determined from distance to gage comments by surveyor).

Discussion

The objective of this study was to predict flow constraints on cottonwood at a regional extent (Yampa, White and upper Colorado basins). There was a significant relationship between plains cottonwood (*Populus deltoides*) and flow alteration (wet-year 90-day maximum flow), which supports the first hypothesis that a reduction in peak flows can constrain the abundance of cottonwood. The relationship was expressed as a constraint (quantile regression 90%ile) because other factors outside the flow managers control can also limit cottonwood abundance, such as logging (see Cade & Noon, 2003). This flow-ecology model is appropriate for water resource planning initiatives, but is not intended for flow prescriptions because it does not portray all components of the flow regime necessary for cottonwood recruitment (see instead Mahoney & Rood, 1998).

The second hypothesis proposed that narrowleaf cottonwood (*P. angustifolia*) would show a response to flow alteration that was equivalent to plains cottonwood. This was not supported because four reaches (out of 39 surveyed) had abundant and reproducing narrowleaf forest, despite pronounced flow alteration in semi-arid wide-valley settings (> 50% abundance, >40% reduction in wet-year 90-day maximum flow). Alteration of peak flows therefore does not represent a universal constraint on abundance and recruitment of narrowleaf. It is not likely that the observed response for narrowleaf was an artifact of flow-metric selection because an *a-posteriori* analysis of alternative flow metrics, including more extreme flood flows, low flows and the IFM, failed to explain why some narrowleaf were not impacted by flow alteration.

The narrowleaf surveys provided a regional perspective on the *spatial* response to flow alteration (north-west Colorado). In an effort to better understand those four reaches supporting abundant narrowleaf forests, despite severe flow alteration, the *temporal* response of narrowleaf to flow alteration was investigated over a smaller spatial extent. All four reaches are located in the Middle Park area below large dams that divert water across the continental divide (e.g., Granby Dam). Aerial photographs revealed that narrowleaf have actually increased in abundance since dam construction, colonizing 32 of the 36 gravel bars that were unvegetated pre-dam in 1938 (for the Colorado River between Windy Gap reservoir and Troublesome Creek confluence). In addition to reduced supply of fine sediment (Verstraeten & Poesen, 2000; Ward & Eckhardt, 1981), flow regulation has lowered stream water levels at one site (75th percentile water-level was 0.35 m lower after Granby Dam), which translated to reduced riparian flooding (from USGS measurements of wetted width) and likely lowered riparian groundwater levels (Woods, 2001, described the surface to groundwater level linkage at sites upstream of Granby Dam).

The increased abundance of narrowleaf appears to contradict the flow-ecology model for plains cottonwood. It also differs from the narrowleaf response on the South Fork Snake River, where Merigliano (1996) found little evidence of narrowleaf forest encroaching on surfaces that stabilized after damming (in a warmer valley than Middle Park, from NHDPlus data). Numerous other studies have shown that recruitment in root-suckering cottonwood species can be associated with snowmelt runoff (Baker, 1990; Gom & Rood, 1999; Merigliano, 1996; Polzin & Rood, 2006; Roberts, 1999; Samuelson & Rood, 2004).

My results show there are some situations in which root suckering by narrowleaf cottonwood is less dependent on high flows compared to seedling recruitment by plains cottonwood. Roberts (1999) proposed that erosional processes are critical for stimulating root-suckering by narrowleaf cottonwood, contrasting to depositional processes for plains cottonwood seedlings. Root-suckering can also be triggered by disturbances unrelated to flooding. High-energy streams (slope >4%), canyons and gorges were excluded from this study based on the assumption that landslides in this setting can trigger recruitment independently of flow (see Friedman et al., 2006). Beaver could trigger root suckering by chewing bark or downing trees (Friedman et al., 2006; Gom & Rood, 1999), and I observed beaver damage at 23 out of 68 sections. Other research has demonstrated that fire can act as an alternative disturbance to floods (Rood et al., 2007). I observed root-suckering at Windy Gap (Colorado River), where 1 in 6 trees had been toppled by winds that reached 134 km/h (wind recorded at Granby, 30/6/2011).

Reproductive traits are not the only point of difference between narrowleaf and plains cottonwood. Rood et al. (2010) demonstrated that narrowleaf have higher flood-tolerance and lower drought-tolerance than a plains cottonwood hybrid (*P.* x *jackii*), and concluded that narrowleaf are a more "willow-like" cottonwood. I observed a transition from narrowleaf forest to willow shrublands (*Salix* spp. excluding *S. exigua*) with increasing precipitation (for wide valleys), and it is possible that excess moisture constrains narrowleaf at their upper elevation limit. Other authors have observed a transition from cottonwood on coarse soils to willow on finer textured soils that better retain moisture (McBride & Strahan, 1994; Roberts, 1999). If narrowleaf are intermediate between willow and plains cottonwood in terms of flood and drought tolerance (see Amlin & Rood, 2002; Francis et al., 2005; Guilloy et al., 2011), then beaver could hasten the transition from narrowleaf to willow by constructing dams that both increase flooding and increase the accumulation of fine sediment that retain soil moisture (Westbrook et al., 2006; Westbrook et al., 2011). Reduced flows could have the opposite effect.

Other physical transitions are associated with the transition between plains and narrowleaf cottonwood (e.g., steeper, more confined streams with coarse substrates at higher elevations), and these make it difficult to establish causality for the difference in flow response between plains and narrowleaf cottonwood. Until we understand what factors constrain narrowleaf response to flow alteration and how these vary across the region, it could be a mistake to assume that narrowleaf are universally tolerant of flow alteration.

Conclusions

The ELOHA framework can provide a scientific basis for informing regional flow management, and I demonstrate this using existing data to describe flow constraints on plains cottonwood. But the flow-ecology methods did not hold true for narrowleaf cottonwood below large dams. The reason for the different flow-response warrants further investigation, including sources of disturbance for root suckering by narrowleaf and how this changes from plains to mountains.

Table S3.1 Flow data revisions

Flow data periods are tabulated over-page with rationale for changes given here. Years with missing data (>10 consecutive days) were omitted from the analysis, which typically only affected the first and last year of record (revised record is summarized in Table A1). Two sites were omitted: the Rio Grande USGS 08332010, for which flow records were no longer available, and the Little Colorado at Woodruff (USGS 09394500), where pre-dam flow records were deemed inadequate. Omitting years with gaps in the flow record reduced the pre-dataset for the Little Colorado at Woodruff to just one year of data; closer examination revealed unlikely spikes in the data (e.g., rising from 33 cfs to 10,000 cfs in one day). A similar 24-hour spike in flow is seen in other years on the exact same date (November 27) and also several times on December 4. Given the date repetition, these may have been an end of year release from Lyman Reservoir or, coincidentally, one of several known dam bursts that occurred at this site (though no record of their dates was found). These unseasonably high flows were therefore omitted as erroneous. To better represent the pre-alteration flows, the data that are available were pieced together. Flows were averaged for each day of the year across the period of 1905-1920. Most days of the year were represented by 5 replicates (ranging from 3 to 6 days) providing an improvement over the one year of complete record available. Data for one additional year were produced by synthesizing a flow record from a nearby gage with an overlapping record:

$$\text{USGS09394500} = 0.315 * \text{USGS09386000}^{1.2249} \qquad R^2 = 0.70 \text{ for 1906-1907}$$

The output of these revisions was a single average year of data that provided more robust flow metrics, but was insufficient for the calculation of a wet year 90 day maximum.

Table S3.1 cont'd Hydrological record used to assess alteration of flow, including the USGS gage number, river and location, duration of pre- and post-alteration, intervening years that were omitted due to missing data ("Omit" column) and the vegetation monitoring sites that each gage record was applied to. See Merritt & Poff (2010) for additional information.

USGS Gage	River	Pre-alt.	Post-alt.	Omit	Vegtn. site no.
08330000	Rio Grande, Albuquerque, NM.	1943-1970	1975-2002		RGM7-1, RGN1-1, RGS1-5
08332010	Rio Grande, Bernardo Floodway, NM.	1958-1974	1975-2002		RG3 (omitted)
08361000	Rio Grande, Elephant Butte Dam, NM.	1936-1958 USGS 8358500	1975-2002		RG2
08362500	Rio Grande, Caballo Dam, NM.	1936-1958 USGS 8358500	1975-2002		RG1
08383500	Pecos River, Puerto De Luna, NM.	1939-1978	1979-2002		PEC-1 & 2
08384500	Pecos River, Sumner Dam, NM.	1913-1936	1937-2002	1926	PEC-3 to 5
09095500	Colorado River, Cameo, CO.	1934-1963	1964-2004		GJ-665 & 666
09128000	Gunnison River, Gunnison Tunnel, CO.	1911-1965	1966-2003		GUN-1 & 2
09163500	Colorado River, State Line, CO.	1952-1966	1967-2004		GJ-667 to 670
09169500	Dolores River, Bedrock, CO.	1918-1983	1984-2003	1971	DOL-2
09177000	San Miguel River, Uravan, CO.	1955-1978	1979-2003	1996	SM-1
09180000	Dolores River, Cisco, UT	1952-1983	1984-2003		DOL-1
09251000	Yampa River, Maybell, CO.	1917-1962	1963-2004		YAM-1 to 3
09384000	Little Colorado River, Lyman Lake, AZ.	1941-1970	1971-2003		LCR-34 to 35
09388000	Little Colorado River, Hunt, AZ.	1930-1949	1950-1972	1934, 1940	LCR-28, 29 & 32
09394500	Little Colorado River, Woodruff, AZ.	1905-1920	1930-2003	see report	LCR-15, 20 & 21
09402000	Little Colorado River, Cameron, AZ.	1948-1985	1986-2003		LCR6 & 10
09429100	Colorado River, Palo Verde Dam, AZ.	1957-1968	1989-2003		LC-T1 to T9, LC-T11 to T16

USGS Gage	River	Pre-alt.	Post-alt.	Omit	Vegtn. site no.
09431500	Gila River, Redrock, NM.	1931-1955	1963-2002		GILA1
09504000	Verde River, Clarkdale, AZ.	1916-1920	1966-2003	1917	VER-1 & 2
09506000	Verde River, Camp Verde, AZ	1935-1989	1990-2005		VER-3
09511300	Verde River, Scottsdale, AZ.	1962-1982	1983-2003		VER-6 & 7
10327500	Humboldt River, Comus, NV.	1895-1947	1948-2002	1910	HUM-1 to 5
10335000	Humboldt River, Rye Patch, NV.	1900-1932	1936-2002	1910, 11, 17 & 28	HUM-6 & 7
10351600	Truckee River, Derby Dam, NV.	1919-1957	1960-2002		TR-1 & 2

Table S3.1 continued

Table S3.2 Site locations and survey dates (m/d/yyyy) for narrowleaf cottonwood sites in north-west Colorado (2 pages).

StateMod Node	Section	date time (MDST)	Latitude (WGS84)	Longitude (WGS84)
CONFL_101	random start	7/5/2011 10:50	39.44223	-108.04763
CONFL_115	random start	7/5/2011 13:30	39.18954	-108.13278
720616	random start	7/5/2011 18:10	39.22049	-107.77624
CONFL_95	random start	7/6/2011 10:20	39.54912	-107.58558
CONFL_95	0.5 km	7/6/2011 10:20	39.54835	-107.59103
09085000	random start	7/6/2011 13:35	39.53238	-107.32769
CONFL_78	1.5 km	7/6/2011 15:45	39.44678	-107.26035
CONFL_78	1.0 km	7/6/2011 16:35	39.44322	-107.26451
CONFL_78	0.5 km	7/6/2011 17:30	39.44203	-107.26074
CONFL_78	random start	7/6/2011 18:20	39.43853	-107.25763
380840	random start	7/7/2011 9:00	39.32537	-107.20866
09080400	random start	7/7/2011 12:30	39.36297	-106.82944
09078600	random start	7/7/2011 15:30	39.35234	-106.69166
CONFL_73	random start	7/7/2011 18:40	39.36753	-107.05505
09084000	0.5 km	7/8/2011 8:55	39.46577	-107.05451
380925	0.5 km	7/8/2011 11:00	39.46348	-107.16381
380925	random start	7/8/2011 11:50	39.46025	-107.16783
380854	random start	7/8/2011 15:25	39.15561	-106.88556
09074000	Steep section	7/8/2011 18:30	39.20405	-106.80834
09074000	1 km	7/8/2011 19:00	39.20559	-106.79797
380925	1.0 km	7/9/2011 9:00	39.46258	-107.15882
09070000	random start	7/9/2011 11:00	39.65277	-106.93012
09070000	0.5 km	7/9/2011 11:40	39.65114	-106.93563
09070000	1.0 km	7/9/2011 12:15	39.65346	-106.94043
09070000	1.5 km	7/9/2011 12:40	39.65277	-106.94633
09069500	1.0 km	7/9/2011 14:00	39.55575	-106.94531
09069500	0.5 km	7/9/2011 14:50	39.55290	-106.94146
09069500	random start	7/9/2011 15:40	39.54900	-106.93800
500601	random start	8/1/2011 9:15	40.36295	-106.57302
09237500	random start	8/1/2011 10:45	40.28673	-106.82687
09238900	random start	8/1/2011 12:45	40.47528	-106.78685
09239500	1.5 km	8/1/2011 14:00	40.47238	-106.8324
09239500	0.5 km	8/1/2011 14:50	40.47983	-106.82747
09244410	random start u/s div	8/1/2011 17:15	40.48654	-107.15665
09244410	0.5 km u/s div	8/1/2011 17:40	40.48403	-107.15133
09244410	1.0 km u/s div	8/1/2011 18:20	40.48236	-107.14738
09244410	random start d/s	8/2/2011 7:40	40.49021	-107.16125

StateMod Node	Section	date time (MDST)	Latitude (WGS84)	Longitude (WGS84)
	div			
09258000	random start	8/2/2011 10:00	40.91399	-107.51999
09247600	random start	8/2/2011 12:50	40.47847	-107.61788
09251000	random start	8/2/2011 13:55	40.50016	-108.03372
09260000	random start	8/2/2011 15:00	40.54649	-108.42474
09260000	0.5 km	8/2/2011 15:25	40.54269	-108.42649
09260000	1.0 km	8/2/2011 15:50	40.53969	-108.42357
09260000	1.5 km	8/2/2011 16:20	40.53616	-108.42391
09306222	1.5 km	8/3/2011 7:35	40.07499	-108.23446
09306222	1.0 km	8/3/2011 8:15	40.07056	-108.23629
09306222	0.5 km	8/3/2011 8:50	40.06687	-108.23993
09306222	random start	8/3/2011 9:25	40.06541	-108.24506
09303000	random start	8/3/2011 11:55	39.97551	-107.63535
09303400	0.5 km	8/3/2011 13:15	39.86559	-107.5349
09303400	random start	8/3/2011 13:50	39.86989	-107.53609
09304000	random start	8/3/2011 15:00	39.97404	-107.63198
CONFL_51	random start	8/3/2011 18:25	39.71101	-107.04618
CONFL_51	0.5 km	8/3/2011 18:45	39.71248	-107.04304
CONFL_40	0.5 km	8/4/2011 8:40	39.95432	-106.55021
CONFL_40	random start	8/4/2011 8:55	39.95263	-106.55546
CONFL_39	random start	8/4/2011 9:15	39.92205	-106.51807
520658	random start	8/4/2011 9:55	39.91408	-106.51881
09060500	random start	8/4/2011 12:00	40.04103	-106.65543
09060500	0.5 km	8/4/2011 12:30	40.04318	-106.65633
CONFL_11	random start	8/4/2011 14:50	40.05220	-106.17831
09038500	random start	8/4/2011 15:40	40.04855	-106.19426
CONFL_14	random start	8/4/2011 18:00	40.06235	-106.20446
CONFL_14	0.5 km	8/4/2011 18:30	40.06324	-106.19871
09034250	random start	8/5/2011 9:05	40.11002	-105.99339
CONFL	random start	8/5/2011 10:40	40.10703	-105.94465
CONFL	0.5 km	8/5/2011 11:05	40.11056	-105.94013
CONFL	1.0 km	8/5/2011 11:25	40.11339	-105.93613

Table S3.3 Spearman rank correlations between the wet-year 90-day maximum flow and other flow metrics. Most high flow metrics were correlated with the wet year 90 day maximum. This is not the case for winter flows (October-February mean) and timing metrics (days change minimum and maximum), which are shaded grey. The "Colorado only" correlations were typically stronger (right column) than "All gages" (mid-column), which likely reflects the more uniform hydrography in Colorado that translates to a more reliable autocorrelation between flow metrics. The flow metrics presented are those used for calculating the IFM (Index of Flow Modification). Two versions of the IFM were calculated for this comparison: one based on instantaneous peak flow metrics (as per Merritt & Poff, 2010) and the other using flow metrics calculated from daily series flow data. The left column uses data from all gages and StateMod nodes used in this study (for plains and narrowleaf cottonwood). The right column uses only flow data from Colorado. Instantaneous maximum flows were synthesized for StateMod nodes not associated with a USGS gage from the daily maximum values (18 of the Colorado sites).

Spearman's rho	Wet year 90-day max. flow	
	All gages	Colorado only
Oct-Feb mean (winter)	0.24	-0.07
Apr-Jun mean (snowmelt)	0.84	0.92
Jul-Sep mean (summer-fall)	0.41	0.46
Days change of Min flow (absolute)	-0.28	-0.19
Days change of Max flow (absolute)	-0.05	-0.34
2 yr return flood (daily series)	0.82	0.87
5 yr return flood (daily series)	0.81	0.87
10 yr return flood (daily series)	0.80	0.82
25 yr return flood (daily series)	0.74	0.76
2 yr return flood (instantaneous series)	0.72	0.84
5 yr return flood (instantaneous series)	0.73	0.81
10 yr return flood (instantaneous series)	0.73	0.83
25 yr return flood (instantaneous series)	0.71	0.80
IFM (daily series)	-0.76	-0.83
IFM (instantaneous series)	-0.66	-0.79
N	58	35

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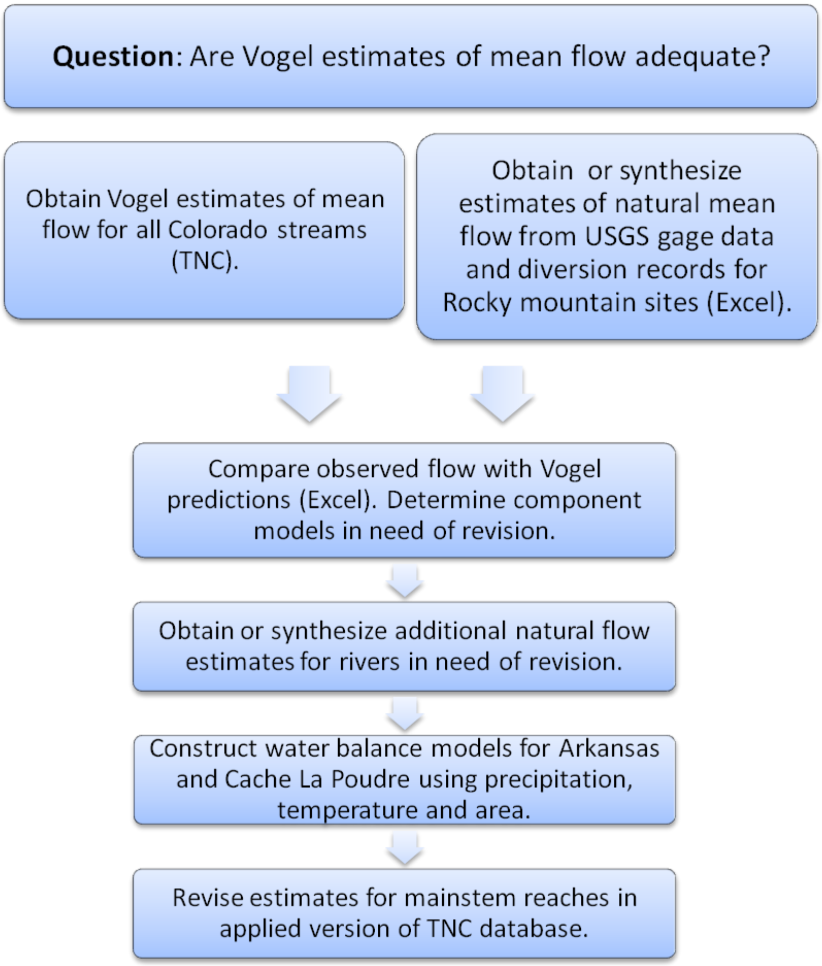
APPENDIX 1: DETERMINING MEAN ANNUAL FLOW

The following flowchart summarizes the steps in this review of *MAF* (mean annual flow) estimates used for predicting hydraulic habitat.



As a starting point, values of MAF were estimated using equations from Vogel et al. (1999). This set of models uses watershed area, precipitation and temperature and were calibrated for individual watersheds (Arkansas, Missouri, upper Colorado, Rio Grande).

The performance of the Vogel estimates was evaluated against gage data for the PHABSIM sites. Natural flows were reconstructed for these sites based on extensive research on flow alteration or by determining the period of record prior to significant flow alteration (alterations listed in Table S2.1). The models from Vogel et al. (1999) provide a reasonable approximation of natural flows (Figure A1.1), especially given the uncertainty in any estimates derived from the gage data (due to uncertain flow alteration, inter-annual variability, etc.).

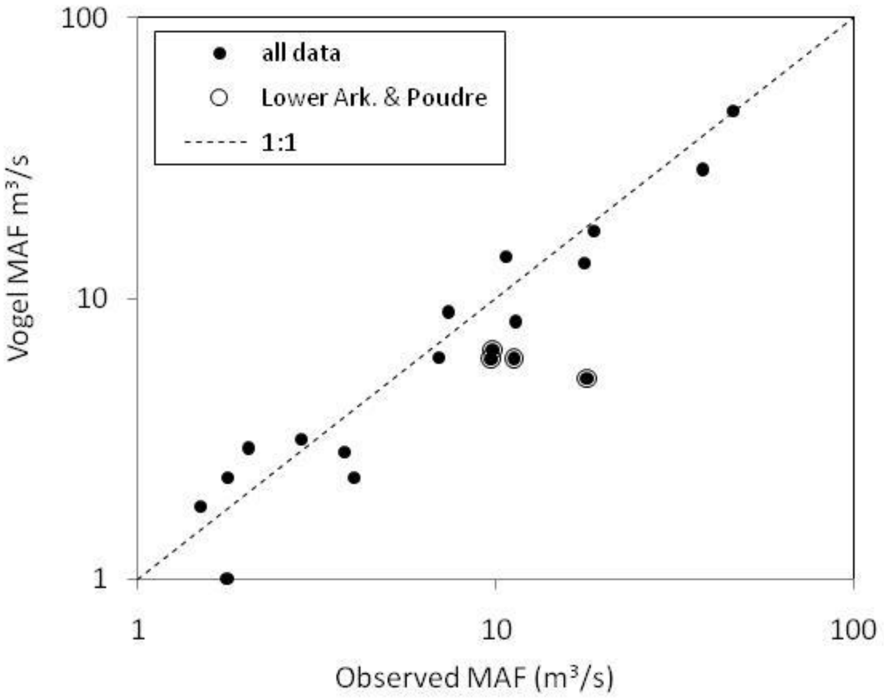


Figure A1.1 Comparison of MAF (mean annual flow) estimates from Vogel et al. (1999) to estimates from nearby gages (pre-alteration or synthetic data). The 1:1 line indicates where points would lay if the predictions matched observed values. Circled points are the Arkansas River (distant outlier) and lower Cache la Poudre River.

The site on the Arkansas River was an outlier, where the Vogel estimate of 5.2 m^3/s falls well short of the gage estimate of 18 m^3/s (natural flow estimate from gage data pre Fry-

Ark diversions). This was not found to reflect any simple calculation errors in the GIS network or model application. The Vogel Model erroneously predicts very little flow increase between the headwaters and the plains (predicted MAF 4.2 m^3/s at Granite and 5.6 m^3/s at Canon City). There was a measurable increase in natural flow between Granite and Canon City (MAF increases from 10.0 to 19.2 m^3/s, using pre-diversion flow records), but the magnitude of this increase is small relative to the change in watershed area (increases from 1060 km^2 to 7940 km^2). Thresholds of annual precipitation are required to produce net annual runoff (Troch et al., 2009), and I expect that much of the Arkansas watershed is below the 450 mm threshold observed for semi-arid watersheds (Flerchinger & Cooley, 2000; MacDonald & Stednick, 2003; Troendle & Reuss, 1997). The Vogel Model for the Arkansas watershed appears to overcompensate for this effect (the upper Colorado model actually produces a better estimate of MAF). The potential therefore exists to improve upon the Vogel estimates for the upper Arkansas.

Using seven gages providing pre-diversion estimates of MAF ranging from 0.8 to 19.2 m^3/s (USGS 07093700, 07091500, 07086000, 07083000, 07086500, 07093500, 07096000), revised models were produced for the upper-Arkansas (Figure A1.2). A revised Equation 1 was produced using a land-area water-balance approach (precipitation input and evapotranspiration losses). The water balance model has the benefit of fewer parameters, with two unknown parameters (estimated from a dataset of seven sites), compared to four parameters for the Vogel equation. The revised model is expected to benefit from constraining the model to the upper Arkansas above Canon City (the Vogel Model was developed for the entire Arkansas watershed).

For Equation 1, MAF (**m^3/s**) was modeled using data from TNC measures database as predictor variables (Area in **km^2**, watershed average precipitation in **mm/year**, and temperature in **^{o}C**).

(*Equation 1*) $\text{MAF}*(\text{seconds per year})/(\text{Area}*10^6) = \text{precip}/1000 - 0.1256*e^{\text{temperature}*0.08944}$

($R^2 = 0.982$ for Arkansas)

The two parameters specified in Equation 1 were empirically calibrated using gage data to describe the increase in evapotranspiration with temperature (the wetter Halfmoon Creek USGS 07083000 was omitted from calibration as an outlier). If using publicly available precipitation and temperature data from the EDNA website (http://edna.usgs.gov), different parameters must be used in Equation 1 (replace 0.1256 and 0.08944 with 0.2447 and 0.01183 respectively).

For the Cache la Poudre River, the Vogel equations produced a downstream decline in flow estimates (for reaches distant from snowpeaks). A revised model for MAF was therefore calibrated using estimates of natural flow derived from gages for seven sites, ranging from 1.6 to 11.3 m^3/s (USGS 06752000, 06751500, 06749000, 06748000, 06747500, 06746110, 06748600). The long history of flow alteration on the Cache la Poudre necessitated the reconstruction of natural flows using diversion records (notably the Michigan Ditch, Grand Ditch, Wilson Ditches, Laramie Tunnel and North Poudre Tunnel). Flows were reconstructed specifically for this study, with the exception of the gage at the mouth of the canyon (USGS 06752000), for which estimates were sourced from Bartholow (2008). MAF was again modeled using the land-area water balance approach, using data from TNC measures database as predictor variables (area in km^2, watershed average precipitation in mm/year, and temperature in ^{o}C) and the natural flow estimates.

(*Equation 2*) $\text{MAF*(seconds per year)/(Area*}10^{6}\text{) = precip/1000} - 0.1395\text{*}e^{\text{temperature*0.09182}}$

($R^2 = 0.998$ for Cache la Poudre)

As for the Arkansas, parameters for the exponential temperature function were calibrated using gage data to estimate evaporative losses (if using precip. & temp. data from the publicly available EDNA website, replace 0.1395 and 0.09182 with 0.3910 and 0.002102 respectively). Predictions from Equation 2 outperformed the Vogel predictions for the Poudre watershed (Figure A1.3), which is to be expected, because of the smaller area of application and the use of the training dataset for model evaluation. Evaluating Equation 2 against all the Rocky Mountain gage data gives a similar level of performance to the Vogel equation overall. But, more specifically, the Equation 2 performed better for larger eastern rivers that have predominantly forested watersheds, compared to the Vogel equations that performed better for streams west of the Continental Divide (large and small) and all *small* streams that were evaluated (east and west).

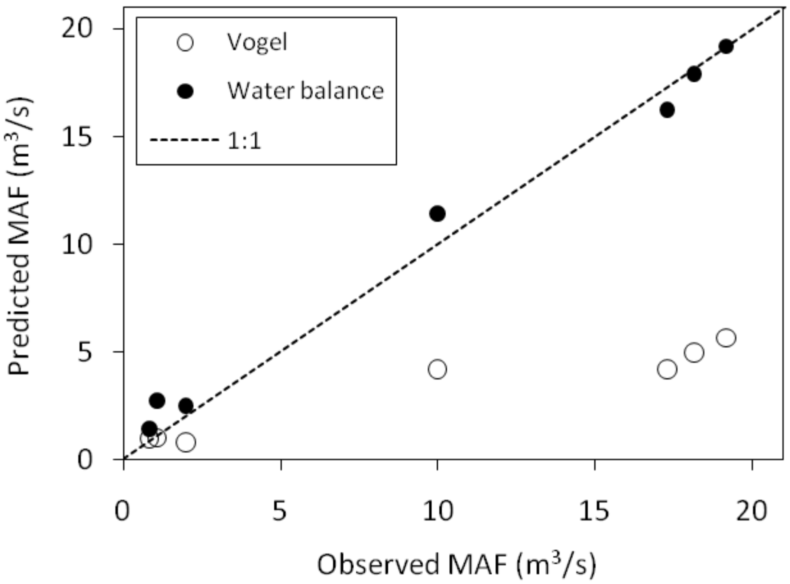


Figure A1.2 Predicted versus observed MAF (mean annual flow), comparing two models for the Arkansas watershed. Predictions of MAF using the "Vogel" model are compared to the water balance model (Equation 1) based on precipitation gains (measured) and evapotranspiration losses (calibrated to temperature). Equation 1 was calibrated using pre-alteration flow data derived from seven USGS gages. The 1:1 line indicates where points would lay if predictions matched observed values.

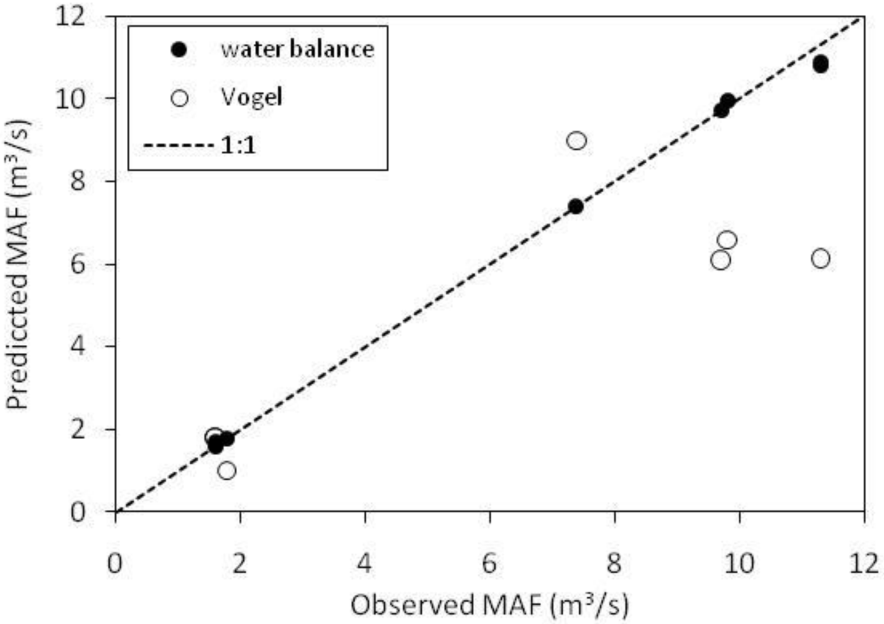
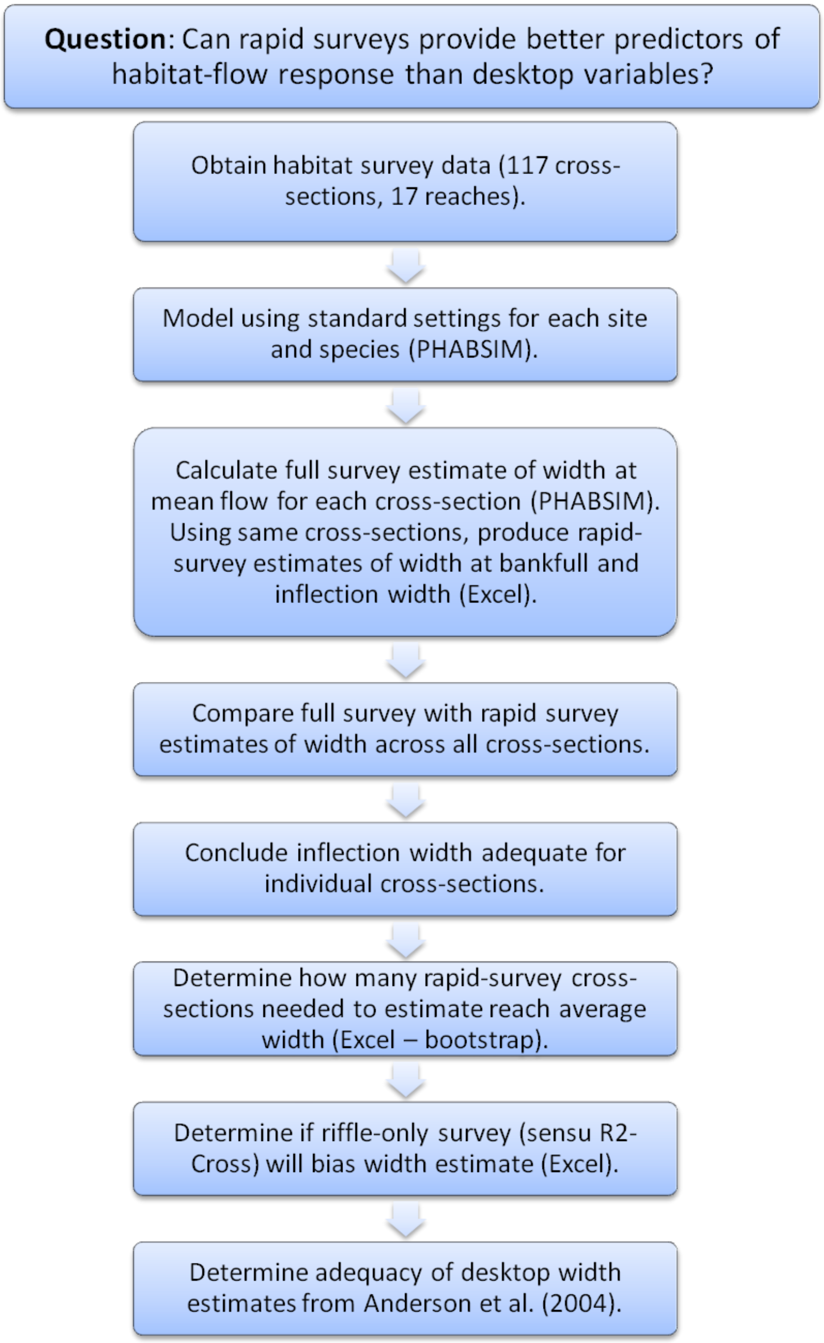


Figure A1.3 Predicted versus observed MAF (mean annual flow), comparing two models for the Cache la Poudre watershed. Predictions of MAF using the Vogel Model are compared to a mass balance function (Equation 2) based on precipitation gains (measured) and evapotranspiration losses (calibrated to temperature using pre-alteration flow data derived from seven USGS gages). The 1:1 line indicates where points would lay if predictions matched the observed values.

For this study, the Vogel equations provide the default estimates of MAF and are replaced only in the Arkansas and Cache la Poudre Rivers for all sites on the mainstem (i.e., not tributaries). The inability to produce a single mass balance model that precisely predicts MAF for Rocky Mountain streams could be attributed to variables not included in the models (e.g., spatially variable vegetative cover, solar aspect, groundwater losses; Dingman, 1994). But I expect a more spatially explicit definition of water balance would go a long way to solving this problem. Most of the runoff is generated at high elevations where precipitation is high and temperatures are low (MacDonald & Stednick, 2003). The model is attempting to account for the small or negligible contributions from semi-arid areas by forcing high evaporative losses onto an average precipitation estimate for the whole watershed. Moving from humid headwaters to more arid plains, this watershed averaging will inevitably overcompensate for evapotranspiration and underestimate flow, with the local calibration performed for this study probably only changing the distance from the source where this effect becomes significant.

Rather than a spatially explicit runoff map, a simple approach for dealing with this problem in the future would be to calibrate water balance models with watershed averages that exclude areas below a runoff threshold (see Troendle & Reuss, 1997). It is possible that forested areas plus areas above the tree line provide a useful delineation of water yielding areas for mean annual flow. Warm lowland areas have higher evaporation potential, but can be excluded because surplus moisture is not there to be lost. The net loss of annual water yield as the river flows through non-contributing reaches is expected to be small for Rocky Mountain streams (compared to error margins in existing models), so this approach could support improved predictions of MAF. I would also advocate calibrating such models to climatic regions, rather than watersheds (sensu Vogel et al., 1999), which has the added benefit of increasing sample size.

APPENDIX 2: RAPID SURVEY WIDTH FOR GHM PREDICTIONS



The above flowchart summarizes the steps in this review of channel width estimates used for the Generalized Habitat Models (Chapter 2). The question addressed in this Appendix is what information can be obtained from rapid-survey methods (e.g., R2Cross) that improve the prediction of habitat response to flow? As demonstrated in Chapter 2, improved predictions are possible using stream width (wetted width at MAF) instead of MAF (mean annual flow) as a predictor of the Q95h (flow providing 95% of maximum habitat). A rapid survey estimate of width therefore presents an opportunity for improved predictions. Rapid survey methods such as R2Cross (Espegren, 1996) and WAIORA (Jowett et al., 2004) are less intensive than PHABSIM, requiring fewer cross-sections to be surveyed with few or no repeat measurements to calibrate the rating curves. Taking this further, we can derive estimates of width from the rapid-survey results (bankfull width and inflection width) without the need for rating curves (see example Figure A2.1). For this investigation, bankfull width was approximated from the maximum survey width (i.e., excluding any obvious overbank measurements). To estimate inflection width, the average cross-sectional depth was plotted against the wetted width for increments of water level (Figure A2.1).

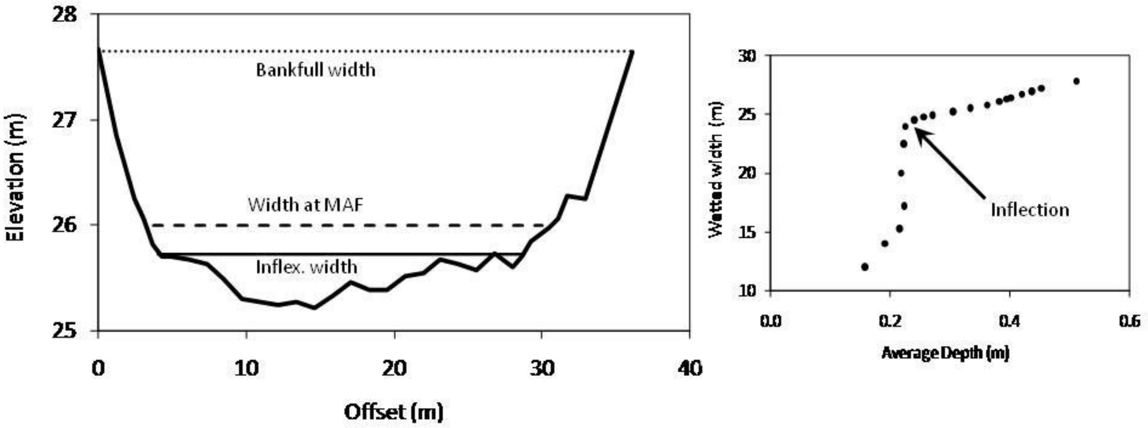


Figure A2.1 Three measures of width are demonstrated in the left plot, which is a cross-section profile from the Cache la Poudre River (site 1, cross-section 1). The water level used to determine the width at MAF (27.5 m) was modeled using PHABSIM (i.e., requires a PHABSIM survey). The other two widths can be determined without water level measurements. Bankfull width is the maximum surveyed width (36.1 m). The inflection width (24.8 m) was determined from the plot to the right, using the point before which there is a marked decrease in the wetted width with decreased depth.

Bankfull width and inflection width were calculated for each cross-section (117 cross-sections from 17 surveys) and compared to the width produced using PHABSIM (predicted wetted width at MAF). There was a close match between the inflection width and the width at MAF (for individual cross-sections), and the two width estimates are close enough to be interchangeable (Figure A2.2). By comparison, bankfull width is more variable and consequently is less reliable as a predictor of the width at MAF (Figure A2.2).

Cross-section width can be estimated from rapid surveys, but how many cross-sections are needed to represent stream width at the reach scale? Within a reach there is considerable variability in cross-section width (Figure A2.3), so basing an estimate of width on a single cross-section introduces error. The number of cross-sections surveyed will determine the level of precision, with little return for the increased survey effort beyond four cross-sections (Figure A2.4). It should be noted that variance was proportionately equivalent for small and large streams, so additional replication is not necessary for large rivers. The consequence of variability in width estimates for the habitat models (prediction of Q95h) was investigated using bootstrap methods to randomly select a sub-sample of cross-sections for estimating mean width. This pilot study differed from the final method by using unit-width discharge (q = MAF/width) as the predictor variable, instead of width alone. Using just one cross-section increased the variability of the mean width estimates, but still performed equal or better than MAF for 95% of the time in predicting Q95h (using randomly selected cross-sections to represent the width of each reach, for q = MAF/W, with 60 replicates performed).

Any increase in the number of cross-sections surveyed will further improve the reliability of flow magnitude predictions (5%ile R^2 increased from 0.616 to 0.690 by using 4 cross-sections instead of 1). Determining a point of inflection from the cross-section data is not always straight forward (cf. Figure A2.1), with ambiguous or multiple points of inflection possible. Surveying additional cross-sections therefore reduces the need for guesswork, and is still a rapid assessment because velocity profiles and return visits are not required.

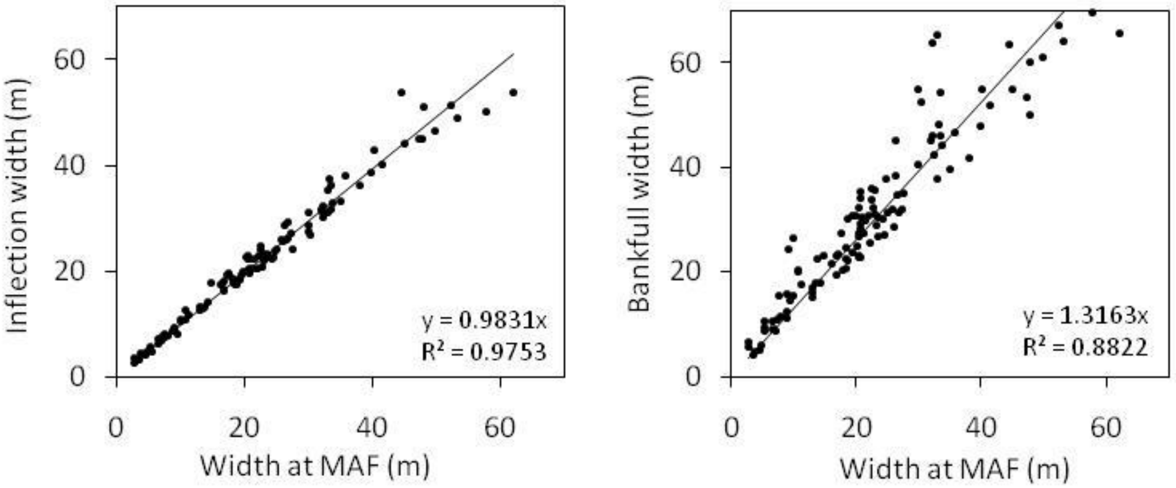


Figure A2.2 A comparison of inflection-width (left) and bankfull-width (right) as rapid-survey predictors of modeled width at MAF. Data points represent individual cross-sections from the 17 surveyed reaches.

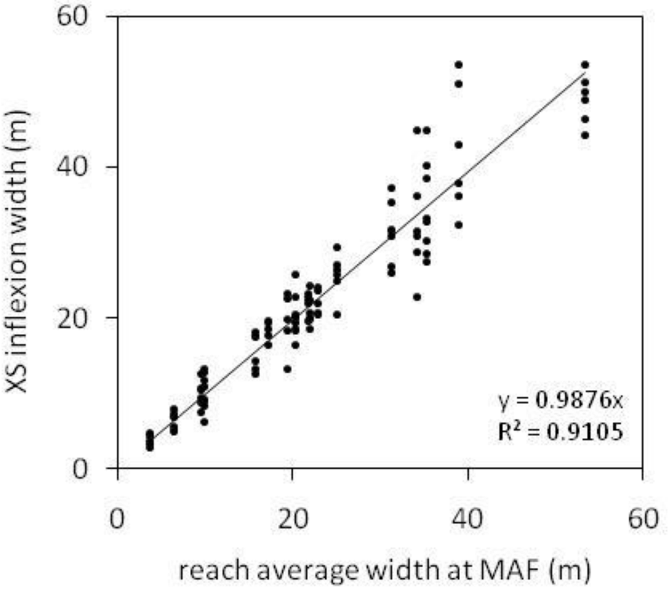


Figure A2.3 Estimates of inflection width from individual cross-sections (y-axis) vary from the reach average estimate of width at MAF (x-axis).

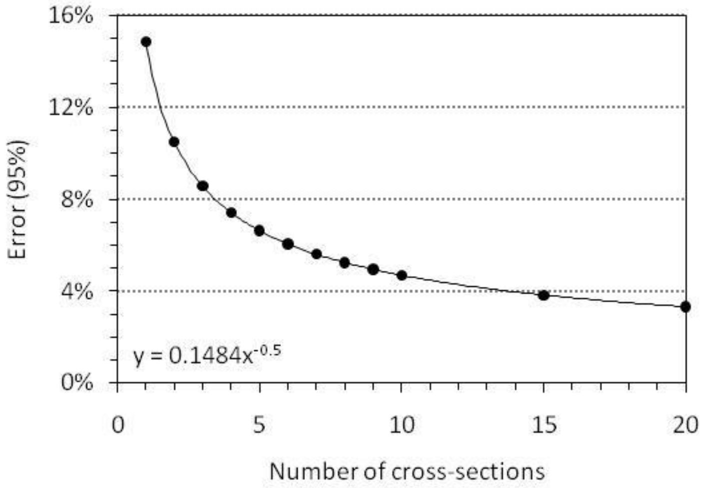


Figure A2.4 Surveying more cross-sections reduces the error for estimates of the reach average width. Individual estimates from 117 cross-sections (17 reaches) were expressed as a percent of the respective reach averages, producing approximately normal data. The standard deviation of widths (15.1%) was used to estimate error (Error = [stdev*1.96 / √n]/2). The y-axis "Error" is the potential deviation from mean width (expressed as a percentage) not exceeded for 95% of mean estimates under replication.

The R2Cross method targets riffle cross-sections as critical habitat. Sampling riffles only has the potential to bias estimates of reach average width, given that Richards (1976) reported greater channel widths for riffles than pools. A riffle bias would explain why Jowett (1998) recommended that rapid-surveys focus on runs to better represent average conditions. Across all Colorado survey sites, riffles did not create a consistent bias in width estimates (Figure A2.5), and this appears to be true for smaller streams (riffles were both above and below average width for streams <15 m^3/s). But riffles were the widest cross-sections for most large rivers (e.g., Rio Grande, Colorado, Arkansas) with low reach slopes (>30 m wide, MAF > 15 m^3/s, reach slope < 0.05%, watershed area > 2000 km^2). In addition to finer bed and bank material in low gradient channels, larger streams may have lower bank strength because of absolute limits on the rooting depth of riparian vegetation (Anderson et al., 2004), allowing for more lateral response to helical flow patterns at the sub-reach scale (Knighton, 1998).

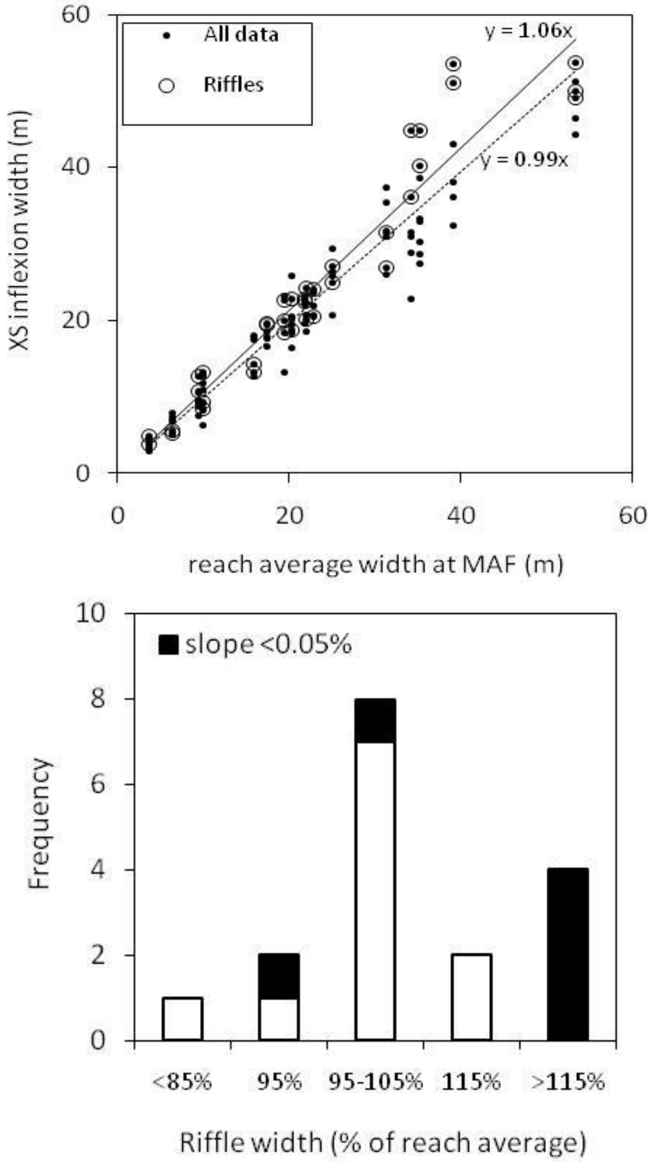


Figure A2.5 Comparing the inflexion width of riffles to all mesohabitats, plotted against the reach average width at MAF (top plot). The shallowest control points from each survey were classified as riffles. The solid trendline is fitted to riffle cross-sections, and the dashed line to all data. The histogram (lower plot) distinguishes the frequency of low-slope reaches (<0.05%), in black, from higher slope reaches (clear) for riffle width expressed as a percent of the reach-average width (i.e., riffles are more likely to be wider in low-slope reaches).

Hydraulic geometry equations (downstream) can provide an estimate of channel width (reach average) using flow as a predictor (e.g., Anderson et al., 2004; Andrews, 1984; Jowett, 1998). But widths estimated from hydraulic geometry equations that are based simply on a flow metric effectively produce a transformed value of flow (square root transformed, with a scaling coefficient), and therefore offer no improvement in the predictive strength over MAF. In order to be useful, the parameters of the hydraulic geometry equations must be varied across the riverscape to reflect the local geomorphology.

Anderson et al. (2004) developed a classification system that predicts equation parameters using watershed characteristics (e.g., precipitation, area). Applying this method to the Colorado survey sites did not improve the predictions of flow magnitude, compared to MAF ($R^2 = 0.49$ and 0.61 respectively). Arguably, the method produces the “correct” width for most sites, with some sites misclassified (Figure A2.6). Therefore future improvements in hydraulic geometry equations may allow improved desktop predictions of width. In the meantime, rapid surveys of width are expected to be the most efficient method for improving the predictions of habitat response.

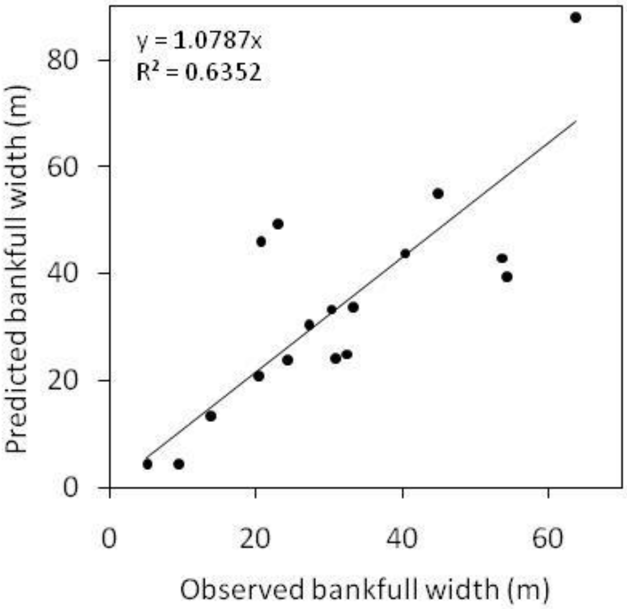


Figure A2.6 Comparison of observed bankfull widths to those predicted using hydraulic geometry equations (data points are reach averages). Parameters for the hydraulic equations were determined using regression trees from Anderson et al. (2004) for gravel-bed rivers based on precipitation and watershed area.

In conclusion, inflection-width estimates from R2Cross surveys might improve the precision of habitat predictions, compared to desktop MAF based models. The more cross-sections, the better the width estimates. Therefore, I recommend surveying four cross-sections with sufficient cross-section offsets to describe the transition from low-water to high-water morphology. Including a representative range of mesohabitats is a sound approach for all streams, even if a bias in width estimates was only detected for large rivers (MAF > 15 m^3/s).

APPENDIX 3: SIMPLIFYING AND IMPROVING HABITAT SUITABILITY CRITERIA FOR TROUT

Summary

PHABSIM (Physical HABitat SIMulation) generates habitat-flow curves (plots of hydraulic habitat versus flow) using a biological model to convert predicted velocities and depths to predicted hydraulic habitat. The biological models, termed *HSC* (Habitat Suitability Criteria), are specifically reviewed in this appendix because the HSC are so critical to the predictive success of the Generalized Habitat Model (Chapter 2). First, I demonstrated that omitting substrate and cover from the HSC was justified for Rocky Mountain streams because it had little effect on predicted habitat-flow curves for juvenile trout at a reach-scale (using 107 cross-sections from the Cache la Poudre River). I then revisited the Cheesman HSC for rainbow and brown trout which were chosen as the best candidate HSC for the Generalized Habitat Model. The Cheesman HSC incorrectly predicted that adult trout avoid deep water (>1 m), which appears to be an artifact of fewer deep-water areas included in the original trout survey (re-analyzed using observations of 191 adult trout and available habitat sub-sampled from 17 reaches of hydraulic habitat data). Using Maxent software, size-guild HSC were then developed that distinguish trout based on size (juvenile or adult), but not species. To justify using the size-guild HSC, I first produced new HSC for both rainbow and brown trout that demonstrated a similar habitat response by the two species. The size-guild HSC were improved by applying a bias to the selection of background data (data representing

available habitat) similar to the bias in sampling trout occurrence. The bivariate models for trout response to depth and velocity (generated using Maxent) are not compatible with PHABSIM, which requires independent univariate models. So the adequacy of univariate plots (e.g., response to depth while holding velocity at its mean value) was tested and found to provide an adequate representation of the bivariate model.

Introduction

Hydraulic habitat methods such as PHABSIM, RHYHABSIM and River2D predict the change in point velocity and depth with flow, based on intensive site surveys and calibrations (Annear et al., 2004). By comparing depths and velocities predicted to occur in a stream (i.e., the hydraulic model) to the depths and velocities used by trout (i.e., the biological model), these methods can generate habitat-flow curves (plots of the change in the weighted usable area with flow; Waddle, 2001). These curves are useful in better understanding how a proposed flow change will constrain hydraulic habitat for trout (see Chapter 1 for hierarchical context for hydraulic habitat). This appendix focuses on the biological model, conventionally referred to as *HSC* (habitat suitability criteria), which describes the depths and velocities used by trout. The HSC are just as important as the hydraulic model in determining the accuracy of PHABSIM predictions (Ayllón et al., 2011).

HSC describe how suitability changes with depth, velocity and substrate on a 0 to 1 scale (1 being most suitable). The combined habitat suitability at each point in a stream is calculated in PHABSIM by multiplying the suitability values for each variable (i.e., depth suitability * velocity suitability * substrate suitability). This is repeated for each modeled flow to describe how habitat suitability changes with flow.

How do we determine the suitability of a given depth/velocity for a given species/life-stage? Bovee (1986) described three options for creating habitat suitability criteria, including Type I (professional judgment), Type II (based on presence only data) or Type III (presence-absence data). More recent modeling methods, such as Maxent (Phillips & Dudík, 2008), provide a fourth option of presence-background data. This approach compares locations where fish are observed (presence) to available habitat without the assumption that absence represents avoidance (cf. logistic regression for presence-absence data).

We know trout inhabit lakes with zero velocity, so why would trout exhibit velocity preferences in streams? The mechanisms behind velocity preferences can be explained in terms of energetics, with a trade-off between the energy gained from the food supplied by the flowing water (e.g., invertebrate drift) and the energy required by the fish to maintain a position in flowing water (Braaten et al., 1997; Fausch, 1984). Much of the research on energetics has focused on salmonids, which hold position mid-water and catch prey items that are washed within sight.

This appendix focuses on brown and rainbow trout in Rocky Mountain streams, and more specifically re-visits an existing dataset with the objective of improving and simplifying the HSC that form the basis of the Generalized Habitat Models (Chapter 2). Unlike PHABSIM, a Generalized Habitat Model does not allow flexibility in terms of which HSC are used, so it is important to get these right from the start.

This appendix investigates three aspects of trout HSC to achieve simplification and improvement:

- Simplification – can substrate/cover be omitted from HSC that predict flow response at a reach scale for trout in Rocky Mountain streams?
- Improvement – is deep-water avoidance by adult trout an artifact of the methods used for the Cheesman HSC?
- Simplification - can HSC for trout be simplified by separating trout only by size-guild (juvenile T1 or adult T2), rather than by size *and* species?

Firstly, does substrate/cover have a marked influence on habitat-flow response for trout in Rocky Mountain streams at a scale relevant to flow management (the reach scale)? Substrate is a more stationary determinant of habitat suitability and is often important for explaining the spatial occurrence of biota (Shuler et al., 1994). But substrate is a product of drivers operating at different scales to velocity and depth (e.g., geology, flood flows). If suitable velocities and depths need to coincide spatially with suitable substrates or overhead cover, this is only likely to affect habitat-flow response *at a reach scale* if suitable substrate/cover is consistently biased in channel position over the length of the stream for which flows are being altered (e.g., macrophytes along stream margins requiring higher flow for inundation).

Secondly, re-examining depth avoidance by adult trout. I chose the Cheesman HSC, which included separate criteria for brown and rainbow trout (Shuler & Nehring, 1994), for inclusion in the Generalized Habitat Models (Chapter 2) because of their common use in Colorado for PHABSIM investigations (from discussions with state and private agencies). But some aspects of the Cheesman HSC concerned me. Why do the models predict that adult trout of both species avoid water deeper than 1 m? At least for juveniles, the mechanism of avoidance of deep water could be intraspecific competition with adult trout, as demonstrated experimentally by Fausch (1984). But I cannot explain depth avoidance for adults, so I investigated if this is an artifact of the modeling techniques that were used. For example, Ayllón et al. (2008) examined the interactive effects of depth and velocity, demonstrating that an observed preference for shallower depths can be an artifact of inadequate velocities in deeper water. Other HSC also cast doubt on avoidance of deep water, with Hayes & Jowett (1994) predicting that adult brown trout *prefer* deep water. To investigate depth avoidance, I specifically examined the effect of different sampling strategies for available habitat (background data for velocities and depths).

Thirdly, new size guild HSC were developed with trout separated only by size-guild (juvenile T1 or adult T2). Size guilds are akin to the habitat guild approach used elsewhere (Lamouroux & Souchon, 2002; Persinger, 2003; Persinger et al., 2011). I combined data for brown and rainbow trout, which belong to different genera (*Salmo* versus *Oncorhynchus*) and originate from different continents (brown from Europe, rainbow from north-west America). There are of course differences between the two, but both employ similar feeding strategies (Elliott, 1973) and any differences must hold true at larger scales to justify consideration by resource managers who can only prescribe one flow value per time step. In pursuing regional-scale flow response (in Chapter 2), do we lose important information by ignoring the differences between brown and rainbow trout? A machine-learning model (Maxent; Dudik et al., 2010) was applied to trout observations from the South Platte River and Cache la Poudre River. Maxent does not assume absence represents avoidance, which avoids the clumsy requirement of habitat saturation, and uses a flexible non-linear function.

Several species and life-stages are not considered in this appendix, including substrate-dependent spawning habitat, because these HSC are not intended to predict population response. I am instead interested in the constraint imposed by flow alteration on hydraulic habitat for trout, which is only one of many processes determining population dynamics (see Chapter 1)

Methods

Substrate & Cover

The effect of substrate on model outputs was examined using 107 cross-sections from the Cache la Poudre River. The cross-sections represent 9 km of river located 75 km west of Fort Collins, Colorado, and used proportional representation of mesohabitats (Table A3.1). These data are described in Thomas & Bovee (1993) and were provided to me by Mark Gard (USFWS, Sacramento, California). The cross-sections were re-modeled using RHABSIM (Version 3.0; Payne & Goforth, 1998) and simulations were run twice: once with substrate off and once with substrate on (substrate *on* indicating that substrate suitability *was* used in determining habitat suitability). The two outputs were then compared to examine the effect that substrate had on reach-average habitat suitability, following the methods outlined in Gard (2005). Cover is treated as static in RHABSIM and PHABSIM, so was assumed to be analogous to substrate in terms of the effect it has on modeled flow response (substrate itself was also one of cover types surveyed). The HSC for juvenile rainbow trout were chosen for this analysis, instead of adult rainbow

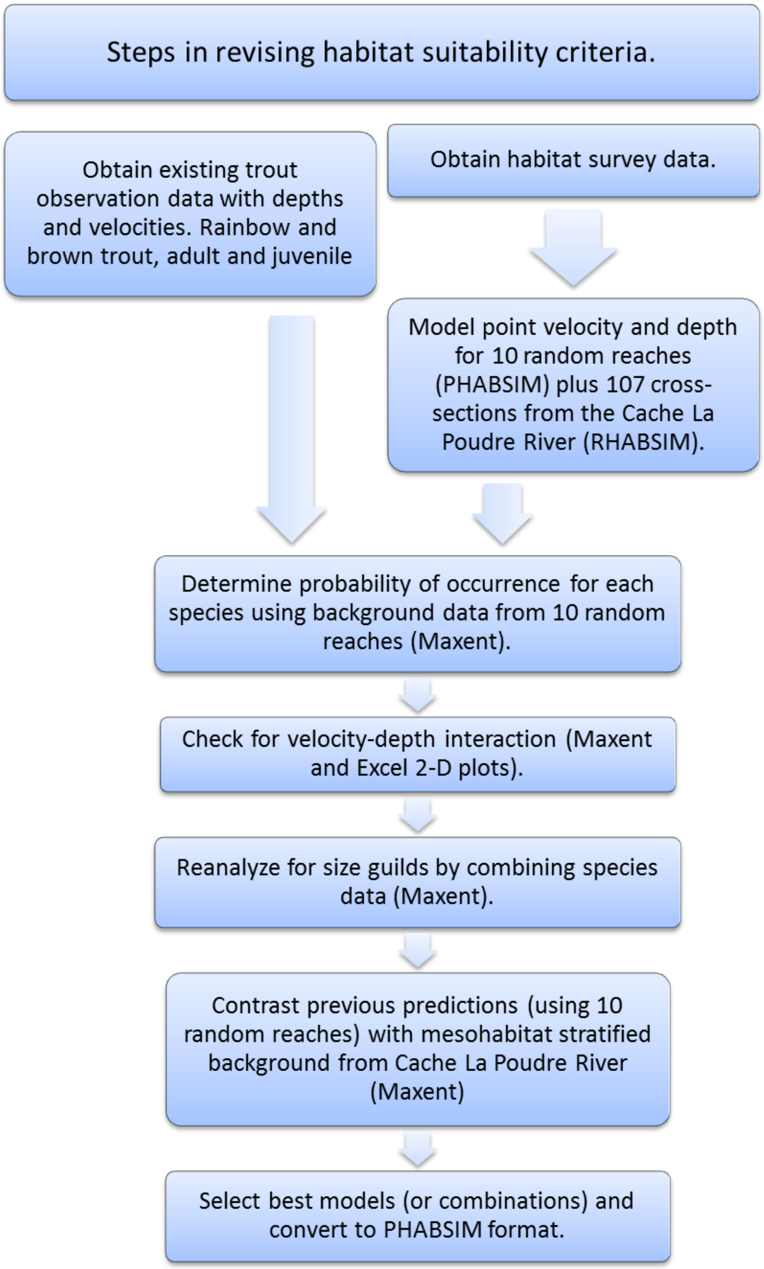
HSC, because of the stronger preference by juveniles for specific cover classes, thereby magnifying any consequence of ignoring cover.

Table A3.1 Reproduced from Gard (2005), this table describes the number of cross-sections per mesohabitat on the Cache la Poudre River in addition to the percent of total habitat that each mesohabitat represented.

Mesohabitat	No. of cross-sections surveyed	Percent of total habitat
Pocket water	20	18.7%
High-gradient riffle	22	10.3%
Low-gradient riffle	11	20.6%
Deep pool	26	24.3%
Shallow pool with boulders	17	15.9%
Shallow pool without boulders	11	10.3

Depth & Velocity for Size Guild HSC

Questions 2 and 3 from the introduction were examined together – deep water avoidance and development of size-guild HSC. The following flow chart summarizes the steps in the analysis of velocities and depths used by trout, with details of the analysis described subsequently.



The revised HSC were based on existing trout observation data from the South Platte River (below Cheesman Dam and Deckers sites) and the Cache la Poudre River (described in Thomas & Bovee, 1993), provided by Miller Ecological Consultants, Ltd. Depth and mean column velocity was measured at each point where trout were observed (all were daylight observations). Juvenile trout were 7-17 cm (assumed age of 1 year) and adult trout ≥17 cm (assumed age of 2+ years), (Thomas & Bovee, 1993). In order to reduce bias in fish observations across a heterogeneous environment, Thomas & Bovee (1993) stratified their sampling effort with equal effort for each of 6 mesohabitats (listed in Table A3.1) and repeated sampling at two flows. I only used their observations of "active" fish, defined as displaying caudal fin movement to hold position (Shuler & Nehring, 1994). The dataset provided adequate replication of occurrence (Table A3.2), exceeding the 55 observation *minimum* recommended by Thomas & Bovee (1993). But the number observations for adult trout fell short of the 150 observation *target* suggested by Bovee (1986).

Table A3.2 Replication of observations for brown and rainbow trout, with each species divided into adults and juveniles.

Species & life-stage			Number of fish observed
BT2+	Brown trout adult	(>170 mm)	61
BT1+	Brown trout juvenile	(70-170 mm)	299
RT2+	Rainbow trout adult	(>170 mm)	130
RT1+	Rainbow juvenile	(70-170 mm)	296

I compared two sampling strategies for quantifying available habitat. The first strategy used 10 PHABSIM surveys (Table A3.3), selected at random from 17 available PHABSIM surveys. For each survey site, two flow calibrations (measurements repeated over time) were randomly selected (if more than 2 available) in order to characterize temporal variability in addition to spatial variability. I excluded all cross-section measurements located above water level. This provided a background matrix of velocity and depth at 3,638 points that were surveyed at the same scale as the trout observations (i.e., point measurements). Negligible model improvement is expected with higher replication of background data (see Figure 4 in Phillips & Dudik, 2008).

There is bias in selection of survey reaches for PHABSIM studies (see Box 1 in Chapter 2), so the 10 reaches better reflect bias in the trout observations at a regional scale (cf. completely random selection of streams across Colorado). But the 10 reaches may not fully account for bias in location of trout observations at a sub-reach scale (i.e., mesohabitat selection). Thomas & Bovee (1993) attempted to achieve equal sampling effort in all mesohabitats by using stratified sampling, compared to the 10 random reaches that used proportional mesohabitat sampling (number of cross-sections surveyed were proportional to areal extent). A second analysis therefore used background data that more closely reflected mesohabitat sampling bias for trout observations. To achieve stratified mesohabitat selection, 10 cross-sections were selected to represent each mesohabitat (random selection without replacement for consistency with survey bias). These data were only sourced from the Cache la Poudre River (the 107 cross-sections described in Gard, 2005), rather than the 10 randomly selected reaches. Thomas & Bovee (1993) considered the South Platte sites and Cache la Poudre sites to be similar in many respects, and I therefore assume the Cache la Poudre River better represents bias in trout observations than the 10 random reaches. The stratified sampling approach netted background data at 1,691 points (cf. 3,638 points for 10 random reaches).

Table A3.3 From all 17 available surveys, the following 10 sites were selected at random for use as background data in the Maxent analysis to define the Target Group environment. Two surveys were selected at random for each site (i.e., measurements at two different flows). More detail on these sites is provided in Table S2.1.

River	Site
Cache la Poudre	1
Cache la Poudre	2
Cache la Poudre	4
Fryingpan	Old Faithful Station
Gunnison	Black Canyon (Duncan-Ute Trail)
South Platte	11 Mile Canyon
North Fork CLP	1
North Fork Sth Platte	below Foxton
Rio Grande	Wason Ranch
Vasquez	downstream DC diversion

I chose Maxent (Dudik et al., 2010; Phillips & Dudík, 2008) to better contrast the occupied depths and velocities (trout presence) with the sampled depths and velocities (target-group background). Maxent is a non-linear method that follows Bayesian principles in deriving an appropriate probability distribution function from the dataset (Phillips et al., 2006), rather than assuming that commonly used probability functions will be adequate. Comparative studies have demonstrated that Maxent and Boosted Regression Trees perform better than most other methods in predicting occurrence from presence-only data (Elith et al., 2006; Phillips & Dudík, 2008), with more recent versions of Maxent achieving better deviance scores than Boosted Regression Trees (Phillips & Dudík, 2008).

Maxent draws on a range of *features* (math functions) to achieve the best fit to the data, including linear, quadratic, interaction terms, thresholds and hinge features. Several of these features are joined end-to-end in describing each species-environment relationship, with overall model complexity restricted for smaller sample sizes. Over-fitting to the data is reduced by minimizing the incorporation of less important variables, as well as by approximating the observed mean for each variable instead of matching the mean exactly. The latter is achieved using *regularization parameters* to govern proximity to the observed mean, with default values developed by Phillips & Dudík (2008) as a function of number of occurrences in the dataset used. The user can then specify a *regularization multiplier* (not reg. parameter) that allows a greater deviance from the observed mean, effectively acting as a smoothing parameter if set >1.

Another useful feature of Maxent is it does not assume absence represents avoidance. Rather than using absence data, Maxent uses background data to represent the environment where species presence has not necessarily been detected (using the union of presence and background data). My analysis used a target-group of background points that I supplied to the model (i.e., not the default terrestrial raster data). Improved predictions can be achieved by using background data that are subject to the same selection bias as the presence data (Phillips & Dudík, 2008). This target-group approach can factor out sample selection bias, and I compared two sampling strategies, as described earlier in this section.

Modeling runs in Maxent were completed using bootstrap re-sampling with replacement to provide an estimate of variability in model predictions. For each species and lifestage, 100 replications were run and each replicate was sampled randomly from the observation dataset (with replacement) to achieve a new dataset of the same sample size but some data loss as a consequence of replication of some observations. Bootstrapping was combined with sub-sampling, where each bootstrap replication was performed on 75% of occurrences that were selected at random (using a random seed for each replication). Sample sizes were considered sufficient to support this double penalty of sub-sampling ($n>1,500$).

A regularization multiplier that allowed a small degree of over-fitting was chosen in the interest of preserving any meaningful steps in the response function (selected from pilot-runs of 10 replicates). Default Maxent settings were used otherwise, including automatic selection of feature type. Adequacy of the models was judged using the AUC statistic (area under the receiver operating curve) for which values of 1 are ideal and values ≤0.5 indicate predictions no better than chance. The AUC describes the models ability to discriminate occurrences across the range of probability thresholds. This will depend not only on the predictor variables and trout study design, but also how much of a generalist the species is in its habitat selection (Lobo et al., 2008).

Results

Substrate & Cover

Cover did change the *magnitude* of habitat (WUA m^2/m) for the Cache la Poudre River (Figure A3.1). But, if we instead consider the *relative* change in habitat with flow (expressed as a % of maximum habitat), the effect of cover is small (Figure A3.1) and arguably of little consequence for flow management (mean absolute deviation 2.8% between substrate off and substrate on). In addition, the use of cover increases the variability of results, with the variance in estimates of the flow at maximum habitat 36% greater with substrate on than substrate off (bootstrap analysis of 200 sub-samples of 6 cross-sections from the population of 107 cross-sections, variance 3.8 with substrate on and 2.8 with substrate off, about a mean 4.2 m^3/s, ANOVA P=0.005, F=7.97). These results should be kept in context, with results applicable to trout in Rocky Mountain streams. Other stream-types may show a more consistent bias in the location of suitable substrate (e.g., undercut banks, littoral vegetation).

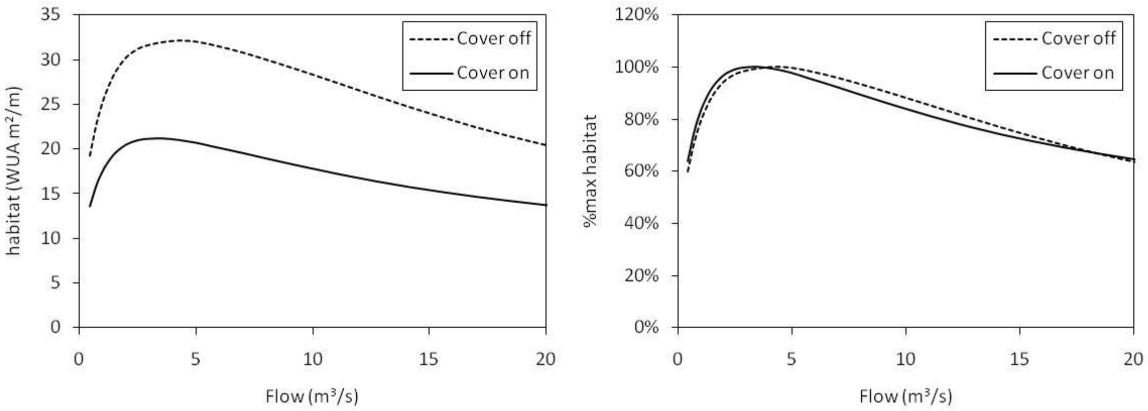


Figure A3.1 Comparison of the effect that cover has on habitat-flow response for juvenile rainbow trout in the Cache la Poudre River (107 cross-sections). Cover affects the magnitude of habitat (left plot, mean absolute deviation 9.5 m^2/m or 55%, paired t-test $P<0.0001$) but has little effect on the flow response (right plot, WUA standardized as a % of maximum habitat, mean absolute deviation 2.8% of max. habitat, paired t-test P=0.28).

Depth & Velocity for Size Guild HSC

The distribution of trout across velocities and depths helps visualize how habitat use contrasts with habitat availability (Figure A3.2). The bias in occurrence of trout to deeper water is apparent compared to the background data, especially for adult trout (Figure A3.2). Though bias in velocity is less pronounced than depth (Figure A3.2), there is still a difference with background measurements that decline in frequency as velocity increases, compared to the unimodal distribution of trout occurrences.

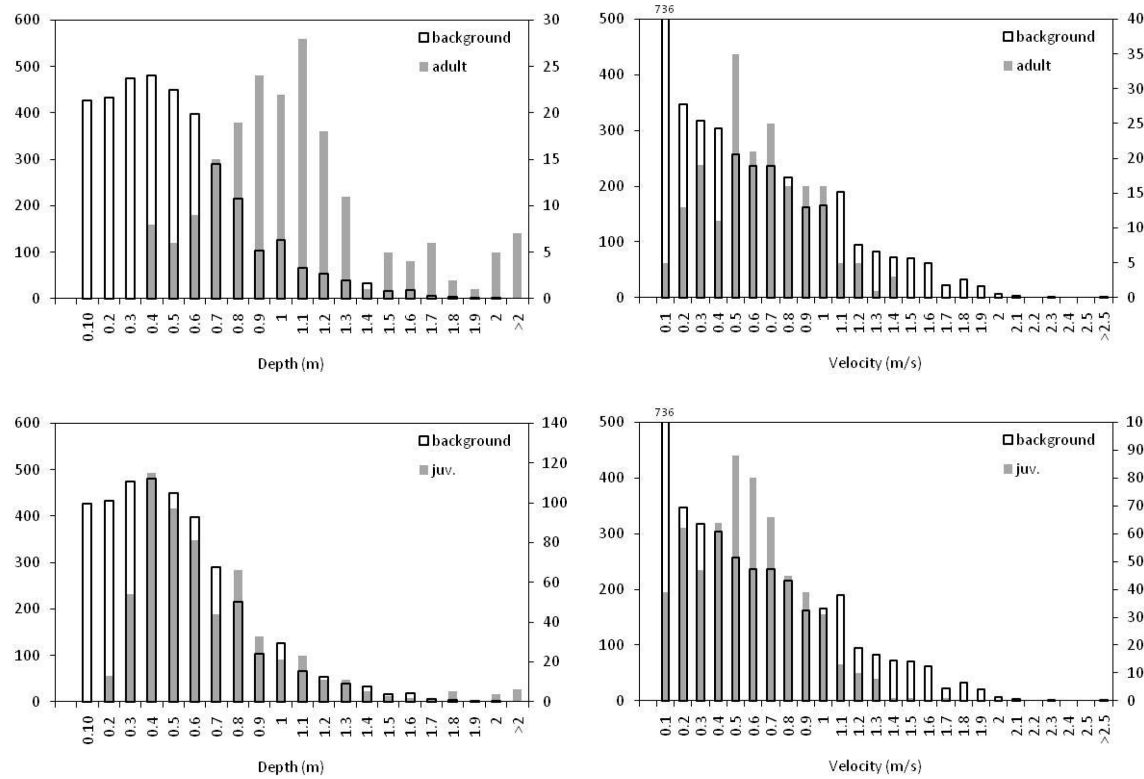


Figure A3.2 Histograms showing the number of observations for velocity and depth, comparing observations of adult (top plots) and juvenile trout (bottom plots) to representative reach background data (all data from randomly selected 10 reaches that used representative mesohabitat sampling). Data for brown and rainbow trout were combined. The number of trout observations are scaled to the right axes, and the number of background observations to the left axes. The leftmost bar in each plot represents the number of observations between 0 and 0.1.

Another set of histograms were produced, this time using *stratified* sampling of mesohabitats to better approximate the stratified sampling bias of trout observations (instead of *representative reach* sampling). For velocity at least, stratified sampling of mesohabitats mostly achieved its objective for an even distribution (Figure A3.3). There was some under representation of fast water (>1.2 m/s), and over-representation of slack water (<0.1 m/s), but few trout were observed at these extremes anyway. Depth was *not* evenly distributed by stratified sampling (Figure A3.3). The representation of moderate depths (0.5-1.0 m) was increased by stratification, but the deeper water where many adult fish occurred (>1.0 m) remained under-represented (compare Figure A3.2 and A3.3). The Cheesman HSC used only observed distributions of fish occurrence (i.e., no adjustment for available habitat). The Cheesman HSC were based on the assumption that the stratified mesohabitat sampling achieved an even distribution of depths and velocities, which appears to be false. In particular, deep water was under-represented and therefore the Cheesman HSC incorrectly predicted that adult trout will avoid deep water. Otherwise, the assumed even distribution appears reasonable for shallower depths and a wide range of velocities.

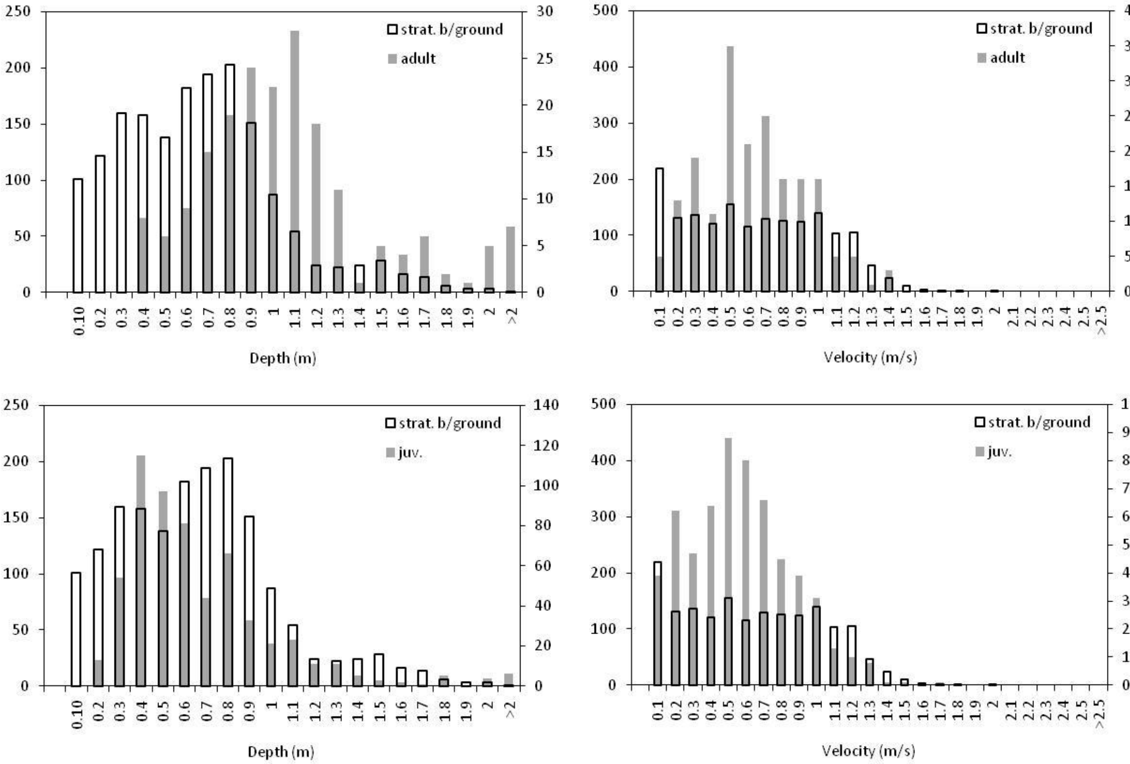


Figure A3.3 As per Figure A3.2, but using stratified background data (all data generated by even weighting across mesohabitats) from the Cache la Poudre River (cf. 10 reaches, representative mesohabitat sampling in Figure A3.2).

The next step in this analysis was to develop new size-guild HSC using Maxent. Models were generated for both species and both life-stages, plus size-guild models that combined the data for rainbow and brown trout (Table A3.4). I first determined whether Maxent was able to detect a response of trout occurrence to depth and velocity. Other authors have used cut-off values for AUC of 0.7-0.75 to distinguish informative models (Phillips & Dudík, 2008). The occurrence of adult trout was very well predicted by Maxent using just velocity and depth (AUC 0.870 to 0.925). In contrast, the juvenile trout occurrence was marginal, with AUC values closer to the 0.7 cut-off (AUC 0.726 to 0.776, Table A3.4).

Table A3.4 Summary statistics for Maxent models that were fit to each species and life stage. AUC values describe how well the model predicts fish occurrence (higher better). Percent contribution to the final model by velocity and depth are also presented (%depth, %velocity). The regularization multiplier effectively describes the degree of smoothing (higher values - more smoothing).

	BT1+	BT2+	RT1+	RT2+	Juv. trout	Adult trout
Reg. multipl.	1.5	1	1.5	1.5	2	2
AUC	0.757	0.87	0.776	0.925	0.726	0.896
%depth	61.8	81.6	67.7	83	67.1	84
%vel	38.2	18.4	32.3	17	32.9	16

Maxent response curves for rainbow trout (Figure A3.4) were compared to brown trout (Figure A3.5) for differences that would invalidate the use of size guild HSC. First contrasting depth, juvenile brown trout were similar to juvenile rainbows, with predicted occurrence increasing rapidly to about 0.3 m deep for both (compare Figure A3.4 and 5). The adults of both species also showed a similar response to depth, with both rainbow and brown trout leveling off after 1 m deep. This is notably deeper than the 0.3 m asymptote for juveniles. As demonstrated by the histograms, occurrence of adults did not decrease in deeper water, and this preference for deep water was not sensitive to different model settings.

Now considering velocity, the response was again similar across species with a unimodal velocity response for rainbow that was within one standard deviation of brown trout. Adults were most likely to occur at velocities around 0.5 m/s, and the similarity to juvenile occurrence was surprising (juvenile peak about 0.4 m/s) given the expected higher velocity preferences of larger fish from trout bioenergetics research (Braaten et al., 1997; Fausch, 1984). The response to velocity and depth was similar for brown and rainbow trout and, in my opinion, justified combining data for the two species to generate HSC that are specific only to the size of the trout. The adult trout HSC (Figure A3.6) had a higher AUC score than juveniles, which is consistent with the individual species results (Table A3.4).

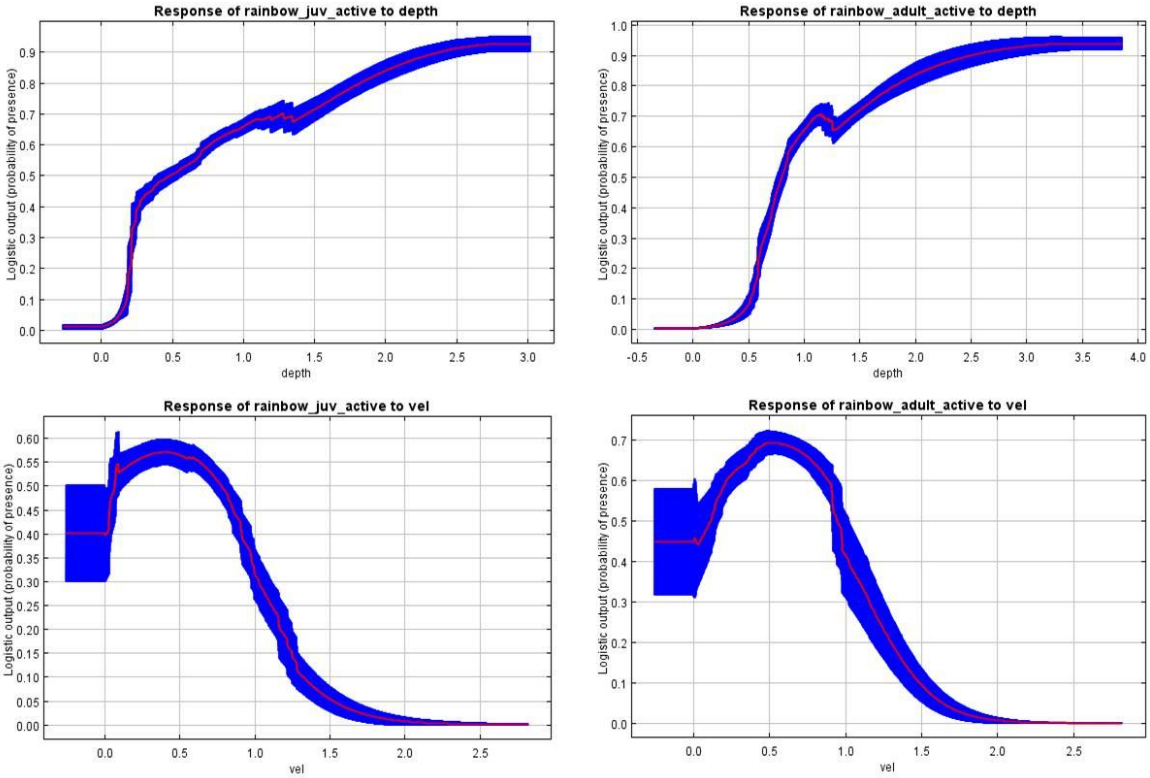


Figure A3.4 Response curves to depth in meters (upper plots) and velocity in m/s (lower plots) for both life-stages of **rainbow** trout (juvenile left plots, adult right). These curves represent the full model including interaction terms, displaying mean response (red line) ± 1 standard deviation (blue area) calculated from 100 bootstrap replicates. AUC values are given in Table A3.4.

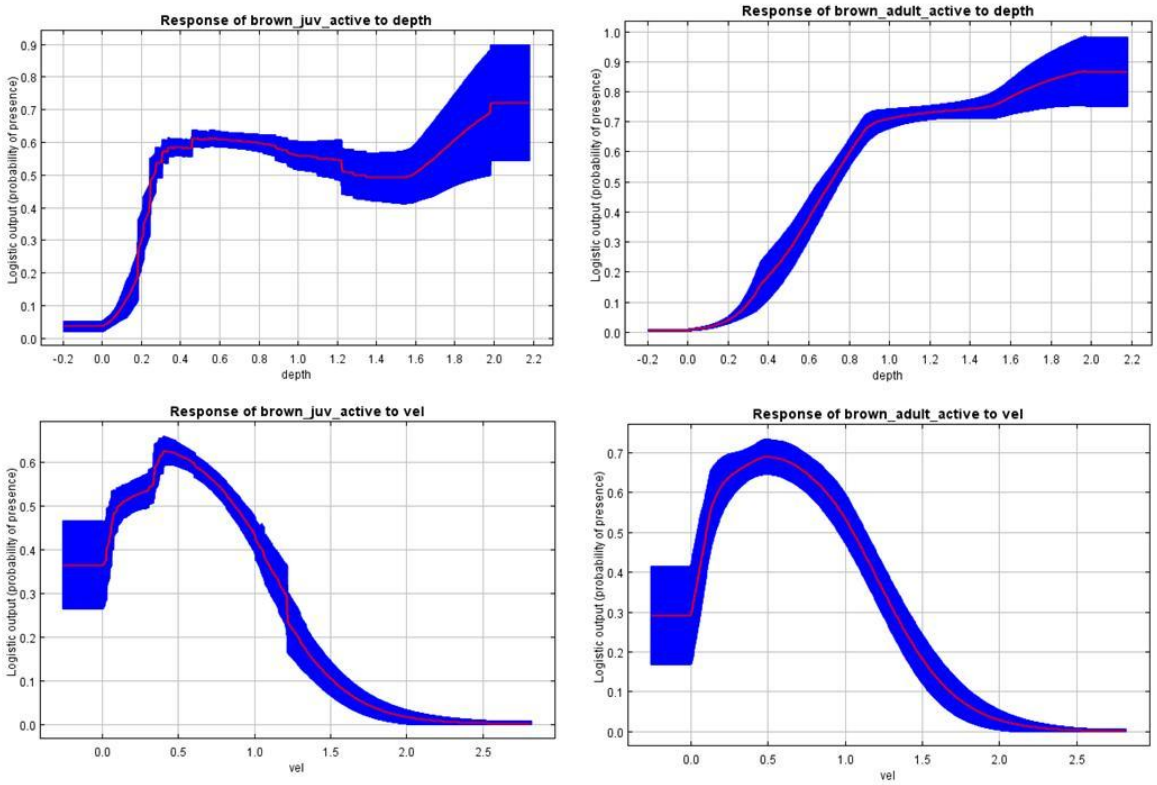


Figure A3.5 Response curves to depth in meters (upper plots) and velocity in m/s (lower plots) for both life-stages of **brown** trout (juvenile left plots, adult right). These curves represent the full model including interaction terms, displaying mean response (red line) ± 1 standard deviation (blue area) estimated from 100 bootstrap replicates of 75% of the data. AUC values are given in Table A3.4.

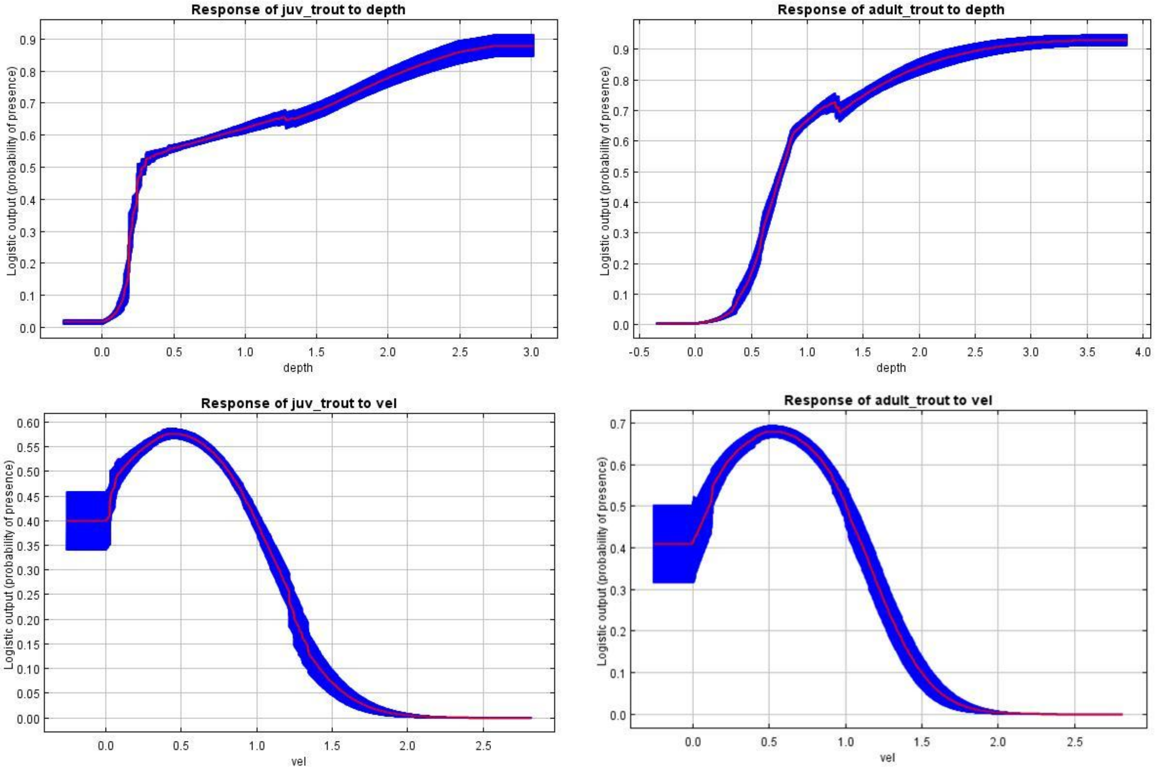


Figure A3.6 Response to depth in meters (upper plots) and velocity in m/s (lower plots) for juvenile trout (left plots) and adult trout (right plots). Datasets for rainbow and brown trout were combined, respectively for juvenile and adult trout to generate the predicted response functions. AUC values are given in Table A3.4.

I next investigated the sensitivity of predictions to sampling bias for background data, comparing representative reach to stratified sampling of mesohabitats in the Cache la Poudre River. The predicted preference by adult trout for deeper water was still apparent, despite the change in background data (using combined or separate species data). But it is not clear whether suitability increases, or remains stable, at depths greater than 1.25 m (dependent on cross-sections included as background data).

Suitability of deep water was more variable for juvenile trout, compared to adults. The increase in suitability at depths >0.5 m that were predicted using representative reach background data contrasted with a leveling off or decline in suitability when using stratified mesohabitats as background data (Figure A3.7). This presumably reflects the greater frequency of moderate depths in the stratified background data (Figure A3.3). Selection of background data (representative reach or stratified) produced a larger contrast in predicted suitability (Figure A3.7) than observed between rainbow and brown trout of the same size class (Figure A3.4 & A3.5).

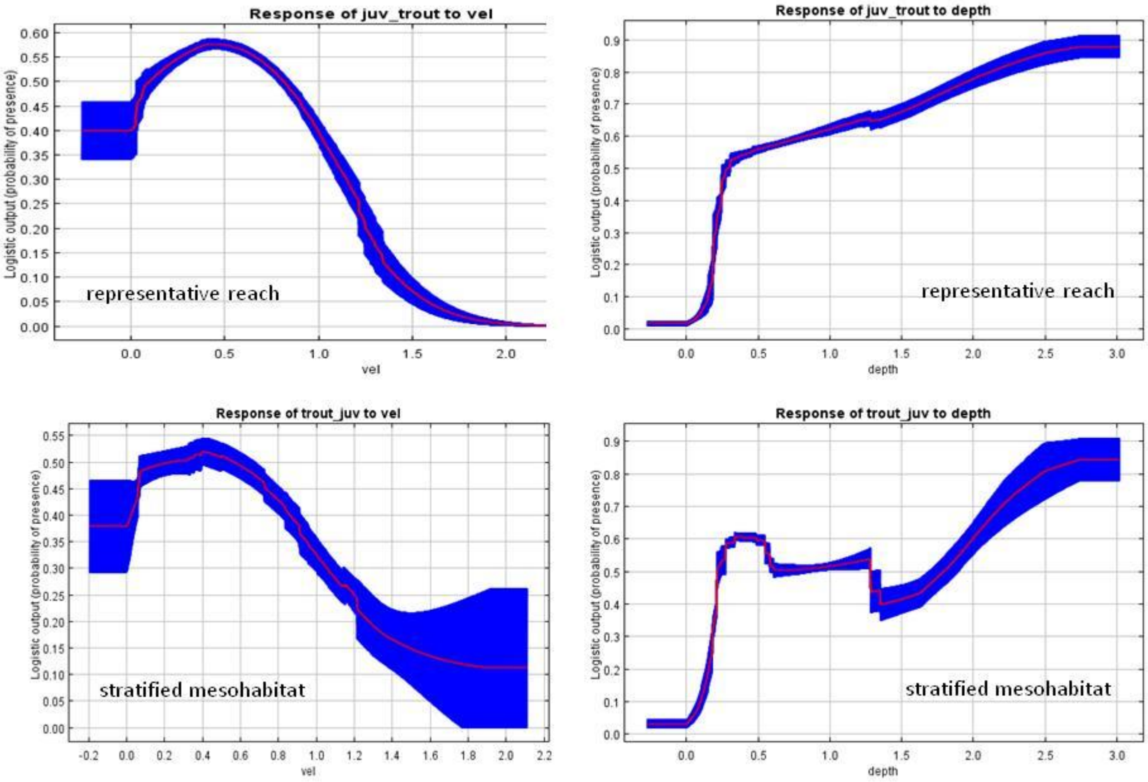


Figure A3.7 Comparison of response curves using different background data, but the same trout occurrence data. The lower two plots use background data with stratified mesohabitat cross-section selection (cf. representative reach in upper plots, as per Figure A3.6). The probability of juvenile trout occurrence was predicted in response to velocity in m/s (left plots) and depth in meters (right plots).

Converting Maxent output to HSC for PHABSIM

The Maxent models are not directly compatible with PHABSIM, which does not accept bivariate formula. PHABSIM treats velocity and depth as independent variables, so I investigated if independence was a reasonable assumption in this case. Maxent was used to produce independent models for velocity and depth, and these were compared to Maxent bivariate models that partitioned variability between velocity and depth (for both species and life stages). The univariate models closely resembled the bivariate models, and the only consistent difference was the suitability of velocities <0.2 m/s. The bivariate models predicted relatively high suitability at zero velocity, in contrast to the univariate models that predicted avoidance of zero velocities (suitability reduced >50%). The question then is - which is true? A plot of velocity versus depth for trout occurrences (Figure A3.8) confirms that trout were often observed at velocities <0.2 m/s, but only where depth exceeded 0.15 m. The univariate prediction that trout avoid zero-velocity was therefore an artifact of avoidance of shallow depths. We can correct for this artifact by using univariate *projections* of the bivariate Maxent models that represent the change in probability of occurrence as one variable changes, keeping the other variable constant (at its average sample value). This univariate projection is an acceptable simplification in this case because velocity was weakly correlated with depth ($R^2 = 0.26$ for background data; $R^2 = 0.03$ for trout locations).

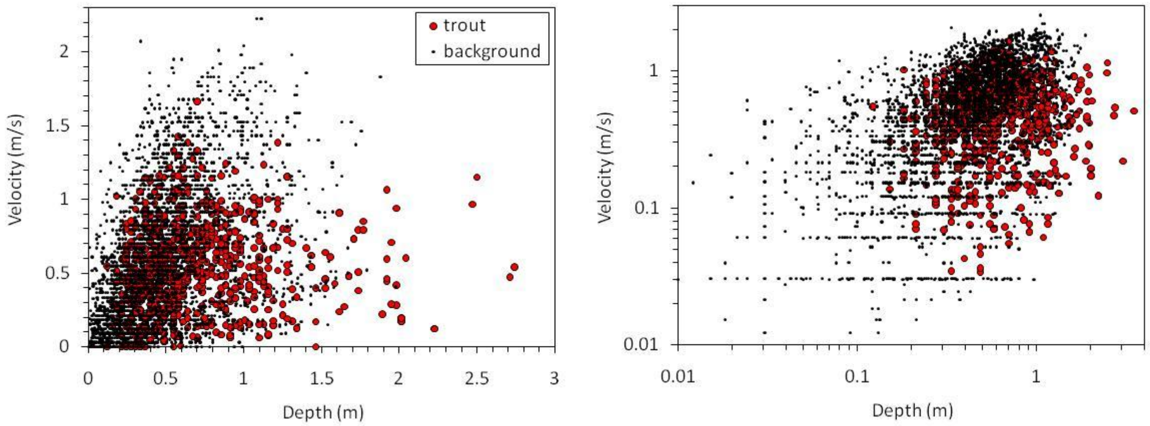


Figure A3.8 To better understand the interaction between velocity and depth, trout occurrence is plotted in two-dimensional space as red points (species and life-stage not distinguished). Background points from 10 sites are overlaid as black dots. The right plot is distinguished from the left plot by log scales on both axes to better visualize small velocities and depths. Two trout observations at >3 m deep were excluded from the left plot for clarity.

The final criteria recommended for application for the generalized habitat models are plotted in Figure A3.9. The Cheesman HSC were modified, having rejected a decline in habitat suitability for water depths greater than 1 m. The velocity criteria were left unchanged, so providing a slightly modified version of the Cheesman HSC that are hopefully acceptable to people preferring the Cheesman HSC.

Maxent derived size-guild HSC were also produced that are intended to represent both brown and rainbow trout, but within size cohorts. The size-guild HSC (Figure A3.9) are not an exact reproduction of the original Maxent output, having been reduced to univariate projections depicted using fewer points (<20) for compatibility with PHABSIM data formats (PHABSIM uses a table of coordinates, rather than an equation). In addition, the HSC were standardized to a maximum suitability of 1. This provides a measure of relative suitability rather than a predicted probability of occurrence (the latter is dependent on habitat saturation drivers, such as recruitment prior to the year of observation). The depth suitability for adult trout was standardized relative to the probability of occurrence at 1.25 m deep, given the less robust predictions of increasing suitability in deeper water (not robust to mesohabitat stratification). Likewise, depth suitability for juvenile trout was standardized to a maximum value at 0.3 m deep, with predictions at greater depths combining predictions from a stratified background and other HSC. None of the juvenile models predicted a decline in suitability between 0.3 and 0.6 m deep (either size guild or Cheesman), so a suitability of 1 was maintained over this depth range. Likewise, none of the Maxent models predicted a further reduction in suitability at depths >1.5 m, and I applied a 50% reduction in suitability at this point as an approximation across Maxent models (of contrasting species and background data).

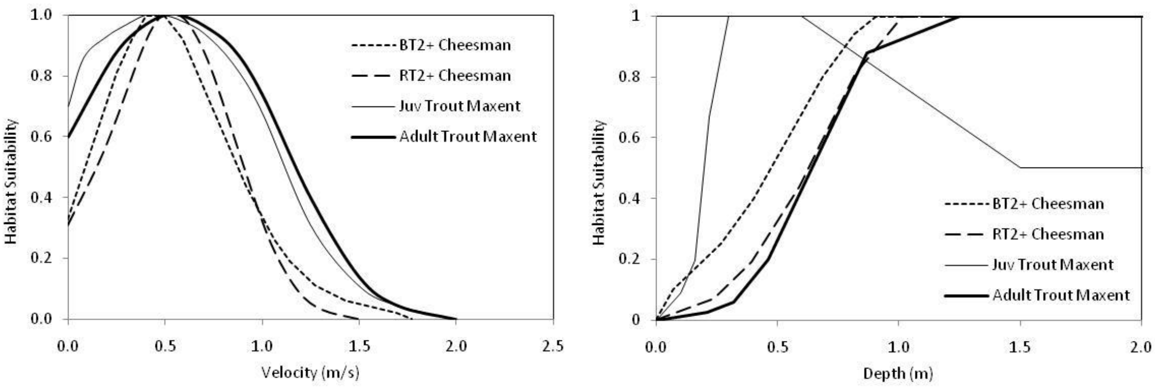


Figure A3.9 Recommended habitat suitability criteria for application using the generalized habitat model (Chapter 2). The Cheesman HSC were modified by increasing suitability of deep water to 1 (deeper than optimum in the original HSC). Size-guild HSC are also presented, with trout separated only by lifestage (juvenile or adult) rather than species, calculated using Maxent.

Discussion

Daytime observations of trout were used in this study, but there is some evidence that adult trout move to faster water after dusk when invertebrate drift (food) increases

(Shuler et al., 1994). The reported velocity change was moderate for brown trout in the Rio Grande, increasing from approximately 0.4 by day to 0.6 m/s at night. Before considering the use of night-time HSC, we must first consider the temporal scale at which flows can be manipulated. The energetic cost to trout from sustained higher velocities night and day may outweigh the gain over a few hours after dusk. Therefore HSC might better incorporate diurnal shifts by extending the range of preferred velocities, rather than ignoring daytime preferences (e.g., suitability score of 1 spread over 0.4-0.6 m/s). All the HSC considered here recognize this velocity range as optimal, so are considered robust to diurnal shifts in habitat preference. For small trout (age 0+ and 1+) the evidence of increased velocity preferences at night is less convincing (Hubert et al., 1994; Shuler et al., 1994).

The habitat suitability at 0.5 m deep for adult trout differed considerably between HSC. This difference is expected to have a big influence on predicted flow response (using PHABSIM) because 62% of background observations were <0.5 m deep (across the 10 background sites at two flows).

This study considered only rainbow and brown trout, so the size-guild HSC do not represent all species of trout in Rocky Mountain streams. I found that bias in background data had a more pronounced effect on predicted suitability than the difference between species. So applying the size-guild HSC to native cutthroat trout (*Oncorhynchus clarkii*) may be a better option than adopting cutthroat trout HSC that were derived using inappropriate background data or few trout observations (cutthroat are a close relative of introduced rainbow trout, with which it hybridizes).

From discussions with people familiar with Colorado fisheries (Division of Wildlife; USGS), the introduced brook char (*Salvelinus fontinalis*) are relatively ubiquitous throughout Rocky Mountains. Populations of brook char can persist with small flows, and a wide tolerance of velocity and depths would explain the paucity of HSC for brook char in Rocky Mountain streams (see Baker & Coon, 1997; Sotiropoulos et al., 2006). There are many possible explanations for their broader habitat range (e.g., more flexible spawning requirements, wider temperature range), but these observations do call into question the relevance of HSC based on rainbow and brown trout in representing brook char. This species is not eagerly sought by Colorado fisherman, limiting the impetus for testing the relevance of size-guild HSC to brook char.

APPENDIX 4: VALIDATION OF GEOMORPHIC CLASSIFICATION

To validate the Geomorphic Valley Classifications of Bledsoe & Carlson (2010), Ryan McShane and I surveyed bankfull width, channel slope, and valley width at 38 reaches throughout the upper Colorado, Yampa and White basins. Bankfull width was measured using two methods – by site survey and by aerial photos. Site surveys were conducted at a subset of reaches where we could safely access the opposite bank (most streams were flowing near bankfull at the time of survey, limiting wading access). Bankfull width was delineated by an absence of bank vegetation (or lichens if rocky), and/or a break point in the channel profile (Leopold et al., 1964; Polvi et al., 2011). Width was measured using an ultrasonic distance meter at 5 points spaced randomly over a 100 m section (distances from random number tables), which extended upstream from a random start point (the same random start selected for the vegetation survey). In addition to this site survey, average channel width was measured for every survey reach using the best available aerial photographs in Google Earth (best in terms of higher resolution and less channel area in shadows). Measured channel width included wet width plus unvegetated sediment along the banks. But wetlands and beaver ponds with no visible connection to the channel were omitted. Channel width was measured at 20 cross-sections spaced randomly over the full reach length (using RANDBETWEEN function in Microsoft Excel).

Despite a good correlation between GVC bankfull width and measured width ($R^2 = 0.86$ for GVC versus aerial-photograph width), the GVC method underestimated widths for larger streams (>10 m) and over estimates widths for smaller streams (Figure A4.1). This bias is seen in the relationship with the site-survey widths *and* with the aerial-photograph widths (open circles and black dots respectively in Figure A4.1).

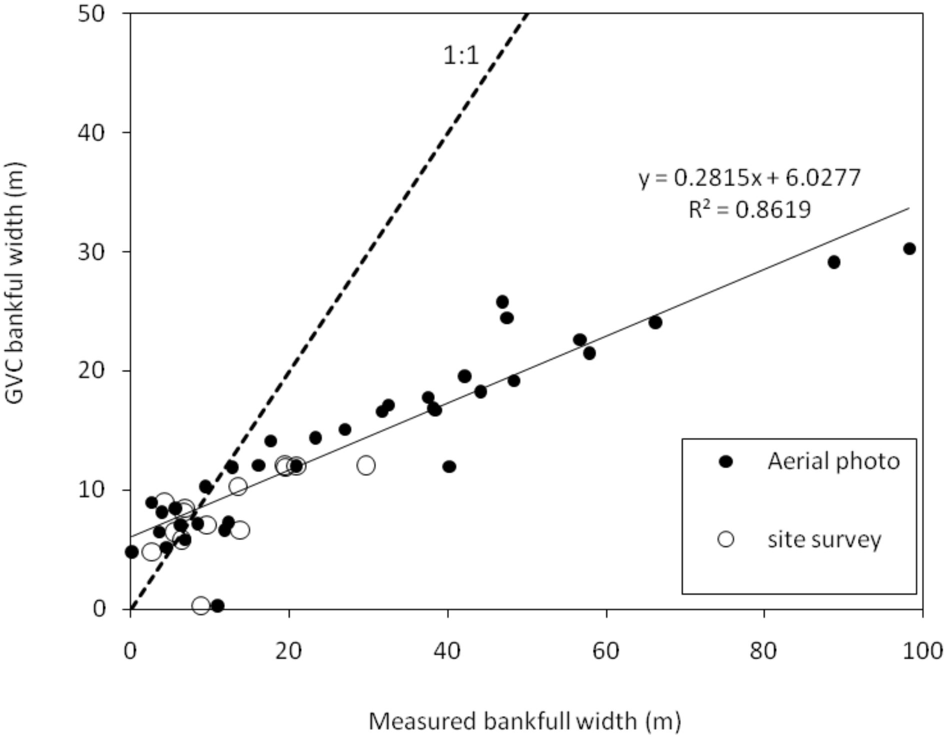


Figure A4.1 Bankfull width used in the GVC (upper Colorado equation from Faustini et al., 2009) plotted against two methods for measuring widths – aerial photograph (black dots) and site survey (clear circle) for a subset of sites. Points would fall on the 1:1 line if GVC width matched observed width, so this demonstrates under estimation of widths by the GVC in larger streams (>10 m) and over estimation in smaller streams.

Comparing the two measured widths - aerial photograph widths were in close agreement with site survey widths ($R^2 = 0.96$ if aerial photograph widths are constrained to the same 100 m site survey section). The median difference was -1.9 m, which may represent concealment of channel margins by bank vegetation. I further validated the use of aerial photographs to estimate width by conducting a more intensive survey on the Williams Fork River. The number of site-survey widths was increased from 5 to 20 and the cross-sections were spaced over a longer section (1015 m instead of 100 m, surveyed 8/4/2011, Lat. 40.0525 Long. -106.188, USGS09038500). For aerial photograph width, the whole reach was sampled (as was done for all sites), but sampling effort was increased from 20 cross-sections to the population width by instead measuring the entire channel area (polygon drawn in Google Earth), then dividing this area by mid-channel length. Width estimates were generated this way for three different photographs (dates 9/24/1994, 9/7/1999, and 6/16/2005).

There were notable differences between the average site survey width and aerial photograph widths (up to 26%), but the differences appear to have resulted primarily from a change in channel width over time, rather than error introduced by aerial photograph measurements. This is evidenced by the strong correlation between preceding flow and channel width, which approaches a deterministic relationship (Figure A4.2). Arguably, the aerial photograph widths might represent bankfull width better than the site surveys (at least for streams with limited vegetation concealment), because more cross-sections were surveyed, and because the entire reach was sampled (instead of 100 m). Change in width over time introduces a potential source of variability to this study. Most aerial photographs used in the broader study were taken during a consistently dry period (85% of reach aerial photographs between 2002 to 2006, during which time the 5 year mean 90 day max. was 67 to 79% of long-term average at USGS09251000), a period that was much dryer than the site survey period (5 year mean 90 day max. for 2011 was 125% of average).

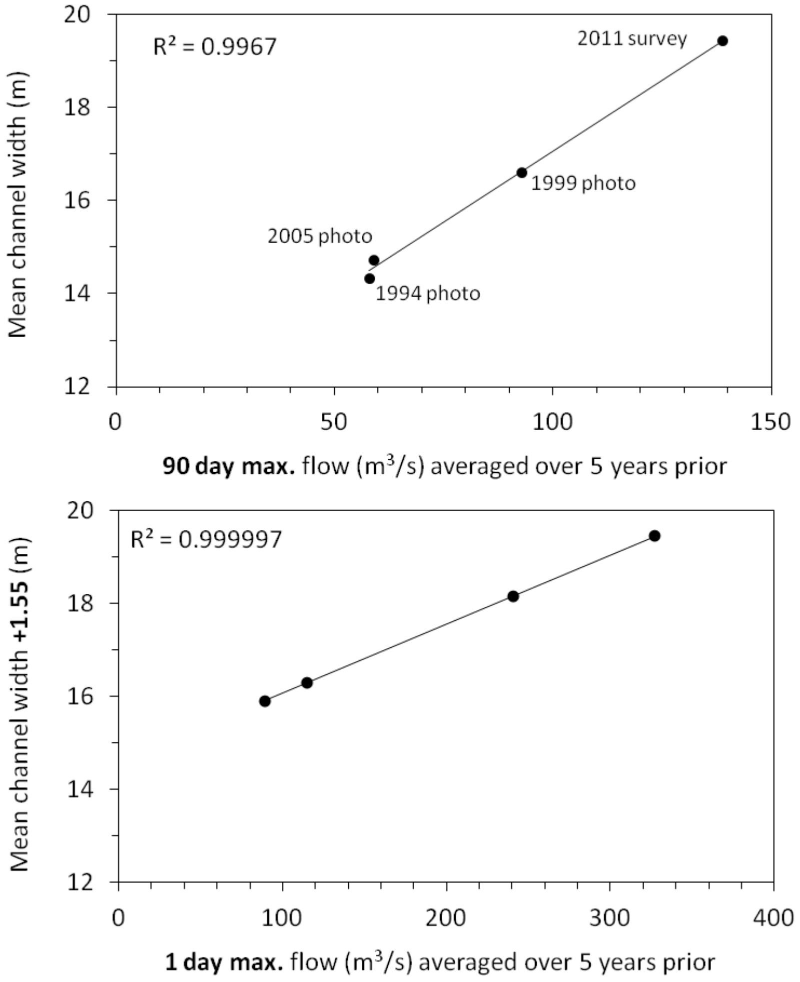


Figure A4.2 Changes in channel width over time were strongly correlated with peak flow, which can account for the difference between the site survey estimate ("2011 survey") and aerial photograph estimates (1994, 1999, 2005) for this reach on the Williams Fork River. The 90 day maximum flow (averaged for the 5 years preceding each survey) was the best predictor (upper plot) among five peak flow metrics (instantaneous, 1 day, 7 day, 30 day or 90 day maximum). This can be improved upon using the 1 day maximum flow (lower plot), but only after solving for a correction factor that maximizes R^2 (+1.55 m for photograph widths).

As an alternative to the equation that was originally used to predict bankfull width for the GVC (upper Colorado, Faustini et al., 2009), I therefore offer the following new equation:

Bankfull width in meters = $8.1331 \times Q^{0.5161}$ ($R^2 = 0.93$, $F=461$, $Prob(F)<0.001$, $N = 38$)

The predictor variable Q is mean annual flow (m^3/s) from the National Hydrography Dataset (Vogel et al., 1999), so can be applied throughout the stream network. This hydraulic geometry equation is based on the validation data set of mean channel widths measured from aerial photographs over the entire reach, after applying a +2 m correction consistent with observed underestimate from site surveys. The exponent of this equation (0.5161) is similar to that reported elsewhere (Andrews, 1984; Park, 1977), with the coefficient (8.1331) unique to the flow metric used here (mean annual flow).

To validate the *Valley Width* estimated for the GVC, site surveys for all 38 reaches included sketching the location of the valley edge on aerial photos, as viewed from various points of access for riparian vegetation surveys (surveyed valley length was 11x to 80x channel width, for the 10%ile to 90%ile respectively). This used valley edge markers described by Polvi et al. (2011), including break points in the valley profile. Valley edge did not always correspond to the base of hillslopes, especially where the terraces adjoining the hillslope appeared long abandoned (from height above the stream and the type of vegetation). For sites lacking obvious break points, I used riparian vegetation to delineate a valley edge (e.g., in confined reaches where hillslopes gradually transitioned to the stream edge). Site sketches on prints of aerial photographs were digitized as polygons onto the same aerial photograph in Google Earth (redrawn using landmarks such as trees and eroded banks). The polygons were exported as KML files and polygon area calculated using GEPath (Freeware Version 1.4.4). Average Valley Width was calculated by dividing total area by valley length (length measured in Google Earth, following the approximate midline of the valley). The GVC Valley Width was recalculated only for the surveyed section, rather than full reach, to enable direct comparison with the survey estimate.

My site surveys of valley width generally described the upper bound of GVC valley widths (Figure A4.3). There was close agreement for about a third of reaches between survey Valley Width and GVC Valley Width (those points close to the dashed line, Figure A4.3). For the other two-thirds of reaches, the site surveys produced wider valley estimates. Site surveys can better discriminate small break points in channel profile, compared to the DEM used to create GVC Valley polygons. But the site survey introduced subjectivity in selecting a valley edge (e.g., choosing one of several break points), compared to the fixed flood heights used for the GVC. The differences between the site survey estimate and GVC estimate of Valley Width were therefore considered acceptable.

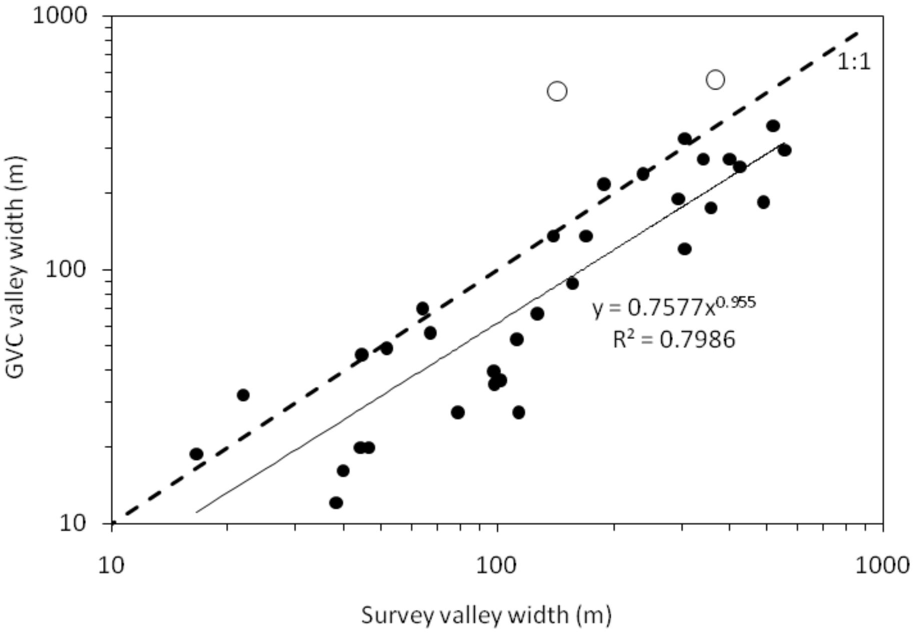


Figure A4.3 The Valley Width from the GVC (recalculated for shorter survey section) plotted against valley widths estimated from site surveys. Points would fall on the 1:1 line if GVC width matched observed. The two open circles are considered outliers because site surveys failed to capture the true valley extent (for one outlier, there was limited visibility of a broad valley and the surveyed section was only 5 x channel width; for the other outlier closer inspection of aerial photographs indicated historic channel avulsions across a wider valley that were missed in the site survey).

The two estimates of Bankfull Width and Valley Width were converted to a ratio to describe channel confinement. A ratio of Valley to Bankfull Width greater than 7 is classed “Unconfined” and less than 7 “Confined” (7 is the ratio at which sinuosity is able to exceed 1.5; Bledsoe & Carlson, 2010). Using the site survey estimates of Valley and Bankfull width produced the same confinement classification as the GVC for 70% of reaches. This increased to 76% of reach classifications matching the GVC classification if only the Bankfull Width estimates were replaced (not Valley Width). The latter is considered a more reasonable representation of classification accuracy, assuming that the GVC Valley Widths are at least as good as the survey estimates.

The channel slope was surveyed using a TopCon AT-G3 autolevel with 30X zoom. These slope surveys were discontinued after six streams, because the digital elevation model appeared to be adequate. Estimates of slope from the six site surveys were close to slopes derived from digital elevation models ($R^2 = 0.92$). The slopes from the DEM were measured over a similar length of stream surveyed (mean survey length 195 m), and the DEM estimates are expected to improve in accuracy over greater lengths.

LIST OF ABBREVIATIONS

AUC - Area Under the receiver operating Curve as per Lobo et al. (2008).

AIC – Akaike’s Information Criterion (statistic for selecting best model).

BBM – Building Block Method from (King et al., 2000).

BIC – Bayesian Information Criterion (statistic for selecting best model).

BT1 – Brown trout juvenile.

BT2 – Brown trout adult.

ELOHA – Ecological Limits Of Hydrologic Alteration from Poff et al. (2010).

GVC – Geomorphic Valley Classification from Bledsoe & Carlson (2010).

HSC – Habitat Suitability Criteria as per Bovee (1986).

HV – habitat value.

IFIM – Instream Flow Incremental Methodology from Bovee et al. (1998).

IFM – Index of Flow Modification, from Merritt & Poff (2010).

LM – Linear Model function implemented in R Stats.

MAF – Mean Annual Flow.

NHDPlus – National Hydrography Dataset, “Plus” distinguishing the revised version.

NLME – Non-Linear Mixed Effects model from (Lindstrom & Bates, 1990).

PHABSIM – Physical HABitat Simulation is the software and method manual used to model hydraulic habitat.

PRISM – Parameter-elevation Regressions on Independent Slopes Model.

Q95h – flow providing 95% of maximum habitat.

R – statistical software freeware.

R2Cross – flow-ecology method used in Colorado from (Espegren, 1996).

RHABSIM – River HABitat SIMulation from (Payne & Goforth, 1998).

RHYHABSIM – River Hydraulic HABitat SIMulation from (Jowett, 1996).

RT1 – Rainbow trout juvenile.

RT2 – Rainbow trout adult.

StateMod – Colorado's surface water flow model from (CDWR & CWCB, 2009).

STGQ – model predicting STaGe-discharge (Q) relationships as a component of PHABSIM.

T1 – juvenile trout (rainbow and brown combined).

T2 – adult trout (rainbow and brown combined).

TNC – The Nature Conservancy.

USGS – United States Geological Survey provided flow data with gage code often presented in text.

VAF – Velocity Adjustment Factor, used by PHABSIM to allow Manning’s n to vary with flow-depth.

VELSIM – VELocity SIMulation model used by PHABSIM to predict velocities.

WFET - Watershed Flow Evaluation Tool from Sanderson et al. (2011).

WUA – Weighted Usable Area (~area of habitat that is usable). Output metric from PHABSIM.