

TWO-DIMENSIONAL MODELLING OF HABITAT SUITABILITY AS A FUNCTION OF DISCHARGE ON TWO COLORADO RIVERS

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ABSTRACT

The quantity of water that should be retained in streams and rivers for the benefit of fish during periods of water scarcity is a question of considerable interest to river managers and biologists. Although instream flow methodologies have existed since the 1970s, no single method has been widely accepted for use on large warm-water rivers because of their high species richness and generalized fish habitat use patterns. In this paper, we present an approach similar to instream flow incremental methodology, but which uses two-dimensional flow models and biomass estimates derived from multiple sites on two Colorado rivers for predicting the effect of discharge on adult standing stocks of two native fish species. Suitability criteria are developed for bluehead and flannelmouth sucker (*Catostomus discobolus* and *C. latipinnis*) by comparing adult biomass in individual meso-habitat units with modelled depths and velocities. We find that roundtail chub (*Gila robusta*) biomass is not correlated with depth and velocity, but appears to be positively associated with indices of habitat heterogeneity. Species biomass and total usable habitat area are predicted as a function of discharge for each site and data show good correlation between predicted and measured biomass. Results suggest that the Colorado and Yampa Rivers have similar potential for native fish biomass, but low summer discharges limit native fish biomass on the Yampa River. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: instream flows; meso-habitat; two-dimensional modelling

INTRODUCTION

Following the water development period of the mid-20th century, biologists and hydrologists recognized the need for 'instream flows' to protect fish and aquatic habitat. Instream flow refers to water that is retained in a river as opposed to being diverted for out-of-stream uses. During the 1960s and early 1970s, several instream flow assessment methodologies were developed to help quantify the amount of water required in rivers for fish and wildlife. Most of these methods were based on hydrologic analysis of water supply coupled with empirical observations of habitat quality and an understanding of riverine fish ecology (Stalnaker, 1994). The most popular instream flow assessment method in the United States is the instream flow incremental methodology (IFIM) and the most widely used instream flow assessment tool is the physical habitat simulation component (PHABSIM) of IFIM (Reiser *et al.*, 1989).

IFIM defines microhabitat by the spatial attributes of a physical location. The spatial attributes of interest are depth, velocity, cover and substrate (Bovee *et al.*, 1998). PHABSIM relies on a variety of one-dimensional step-backwater hydraulic models to calculate depth and average velocity at cross-sections over a range of flows (Tarbet and Hardy, 1996). Modelled velocity is distributed across the channel based on measured velocity distributions over some range of flows. The probability that an individual of a specific species and life stage has been observed occupying a range of depth, velocity, substrate/cover provides habitat suitability criteria. Weighted usable area (WUA), a measure of habitat area based on observations of habitat suitability, represents microhabitat availability

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for a target species (Stalnaker *et al.*, 1995). Temporal variability is accounted for by integrating hydrologic time series and 'habitat versus discharge' relationships to generate a habitat time series (Hardy, 1998).

PHABSIM has been criticized for both physical and biological reasons including: (1) difficulties in establishing a relationship between WUA and population response; (2) the focus on single species and life stages; and (3) the use of one-dimensional flow models which, by definition, cannot accurately represent velocity distributions in rivers with significant lateral flow components (Bovee, 1996; Espegren, 1998; Mathur *et al.*, 1985; Scott and Shirvell, 1987). Carrying capacity (potential biomass) of species in a community is only partially set by habitat availability; factors including forage availability, predation and competition can reduce a particular species biomass below the habitat potential. Increased microhabitat availability for specific species and life stages cannot, therefore, be assumed to result in increased biomass (Mathur *et al.*, 1985). PHABSIM relies on the assumption that habitat parameters can be modelled at a biologically significant level, as do almost all instream flow methodologies (Hardy, 1998). However, with step-backwater models (like those used in PHABSIM) it is difficult to obtain reliable results for areas less than 10 m², making habitat description difficult at a scale relevant to fish, which commonly occupy a space smaller than 1 m² (Leclerc *et al.*, 1995).

Assessing the habitat requirements of fish in warm-water rivers using PHABSIM is especially problematic (Rose and Hahn, 1989; Nestler, 1990). In warm-water rivers, habitat suitability based on microhabitat observations may not be appropriate because of the high species richness and generalized habitat use patterns of fish (Bain and Boltz, 1989; Bowen *et al.*, 1998). Instead, a broader community-level perspective that simultaneously considers multiple species is required for examining the relationship between flow and habitat given the likelihood of differential species response to varying stream flows (Lobb and Orth, 1991; Anderson, 1998).

A number of authors have suggested that two-dimensional flow models should offer significant improvement over one-dimensional modelling in determining habitat metrics as a function of flow (Leclerc *et al.*, 1995; Bovee, 1996; Ghanem *et al.*, 1996; Hardy, 1998; Kondolf, 2000; Guay *et al.*, 2000). One-dimensional flow models calculate downstream changes in water-surface elevation and velocity between individual channel cross-sections, while two-dimensional flow models calculate downstream and lateral flow components of flow (three-dimensional models include vertical velocities). Instream flow assessments based on one-dimensional modelling can account for temporal variability in discharge, but are poorly suited to the analysis of spatial metrics. Spatially explicit flow models (two- and three-dimensional) are necessary to describe the spatial and temporal heterogeneity in a river system, not only to model the physical features of the habitat, but also to permit a better understanding of the processes that can be limiting to fish existence, including habitat heterogeneity/diversity (Bovee, 1996; Ghanem *et al.*, 1996). Two-dimensional models are ideally suited for computation of landscape ecology metrics across a variety of spatial scales, including examination of habitat utilization and fish community structure (Bovee, 1996; Hardy, 1998).

Our primary objective in this study was to determine whether two-dimensional (2D) models and community biomass estimates could be used within an IFIM framework to predict fish biomass as a function of discharge. We use community biomass estimates and meso-habitat abundance, rather than microhabitat suitability indices, for determining habitat suitability. Data are collected and analysed at the meso-habitat unit scale, which consists of a single habitat type (e.g. pool, riffle, run) one to ten channel widths in length, because biological data are most efficiently collected at the meso-habitat scale and 2D hydraulic models are most likely to accurately simulate meso-scale flow patterns (Crowder and Diplas, 2000; Parasiewicz, 2001). Suitability criteria collected at the meso-habitat scale are also more likely to be transferable to sympatric species or guilds (Parasiewicz, 2001).

A major assumption explicit in this approach is that fish distribute themselves in the river as a function of habitat suitability. While we recognize the need for channel maintenance flows and rearing habitat, we do not address those issues in this paper.

STUDY AREAS

Three study sites were chosen on the Yampa River, which flows through the northwest portion of Colorado from its headwaters near Steamboat Springs to its confluence with the Green River in Utah (Figure 1). The Yampa River is unusual in Colorado because it contains no mainstem dams. As such, spring peak discharges have been relatively unaffected by development in the basin, whereas late summer base-flows have been significantly affected by

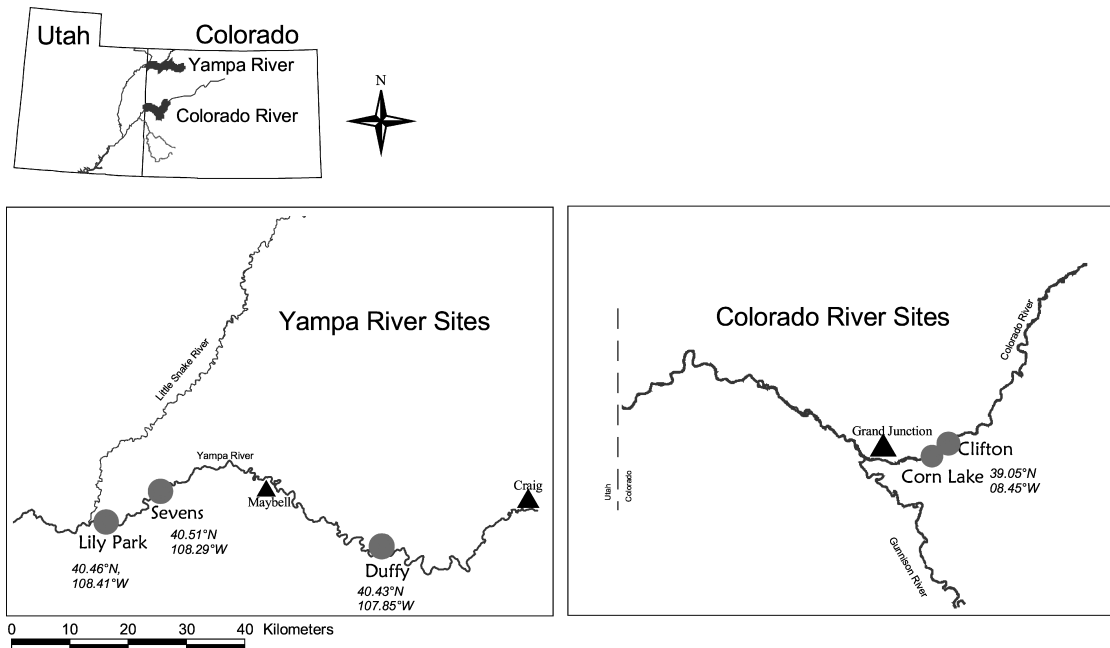


Figure 1. Site map showing Yampa and Colorado River study sites. Flow is from right to left

agricultural withdrawals. According to Colorado River Decision Support System (CRDSS) models, Yampa River discharges in August and September average only 70% of native late summer low flows (Modde *et al.*, 1999). The three study sites on the Yampa River are Duffy, Sevens, and Lily Park. Each site exhibits slightly different fish and habitat characteristics though all have riffle–run morphologies (Table I). The Duffy site is slightly unique, with a large population of non-native fish including white suckers (*Catostomus commersoni*), smallmouth bass (*Micropterus dolomieu*) and sucker hybrids. Both Sevens and Lily Park sites have a higher proportion of native fish species than Duffy. Lily Park is located just upstream of the Little Snake River confluence and was added in 2000 because it had a higher gradient and greater proportion of native fish than Duffy or Sevens.

Two study sites were chosen on the ‘15-Mile reach’ of the Colorado River, which extends from Palisade, Colorado, to the Gunnison River confluence. The Colorado River contains a large number of upstream water projects that store water for delivery out of the basin. In an average year, peak flows are only 60% of pre-impoundment flows at the Cameo gauge 10 km upstream of the study reach. During the early summer, base flows are typically higher than native summer low flows but can be reduced in late summer by upstream irrigation withdrawals. The Colorado River Recovery Program (Osmundson *et al.*, 1995) considers the 15-Mile Reach important for endangered fish recovery. The two Colorado River sites, Clifton and Corn Lake, are located adjacent to one another and taken together cover 8.1 km. Both sites have riffle–run morphologies and mean channel slopes of approximately 0.16–0.2%. The greatest difference in the sites is that Clifton is wider with an anastomosing channel planform whereas Corn Lake is more constrained.

Table I. Site data. Channel width calculated at 17 m³/s

	Clifton	Corn Lake	Duffy	Lily	Sevens
Length (km)	4.2	3.9	2.1	3.1	2.9
Width (m)	59	50	68	57	60
Slope (%)	0.20	0.16	0.06	0.20	0.05

METHODS

Fish sampling

Fish were sampled by electro-shocking and netting from a 4.8 m raft rigged with a Smith-Root electro-fisher, 5000 W generator, and anode array mounted on a forward boom. The boat was manoeuvred with oars and/or a battery-powered 18.1 kg thrust trolling motor. Two netters caught fish, and all were measured to the nearest millimetre. Only fish over 150 mm were used for mark-and-recapture population estimates. Density estimates were made for each year at each of the five study sites on the Yampa and Colorado rivers.

The Darroch multiple mark method (Everhart and Youngs, 1981) was used to make population estimates with 95% confidence intervals. Total fish estimates were made for each site and for each species. Recapture rates varied between species and size-groups. In general, larger suckers had the highest recapture probabilities; channel catfish (*Ictalurus punctatus*), largemouth bass (*Micropterus salmoides*), smallmouth bass, northern pike (*Esox lucius*) and common carp (*Cyprinus carpio*) had appreciably lower recapture probabilities.

Within sites, electro-fishing was performed at the meso-habitat scale (individual runs, riffles, pools). Sub-reach sampling units had the same starting and end locations between passes and years and were digitized into a geographic information system (GIS) format from aerial photographs. Species density and biomass were calculated by multiplying the percentage of a given species caught in each sub-unit by the total-reach estimate (determined from mark-and-recapture probabilities) for that species and year. Biomass was estimated for flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*Catostomus discobolus*) and roundtail chub (*Gila robusta*) over 20 cm in length. Individuals smaller than 20 cm in length were not included in biomass estimates.

Channel mapping

A Javad Oddyssey L1/L2 Real Time Kinematic (RTK) Global Positioning System (GPS) was mounted on the side of a boat directly over an ODOM Hydrographic Systems, Hydrotrac—Single Frequency, Portable Survey Sounder. The Javad RTK GPS was optionally equipped with advanced multi-path reduction and the ability to receive both GPS and Glonass satellites. Published vertical accuracy for the GPS system is 15 ± 1.5 mm per kilometre of distance between the base station and rover GPS units. Repeat field measurement of a single monument located 1 km from the base-station gave a vertical standard deviation of 2 mm. The ODOM Hydrotrac Sounder operated at 200 kHz and output readings at a rate of 10 Hz with a published accuracy of $1 \text{ cm} \pm 0.1\%$ of depth.

The GPS and sounder output data at different rates (1 Hz and 10 Hz, respectively), so a Comlog program tagged incoming data with the time to the nearest millisecond. An XYZ dataset was created by linearly interpolating depths for each GPS reading. To ensure that the entire channel was mapped without large gaps in coverage, GPS data were also logged using ArcView Tracking Analyst to create real-time maps showing locations where bathymetric data had been collected. Mapping was done through a combination of longitudinal and cross-sectional surveys.

Two-dimensional models require calibration, so water-surface elevations and extents were mapped using the RTK GPS mounted on a range pole. Additionally, water depth and velocity were measured with a 3 MHz Sontek River Surveyor Acoustic Doppler Profiler (ADP) at some sites for use in model calibration/validation. Velocity measurements were depth-averaged in 15 cm increments over channel depth. Individual measurements were time-averaged over a 30-s period by holding the boat steady at one place in the river. RTK GPS was used to reject readings in which the boat moved over 3 m during the 30-s period.

Hydraulic simulation

In the first two years of the project, hydraulic modelling was performed using RMA2 (version 4.3), a two-dimensional hydraulic model distributed with the Surface Water Modeling System (SMS) software package from EMSI. Although modelling with RMA2 presented only moderate difficulties (Stewart, 2000), it was decided that modelling of additional sites would be contracted to C. Addley at Utah State University (USU). The USU laboratory used a two-dimensional model developed by J. Nelson of the United States Geological Survey. The technical description of this model and underlying equations can be found in Nelson *et al.* (1995), Nelson (1996), Thompson *et al.* (1998), McLean *et al.* (1999), and Topping *et al.* (2000). Finite element meshes used rectangular elements

(RMA2 meshes had a limited number of triangular elements) with maximum nodal distances of 3 m laterally and 5 m longitudinally. In smaller channels, smaller elements were used. Unless otherwise noted, results presented in this paper reflect USU modelling data with the exception of the Duffy site, which was only modelled with RMA2. Hydraulic simulations were performed over a range of discharges at each site.

Meso-habitat availability/suitability

In order to quantify meso-habitat availability, solutions from the 2D model runs were imported into ArcInfo GIS and linearly interpolated into 1×1 m depth and velocity grid coverages. Depth and velocity grids for each site/discharge were sampled to create generic habitat coverages based on 16 non-overlapping habitat types (Table II). The generic habitat types were defined prior to 2D modelling to characterize overall site morphology and for the purpose of evaluating habitat diversity as a function of discharge.

Suitability criteria for individual species were developed from mean depth and velocity for each meso-habitat unit using Fragstats 3.3 (McGarigal *et al.*, 2002). Mean depth and velocity were calculated at the modelled discharge closest to the actual discharge during periods of fish sampling. Depth, velocity and species biomass for each meso-habitat unit were subsequently imported into Sigma Plot and smoothed using a 3D running median function (nearest 10%) to create a regular matrix of predicted biomass as a function of depth and velocity.

Both the spatial and temporal distributions of habitat are important to understanding how changes in discharge are likely to affect fish communities. A number of studies have shown that habitat diversity is positively correlated with species diversity in aquatic environments (Schlosser, 1982; Shields *et al.*, 1994; Eckmann, 1995; Katano *et al.*, 1998). The idea is that a landscape with a large diversity of habitats presents more opportunity for individual species to find habitat patches that they can exploit (Connell, 1980). In communities with significant predator/prey interactions, the diversity of habitats may provide the opportunity for prey species to avoid predation by seeking habitats that predators are either unwilling or unable to utilize (Power, 1992).

To evaluate habitat diversity, Shannon's diversity index (Shannon and Weaver, 1949) was calculated for each meso-habitat sub-unit using Fragstats 3.3. Shannon's diversity index evaluates the richness and evenness of habitat types (richness refers to the number of patch types; evenness refers to the distribution of area among different types) and is used as a relative index for comparing differences in landscape heterogeneity at different times (McGarigal and Marks, 1995).

Table II. Depth and velocity criteria used to define meso-habitat types

Habitat types	Depth (m)	Velocity (m/s)
Wetted pool	0.01–0.2	<0.15
Shoal pool	0.2–0.5	<0.15
Shallow pool	0.5–1.0	<0.15
Medi pool	1.0–2.0	<0.15
Deep pool	>2.0	<0.15
Wetted run	0.01–0.2	0.15–0.6
Shoal run	0.2–0.5	0.15–0.6
Shallow run	0.5–1.0	0.15–0.6
Medi-run	1.0–2.0	0.15–0.6
Deep run	>2.0	0.15–0.6
Shallow riffle	0.01–0.2	0.6–1.5
Riffle	0.2–0.5	0.6–1.5
Deep riffle	0.5–1.0	0.6–1.5
Extra deep riffle	>1.0	0.6–1.5
Shallow rapid	<0.5	>1.5
Deep rapid	>0.5	>1.5

RESULTS

Model validation

In this study, USU 2D hydraulic models were calibrated against measured water-surface elevations, whereas RMA2 models were calibrated with measured depth and velocity data at the highest modelled discharge. Model results were later evaluated for their ability to reproduce hydraulic conditions by comparing model results against field measurements of depth and velocity. RMA2 was calibrated at $17 \text{ m}^3/\text{s}$ and $51 \text{ m}^3/\text{s}$ for Duffy and Corn Lake respectively, and was validated at $8.5 \text{ m}^3/\text{s}$ and $34 \text{ m}^3/\text{s}$. ADP depth and velocity data were collected at only three sites: Duffy (RMA2), Clifton (USU), and Corn Lake (RMA2 and USU), so only four simulations were validated. In each case, the simulation data appeared to reproduce patterns in the observed data, although water depth was slightly, yet consistently, over-predicted or under-measured (Table III, Figure 2).

Fish density and biomass estimation

At Duffy Tunnel on the Yampa River, total fish biomass was similar in 1998 and 1999, but decreased significantly in 2000 and 2001, years when summer flows were reduced (Table IV). The only species whose density and biomass increased in 2000 and 2001 was smallmouth bass, a non-native small-bodied predator that can utilize shallow habitats. Similarly, at Sevens, total fish density and biomass estimates were high 1998 and 1999, but decreased significantly during the low-flow years of 2000 and 2001. Lily Park was added to the study in 2000,

Table III. Regression between measured and computed depth and velocity. Slope is the slope of the regression line

Site	Model	n	Depth (m)		Velocity (m/s)	
			r^2	Slope	r^2	Slope
Duffy	RMA2	40	0.98	1.00	0.57	0.52
Clifton	USU	60	0.73	1.00	0.74	1.06
Corn Lake	RMA2	23	0.68	0.74	0.91	1.12
Corn Lake	USU	26	0.65	0.74	0.81	0.96

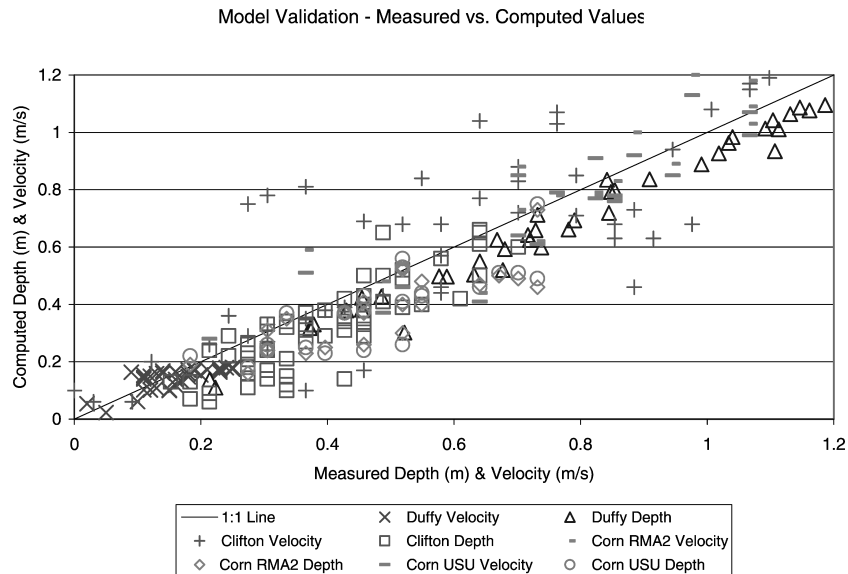


Figure 2. Measured versus computed depth (m) and velocity (m/s)

2D HABITAT SUITABILITY

Table IV. Biomass estimates (kg/km) of stream channel. Flow represents the modelled discharge used for habitat/biomass comparisons

	1998	1999	2000	2001
Sevens				
Flow (m ³ /s)	9.9	8.5	5.7	4
Total fish	1137	1005	633	492
Flannelmouth sucker	413	412	361	228
Bluehead sucker	111	94	26	30
Roundtail chub	44	27	14	15
Duffy				
Flow (m ³ /s)	9.9	8.5	5.7	4.2
Total fish	510	454	341	292
Flannelmouth sucker	34	19	16	6
Bluehead sucker	14	10	10	12
Roundtail chub	12	27	5	10
Lily Park				
Flow (m ³ /s)			8.5	5.7
Total fish			2369	1760
Flannelmouth sucker			1316	801
Bluehead sucker			195	114
Roundtail chub			3.0	0.1
Corn Lake				
Flow (m ³ /s)		42.5	31.1	25.5
Total fish		2761	2854	2605
Flannelmouth sucker		1261	1269	1281
Bluehead sucker		806	504	596
Roundtail chub		57	68	41
Clifton				
Flow (m ³ /s)			31.1	25.5
Total density estimate			3207	3341
Flannelmouth sucker			1280	1075
Bluehead sucker			452	496
Roundtail chub			100	94

so data were not available for the higher base flow years. In both 2000 and 2001, Lily Park adult flannelmouth suckers were observed to use different meso-habitats at different flows. At flows below 3.4 m³/s, flannelmouth suckers were found in deep pools and eddies; but flannelmouth suckers were found in deeper runs at flows above 3.4 m³/s (Anderson and Stewart, 2003).

The Colorado River sites had the highest biomass of all the sites and the greatest composition of native fish. Flannelmouth sucker, bluehead sucker and roundtail chub were the most common species captured, representing over 65% of the fish caught on the Colorado River.

Habitat composition/diversity and fish biomass

To evaluate the effects of low-flow channel morphology on biomass and community composition, we compared a number of biological metrics with generic habitat metrics calculated at the median low-flow discharge for each sample year. Riffle habitat, commonly associated with increased invertebrate productivity, was significantly positively correlated with total biomass at each site ($r^2 = 0.82$, $n = 17$).

Biomass for bluehead sucker, a native species of interest, was positively correlated with the abundance of 'deep-riffle' habitat ($r^2 = 0.92$, $n = 17$). Field observations suggested that large-bodied fish required deeper habitats than smaller-bodied fish. Two of the most common large-bodied non-native species, carp and channel catfish, were positively correlated with pool and run habitat over 1 m deep ($r^2 = 0.51$ and 0.57 , respectively, $n = 17$).

Roundtail chub biomass was not correlated with any generic habitat type, though roundtail chub biomass did appear to increase as a function of habitat diversity. Shannon's diversity index was calculated for each site and discharge using the 16 generic habitat types. At study sites with a Shannon's diversity habitat index greater than 2.0, Shannon's diversity index was positively correlated with roundtail chub biomass ($r^2 = 0.93$, $n = 8$). At Corn Lake, where habitat diversity was calculated for each riffle-run reach within the site, Stewart (2000) found that reach-scale Shannon's habitat diversity was also positively correlated with roundtail chub abundance ($r^2 = 0.93$, $n = 6$).

Determination of habitat suitability

Habitat suitability indices were developed for bluehead and flannelmouth sucker using fish and modelling data from Clifton, Corn Lake, Sevens and Lily Park. Duffy Tunnel was not included because it did not contain significant numbers of adult native fish. An attempt was made to develop suitability indices for roundtail chub, though neither biomass nor species density could be correlated with any range of depth and/or velocity.

Regressions between log-transformed observed and predicted biomass for bluehead sucker ($x = 0.96y$, $r^2 = 0.92$, $n = 145$) and flannelmouth sucker ($x = 0.98y$, $r^2 = 0.89$, $n = 145$) demonstrates a good agreement in those areas where data exist (Figure 3). Unfortunately, smoothing results in biomass predictions where fish were neither

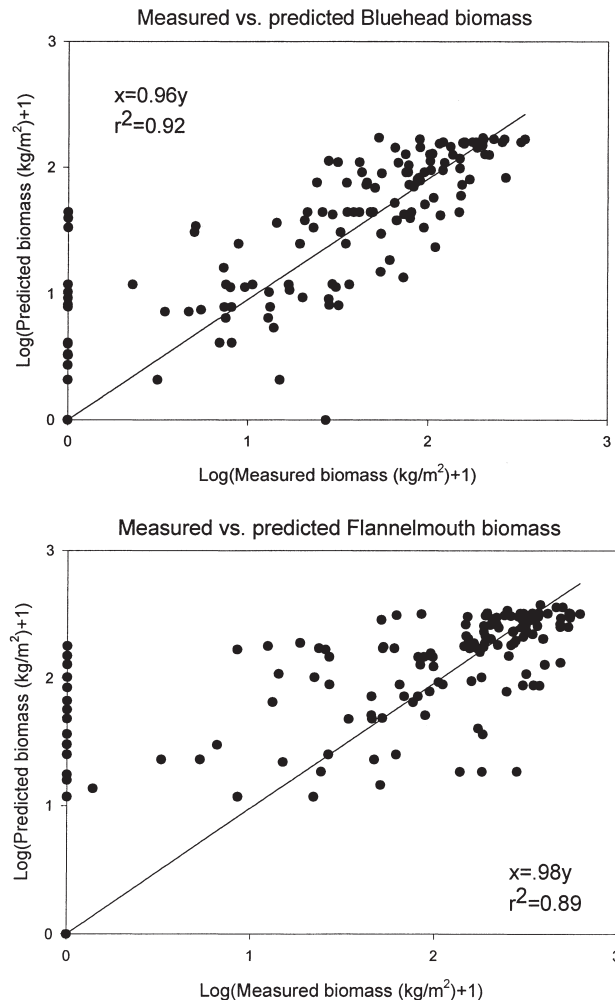


Figure 3. Measured versus predicted biomass of bluehead and flannelmouth sucker

observed nor likely to occupy, and does not predict biomass beyond the range of observed depth and velocity. To account for these discrepancies, we modified the matrix by eliminating biomass where no biomass was observed and extended the range of depths and velocities by mirroring data beyond the observed range. Data were then grouped into four general habitat suitability categories (unusable, unsuitable, marginal and optimal) representing 0%, 15%, 25% and 60% of the sampled biomass, respectively (Figure 4).

To check for bias that may have been introduced by manually modifying the suitability matrix, we used the depth/velocity criteria shown in Figure 4 to calculate total predicted biomass for each site from the depth and velocity grids. A comparison between observed and predicted biomass shows that the generalized model reasonably predicts both bluehead sucker ($r^2 = 0.90$, $n = 11$) and flannelmouth sucker ($r^2 = 0.81$, $n = 11$) biomass at the four sites from which it was developed (Figure 5).

Habitat suitability versus discharge

To evaluate the incremental effects of discharge on species biomass, we plot the amount of unusable habitat and predicted biomass for both bluehead and flannelmouth sucker as a function of discharge. As shown in Figure 6, the area of unusable bluehead sucker habitat decreases linearly from the lowest modelled flow (1.1–2.8 m³/s) to 8.5 m³/s on the Yampa and 14.2 m³/s on the Colorado River. Predicted bluehead biomass at Lily Park, Clifton, and Corn Lake increase linearly up to 19.8 m³/s ($r^2 = 0.99$, 0.995 and 0.997, respectively) and continue to increase linearly beyond 34 m³/s, but at significantly reduced slopes. Duffy and Sevens were modelled to 17 m³/s and 24.9 m³/s, respectively and, at those sites, predicted biomass increases linearly over the entire range of modelled data ($r^2 = 0.99$ and 0.994, respectively). Area of unusable habitat for flannelmouth sucker decreases linearly from the lowest modelled flow (1.1–1.7 m³/s) up to 11.3 m³/s ($r^2 = 0.97$ –0.995), while predicted flannelmouth biomass increases linearly to 14.2 m³/s ($r^2 = 0.98$ –0.999) (Figure 6).

DISCUSSION

Using two-dimensional modelling results and meso-habitat biomass estimates, we tested the hypothesis that adult fish biomass on the Yampa and Colorado rivers could be predicted as a function of hydraulic characteristics during periods of low discharge. Significant relationships were established between depth, velocity and bluehead/flannelmouth sucker biomass. Three-dimensional plots of depth, velocity and biomass show that certain ranges of depths and velocities are associated with greater adult fish biomass than others. When data are smoothed into a regular matrix, biomass can be predicted as a function of depth and velocity. Results show good agreement between predicted and measured biomass at the meso-habitat scale for bluehead and flannelmouth sucker.

By applying a suitability class to each depth/velocity combination generated by the two-dimensional hydraulic models, and summing the predicted biomass over the entire site, we were able to generate biomass estimates for each site and discharge. Again, measured and observed biomass at the site scale was strongly correlated, though the suitability model underestimated flannelmouth biomass at the site level by nearly 20%.

Plots of predicted biomass as a function of discharge are strikingly similar between the Yampa and Colorado rivers. The Yampa and Colorado rivers have similar morphologies and the same native fish communities, yet widely different base flows and different community structures (composition and abundance). These data suggest that low summer base flows are acting to limit adult native fish biomass on the Yampa River. While we do not rule out that other mechanisms including hybridization, channel alteration, and/or water quality changes may be affecting native fish biomass on the Yampa, we can find no evidence to suggest that adult bluehead sucker and flannelmouth sucker biomass could not be increased by increasing summer base flows on the Yampa river (at least up to flows of 8.5 m³/s).

While we attempted to develop physical habitat suitability indices for roundtail chub, no relationship between roundtail chub biomass (or density) and water depth/velocity could be established. Preliminary evidence supports the hypothesis that roundtail chub biomass can be predicted as a function of habitat heterogeneity at the reach scale. Roundtail chub are predators that use different meso-habitats for different activities (patrolling, feeding, and holding) and more diverse habitats may allow roundtail chub to expend less energy travelling between suitable habitats.

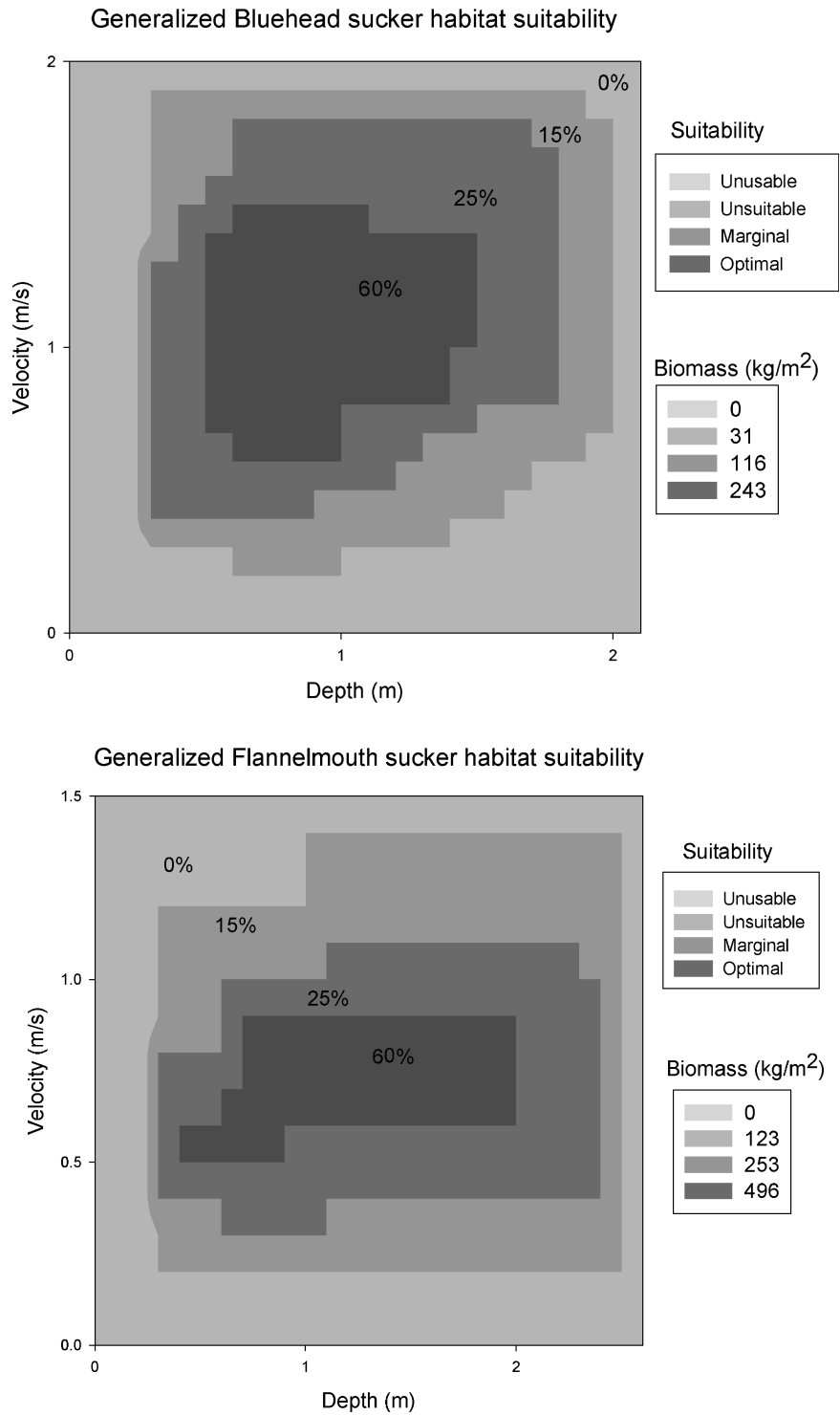


Figure 4. Generalized bluehead and flannelmouth sucker habitat suitability. Darker colors represent more suitable habitat with higher biomass estimates

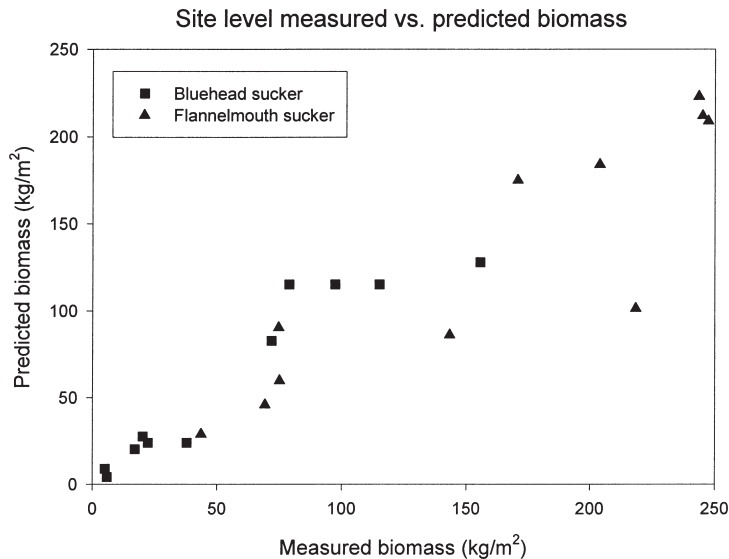


Figure 5. Measured versus predicted biomass for bluehead and flannemouth sucker based on site estimates

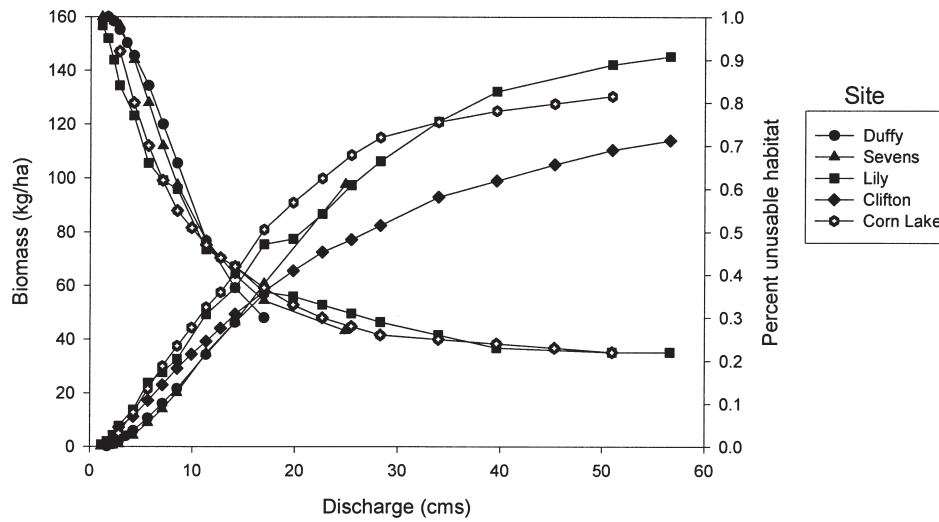
Benefits and limitations of the study approach

Biological data used in this study were collected over multiple years and sites on three different rivers. Although these data took considerable time to collect, consistency in the fish community through time suggests a strong dynamic relationship with habitat conditions. During the formulation of the suitability criteria, it became clear that species biomass (predicted as a function of depth and velocity) was consistent among sites on the Yampa and Colorado rivers (with the exception of Duffy which was significantly affected by hybridization). By combining data from the Yampa and Colorado rivers in development of the suitability criteria, we were able to incorporate a wide range of biomass estimates. Consistency in predicted biomass and habitat availability between sites and rivers suggests that the suitability indices are relatively robust and can be applied to other sites with similar morphology and fish community structure. We recognize and accept that biomass estimates may be biased towards shallower depths where electro-shocking is generally more efficient.

Two-dimensional flow models were used for calculating hydraulic variables. Modelled sites exhibited significant lateral variations in depth and velocity that could not have been accounted for with one-dimensional or quasi-two-dimensional model approximations. It is interesting to note that although depth and velocity were defined at 1 m increments both longitudinally and laterally, we found mean meso-habitat depth and velocity adequate for developing habitat suitability indices. It is reasonable to assume that mean depth and velocity could have been approximated in much less time using one-dimensional models with cross-sections spaced within and between meso-habitat units. The primary advantages of two-dimensional modelling were expressed in our ability to validate model results over a range of channel conditions, explicitly map hydraulic data, and extrapolate habitat suitability into biomass estimates by mapping suitability as a function of spatially explicit depth and velocity. Meso-habitats were chosen as the biological scale of interest because they were the smallest unit from which fish community structure could be sampled and expected to demonstrate consistency through time. Because meso-habitat units are spatially explicit (i.e. can be mapped), biomass estimates collected at the meso-habitat scale can be correlated with any other congruent spatially explicit dataset (i.e. datasets with spatial scales that are multiples of meso-habitat scale).

With IFIM, species occurrence probability distributions are developed for physical habitat variables and an assumption is made that fish biomass is correlated with microhabitat suitability. With the approach described above, relationships between biomass and physical habitat variables are generated from field measurements, and alternative hypotheses related to spatially explicit data (e.g. relationship between biomass and hydraulic variability or groundwater inputs) are readily tested. If multiple relationships exist, they can be evaluated in the context of multivariate analysis. We feel that the ability to directly evaluate relationships between any number of spatially

Predicted biomass and percentage of unusable Bluehead sucker habitat



Predicted biomass and percentage of unusable Flannelmouth sucker habitat

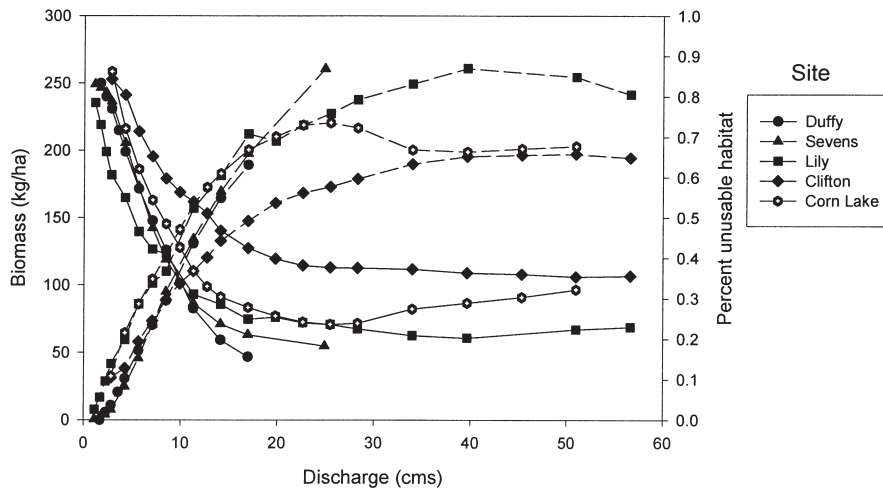


Figure 6. Biomass and percentage of 'unusable' habitat. Biomass on the left axis increases with discharge over the first 100 cfs while percent unusable habitat decreases

explicit variables (i.e. biomass, physical habitat, temperature, large woody debris, distance to tributary junctions, etc.) provides significant advantages over traditional IFIM studies.

A significant limitation of this study approach is that it cannot be used to evaluate effects of discharge on very rare species. Colorado pikeminnow (*Ptychocheilus lucius*) and razorback chub (*Xyrauchen texanus*) are both federally listed endangered species whose historic range was inclusive of the Colorado and Yampa river study sites. Unfortunately, Colorado pikeminnow and razorback chub are now so rare that few were ever caught in the study area, so we were unable to generate biomass estimates.

ACKNOWLEDGEMENTS

The Colorado Division of Wildlife under Federal Aid Project F-289 funded this study. We would like to thank Dr Craig Addley and Jennifer Ludlow at Utah State University for help with the two-dimensional modelling.

Thanks to Shannon Claeson at Oregon State University, Sara Rathburn at Colorado State University, and Gigi Richard at Mesa State College for all their support.

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