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MODELLING EFFECTS OF DISCHARGE ON HABITAT QUALITY AND DISPERSAL OF JUVENILE HUMPBACK CHUB (*GILA CYPHA*) IN THE COLORADO RIVER, GRAND CANYON

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ABSTRACT

A two-dimensional hydrodynamic model was applied to seven study reaches in the Colorado River within Grand Canyon to examine how operation of Glen Canyon Dam has affected availability of suitable shoreline habitat and dispersal of juvenile humpback chub (*Gila cypha*). Suitable shoreline habitat typically declined with increasing discharges above 226–425 m^3/s, although the response varied among modelled reaches and was strongly dependent on local morphology. The area of suitable shoreline habitat over cover types that are preferred by juvenile humpback chub, however, stayed constant, and in some reaches, actually increased with discharge. In general, changes in discharge caused by impoundment tended to decrease availability of suitable shoreline habitat from September to February, but increased habitat availability in spring (May–June). Hourly variation in discharge from Glen Canyon Dam substantially reduced the amount of persistent shoreline habitat at all reaches. Changes in suitable shoreline habitat with discharge were shown to potentially bias historical catch per unit effort indices of native fish abundance up to fourfold. Physical retention of randomly placed particles simulating the movement of juvenile humpback chub in the study reaches tended to decline with increasing discharge, but the pattern varied considerably due to differences in the local morphology among reaches and the type of swimming behaviour modelled. Implications of these results to current hypotheses about the effects of Glen Canyon Dam on juvenile humpback chub survival in the mainstem Colorado River are discussed. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: instream flow; humpback chub; Grand Canyon; Colorado River; suitable habitat; dispersal; hydrodynamic modelling; Glen Canyon Dam

INTRODUCTION

The Colorado River in Grand Canyon was impounded by Glen Canyon Dam (GCD) in 1963. Since that time, much effort has been expended to assess the downstream effects on aquatic and terrestrial resources (Valdez and Carothers, 1998). Although the range of ecological issues being evaluated is diverse, the most critical set driving potential changes to the operation of the dam relate to humpback chub (*Gila cypha*). The humpback chub is a large, warm-water, cyprinid fish endemic to the Colorado River drainage that was listed as endangered in 1967 and protected under the Endangered Species Act (ESA) in 1973. One element of the Reasonable and Prudent Alternative (RPA) of the US Fish and Wildlife Service's (USFS) Biological Opinion on the operation of GCD called for the experimental implementation of a seasonally adjusted steady flow (SASF) consisting of sustained high releases during the period of April–May, followed by low steady releases during June–October (US Fish and Wildlife Service, 1994). The low steady summer flow (LSSF) experiment conducted in the spring and summer of 2000, at an estimated cost of approximately $21 million in additionally purchased power (Palmer and Burbidge, 2001), was the first implementation of the SASF.

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In the Colorado River in Grand Canyon, nine aggregations of humpback chub have been identified. The Little Colorado River (LCR)/mainstem aggregation is the largest with an estimated population size of 3500 adult chub >200 mm total length (TL). A large portion of this aggregation moves into the LCR to spawn between March and May and then returns to the mainstem in late June–July. Their distribution in the mainstem ranges from river km 91 to 110 (Figure 1; Valdez and Ryel, 1995). Temperatures of water released from GCD are too low to support mainstem spawning and are hypothesized to severely limit larval survival (Valdez and Ryel, 1995; Converse *et al.*, 1998). Many humpback chub hatched in the LCR descend into the mainstem beginning in May (Valdez and Ryel, 1995; Robinson *et al.*, 1998). The proportion of fish leaving the LCR as larvae (<15 mm TL), young-of-the-year (YOY; <90 mm TL), or juveniles (90–200 mm TL) relative to those that remain is unknown, but it is likely to be highly variable and dependent on floods and fish densities in the LCR (Robinson *et al.*, 1998). Survival rates of YOY and juveniles that enter the mainstem are difficult to estimate; Valdez and Ryel (1995) and Robinson *et al.* (1998) suggest that fish entering at sizes <52 mm TL do not survive.

Juvenile humpback chub in Grand Canyon are highly aggregated. The majority of fish are found in the vicinity of the LCR from its confluence at river km 99 downstream to river km 136 (Valdez and Ryel, 1995). Juveniles

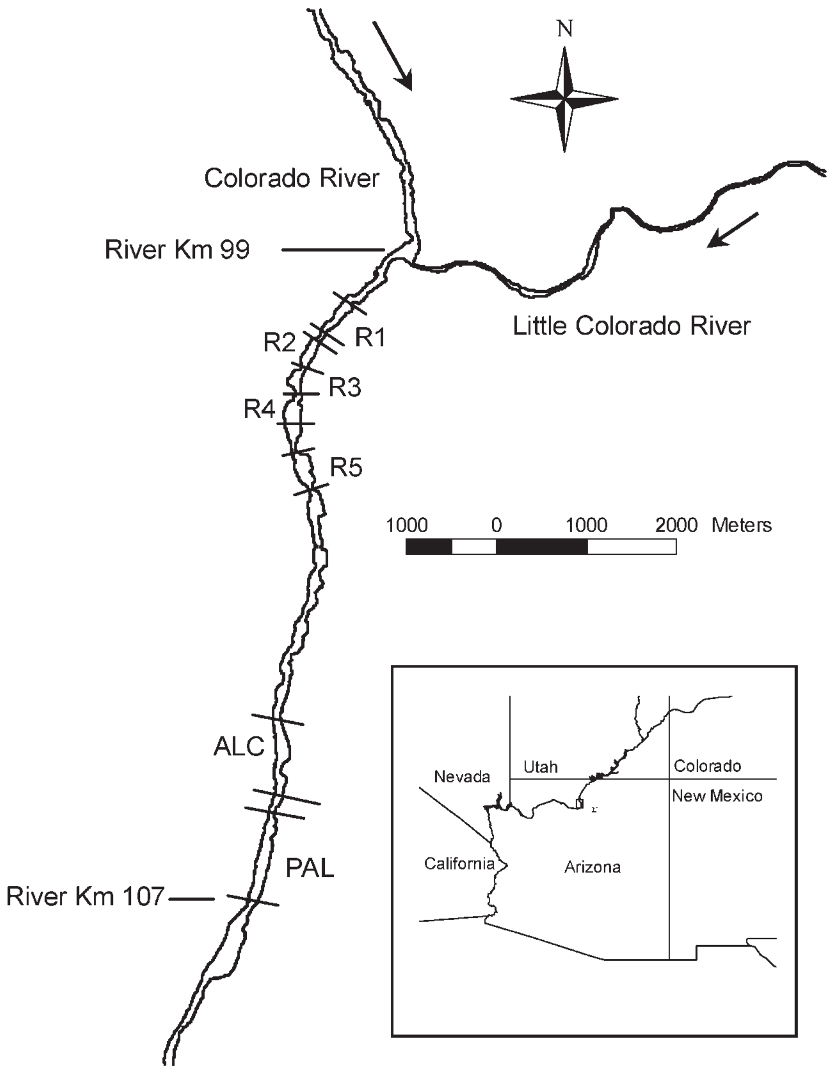

Figure 1. Map of the Colorado River in Grand Canyon near its confluence with the Little Colorado River showing study reach locations. The overall study location is shown in the box highlighted with an asterisk within the inset map

preferentially select shorelines composed of vegetation, talus, or debris fans and are found in much lower densities over cobble, bedrock, and sandy substrates (Converse *et al.*, 1998). It is hypothesized that a decrease in the frequency of low-flow periods due to dam operations has reduced suitable habitat availability and, coupled with lower water temperatures, have probably inflicted an extreme negative effect on juvenile humpback chub (Converse *et al.*, 1998). This hypothesis is a critical component of the logic used to develop the SASF regime. Valdez and Ryel (1995) also hypothesized that 'recruitment of young [chub] may be dependent on their ability to remain and mature in habitats required by adults', that is, in habitat within relatively close proximity to the LCR. Thus, differences in discharge and water temperatures in the mainstem during the dispersal period could potentially affect the ability of YOY and juvenile chub to find and remain in their preferred habitats in the mainstem downstream of the LCR. Young fish dispersed further downstream are assumed to have much lower survival rates because of reduced habitat availability and large predator populations and a reduced likelihood of being able to migrate back to the LCR to spawn if they do survive as juveniles.

Numerical habitat models have been widely used to predict the effects of flow regulation on fish habitat (Reiser *et al.*, 1989), but such models have not been used to date to evaluate hypotheses related to GCD effects on humpback chub in Grand Canyon. The most commonly applied tool is the physical habitat simulation model (PHABSIM), which combines predictions of water depth and velocity from one- or two-dimensional hydraulic models with data or professional judgment on fish habitat preference to predict the potential effect of flow regulation on fish habitat quality, which is indexed by what is termed 'weighted useable area' (WUA; Bovee, 1982). The validity of modelling approaches like PHABSIM to assess instream flow requirements has been repeatedly questioned (Mathur *et al.*, 1985; Studley *et al.*, 1996; Williams *et al.*, 1999). Fish preference for depth, velocity, and substrate changes with a variety of factors including time of day, season, physical conditions (turbidity, temperature, discharge), and biological factors (food availability, predation risk). More importantly, the link between WUA and population parameters such as abundance, growth, survival, or recruitment has never been well documented. These weaknesses apply to all numerical habitat models, including those based on two-dimensional flow fields (e.g. Guay *et al.*, 2000) or that include more details about biology (e.g. individually-based models; see Van Winkle *et al.*, 1997).

Managers and scientists involved in the decision-making process on the future operation of GCD are faced with managing releases to meet existing water delivery agreements, hydropower generation, and the needs of environmental resources in Grand Canyon, including threatened and endangered species. Although a conceptual model for the effects of flow on humpback chub has been articulated (Walters and Korman, 1999; Walters *et al.*, 2000), there is not sufficient information to develop a numerical model to help design experimental flow regimes. The Glen Canyon Dam Adaptive Management Program has a mandate to evaluate flow regimes and other management actions by monitoring changes in a wide range of resources, including the abundance and distribution of native and exotic fish species. The well-publicized experimental flood in 1996 and the LSSF experiment conducted in 2000 are the most notable experiments conducted to date; however, there was also considerable experimentation with steady flow regimes in the early 1990s. A new experimental flow regime, which includes increases in daily flow fluctuations over the winter to disadvantage non-native rainbow and brown trout, was implemented in 2003. Managers are well aware that it will take years, if not decades, before the native fish responses to alternative flow regimes are potentially known. In the short term, the ESA essentially requires that the Bureau of Reclamation design and implement the experimental flow regime identified in the Biological Opinion. In the face of this management dilemma, the use of a numerical habitat model seems warranted, at least as a first-cut tool to examine some of the assumptions regarding juvenile chub habitat availability and dispersal that are currently being used in a qualitative way to design these experimental flow regimes (e.g. Valdez *et al.*, 1999).

Prediction of changes in suitable habitat as a function of discharge from GCD is also relevant to the interpretation of results from the sampling programmes being used to monitor fish populations in Grand Canyon. A significant component of current and previous monitoring consists of measuring catch per unit effort (CPE) at index sites throughout the canyon. In Grand Canyon, CPE for boat electrofishing is computed as the catch divided by the number of seconds of electofishing effort. The use of CPE to index abundance relies on the assumption that catch rates are proportional to stock size (N):

$$\mathrm{CPE} = qN \tag{1}$$

where q is the catchability coefficient (Hilborn and Walters, 1992). Catchability can be defined as the proportion of the stock caught by one unit of effort, or more explicitly as the ratio of the area swept by the sampling gear (a) to the area over which the fish are distributed (A), that is, $q = a/A$. The majority of sampling in Grand Canyon for juvenile fish is conducted in relatively shallow and low-velocity habitat, and the area swept at each site (a) is relatively constant among trips. The area over which fish are distributed (A), however, will presumably increase with increases in the amount of suitable habitat. If we assume that reductions in discharge from GCD increase the amount of low-velocity shallow habitat and, hence, increase the amount of suitable habitat, we would expect a/A ($= q$) to decrease. In this situation, CPE would decline proportionally with the increase in A even though stock size remained unchanged. The use of a numerical habitat model to estimate the degree of change in suitable habitat area is warranted, even if the objective is simply to examine the potential for changes in discharge to introduce bias and variation in CPE data.

In this paper, we use a two-dimensional hydrodynamic model (Wiele *et al.*, 1996) to examine how operation of GCD has affected the availability of suitable habitat and the dispersal of young native fish. We apply the model to seven reaches in the critical humpback chub rearing area immediately downstream from the LCR to develop a series of relations between the availability of suitable habitat and discharge. The effect of impoundment and historical operating regimes on habitat is evaluated by comparing monthly statistics of suitable habitat availability computed from the habitat–discharge relations and hourly discharge data. We also quantify the amount of suitable habitat that persists over a typical 24-hour period, and examine how it changes in response to historical differences in the amount of variation in hourly discharge. We compute changes in suitable area that occurred during fish sampling trips conducted in 1993 to examine the potential for discharge-driven changes in suitable habitat area to introduce bias and variation into CPE data. Finally, we use a particle-tracking algorithm to examine how discharge and assumptions about swimming behaviour affect the ability of young fish to remain in critical rearing areas downstream from the LCR. We discuss our results in the context of current hypotheses about humpback chub juvenile survival in the Colorado River and operational flow regimes from GCD.

STUDY SITE

Hydrodynamics and habitat availability were modelled in seven study reaches in the mainstem Colorado River below the confluence of the LCR (Figure 1). The spatial distribution of reaches that we modelled has considerable overlap with the range of the LCR/mainstem humpback chub aggregation (river km 91–110; Valdez and Ryel, 1995). Our study reaches cover 3.6 km of this habitat (19%) between river km 99 and 107 (Table I).

The complex flow patterns in the study reaches result from the irregular bedrock channel, large-scale blocks along the channel sides, and debris fans (Figure 2). Debris flows and floods from streams in side canyons (Howard and Dolan, 1981; Schmidt, 1987; Webb *et al.*, 1989; Schmidt and Graf, 1990; Schmidt and Graf, 1990; Melis *et al.*, 1994; Schmidt and Rubin, 1995) form debris fans that partially constrict the channel, and recirculation zones are generated in the lee of the channel constrictions. Deep holes typically occur in the bedrock channel downstream from debris fans. The spacing between debris fans is controlled largely by bedrock structure (Dolan *et al.*, 1978).

Table I. Length and wetted areas at two different discharges for model reaches

Reach	Length (m)	Wetted area ($m^2 \times 10^3$)	
		84 m^3/s	907 m^3/s
R1	498	39	57
R2	328	34	41
R3	258	26	32
R4	253	25	41
R5	448	68	78
ALC	890	83	117
PAL	993	111	165
Total	3668	386	531

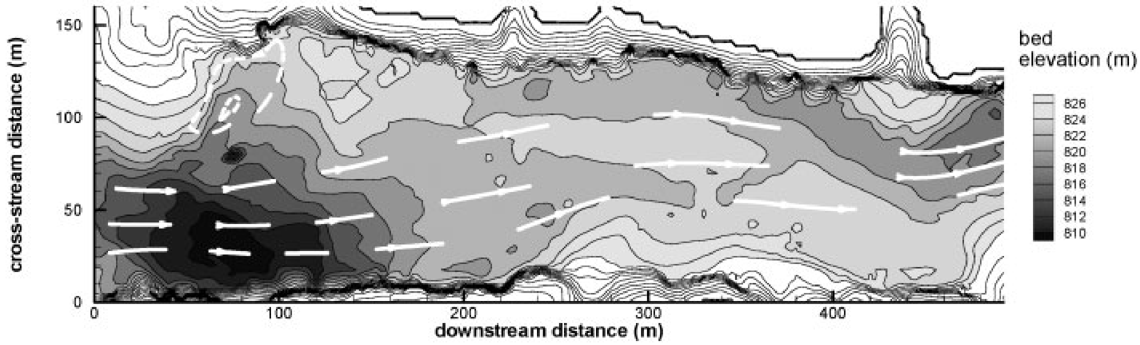

Figure 2. Shaded contour plot of the first study reach (R1). Most of the study reaches have a similar shape, with recirculation zones in the lee of debris fans, a deep hole in the bedrock channel downstream from the reach inlet, and irregular banks. Contour interval is 2 m. Dashed lines are stream traces. Length of each dash represents travel distance in 30 s. Flow is from left to right

The bed of the Colorado River in Grand Canyon is about 60% bedrock, talus blocks, or boulders, with sand deposits primarily in the recirculation zones and, to a lesser degree, along the channel sides (Howard and Dolan, 1981; Wilson, 1986; Schmidt and Graf, 1990). Each of the study reaches, with the exception of the Above Lava-Chuar (ALC) reach, is bounded by rapids and has a recirculation zone near the reach inlet (Figure 2). The ALC reach is bounded on the upstream end by a narrow part of the channel that expands too gradually to form a rapid. A debris fan on the east side of the river (river left) midway through the ALC reach forms a constrained recirculation zone. The reaches vary in length from 0.25 to 1 km, with roughly proportional differences in wetted area (Table I).

METHODS

Our methods are described in four sections. First, we describe the hydrodynamic model used to predict two-dimensional fields of depth and velocity under a range of discharges in each study reach. Second, we describe our methods for developing maps of shoreline type so that our index of suitable habitat can be stratified by cover type. Third, we summarize how our indices of suitable habitat availability are computed and the analyses used to evaluate the effects of impoundment and alternative operating regimes. Finally, we describe the particle-tracking algorithm used to simulate the dispersal of young fish.

Hydrodynamic model

The topographic data used by the hydrodynamic model consist of combined sets of bathymetric measurements taken from hydrographic surveys and contours developed photogrammetrically from aerial photographs for elevations above the water surface at the time of the hydrographic surveys (Wiele *et al.*, 1996). Computational grids representing 6.25 m^2 (2.5 m per side) were derived from these combined data.

The hydrodynamic model is the flow component of a two-dimensional flow and sand transport model that has been applied to reaches of the Colorado River in the Grand Canyon to study depositional processes and to predict the response of sandbars to dam operations and sand supplied by tributary floods (Wiele *et al.*, 1996, 1999; Wiele, 1997). Model predictions of sand erosion and deposition have agreed well with cross-sections measured before and after a tributary flood (Wiele *et al.*, 1996) and with daily bathymetric measurements during a high dam release (Wiele, 1997; Wiele *et al.*, 1999). Accurate predictions of erosion and deposition provide a sensitive test of the accuracy of calculated flow fields. Flow depths in the model are largely determined by the downstream boundary condition for the flow component of the model, which specifies the water surface elevation for the modelled discharge. The flow model solves a combined form of the vertically averaged momentum and continuity equations using the finite difference method of Casulli (1990). The local friction coefficient is derived from the logarithmic velocity profile (Keulegan, 1938) and the roughness parameter, z_0, is related to the measured deviations of the bed around the smoothed gridded bed topography. Details of the model can be found in Wiele *et al.* (1999).

The flow and sand transport model uses a simple turbulence closure to approximate the vertical structure of the velocity profile. This method does not account for regions with abruptly changing bed topography where the assumption about the flow structure is violated. The regions where the flow patterns are more complicated than is represented by the use of a vertical velocity profile based on a turbulence closure tend to occupy a small part of the channel and have not had a significant effect on the calculations of erosion and deposition. For this study, we have neglected the vertical structure of the flow and used only the vertically averaged velocity. With the logarithmic velocity profile used in the model, the velocity in the upper 80% of the flow is nearly constant. The main compromise with our approach is in neglecting the velocity structure in the lower 20% of the flow. The overall channel shape in our study reaches is fixed by bedrock, large talus blocks, and debris fans that are stabilized by cobbles and boulders that are rarely transported by dam-controlled flows. We modelled one channel shape in each of our study reaches, although channel shape, and consequently flow fields, can be altered by changes in the volume and location of sand deposits. Comparisons of area of favourable habitat with differences in discharge could be influenced by variations in sand deposition within the study reaches, but relative changes between reaches are likely to be less sensitive to variations in sand deposition. Historical comparisons may be complicated by the variability in sand deposits in the low-velocity zones as a result of the decreased sand supply after the closure of Glen Canyon Dam. The difference between pre- and post-dam sand supply in our study reaches is partly mitigated, however, by their proximity to the Little Colorado River (Figure 1), one of two major sand-contributing tributaries. All study sites are located within 8 km below the confluence with the Little Colorado River.

Mapping of shoreline types

Field-surveyed bathymetric and shoreline topographic data (Hazel *et al.*, 2000) were combined with photogrammetrically generated contour data (US Bureau of Reclamation, 1990). A triangulated irregular network (TIN) surface model was created using the Delauney method of triangulation, implemented by ARC/INFO (Environmental Systems Research Institute, Inc., 1991). The TIN surface was then interpolated using a bivariate quintic interpolation scheme in order to generate 6.25 m^2 resolution grids. The interpolated surfaces were then combined with riparian vegetation maps (US Bureau of Reclamation, 1990) established on the basis of elevation, vegetation density, and surficial geology (Schmidt *et al.*, 1999). The mapping units of these data sets were merged and reclassified to match the six shoreline types used by Converse *et al.* (1998) to describe the habitat preference of juvenile humpback chub in Grand Canyon: bedrock, cobble, debris fan, sand, talus, and vegetation.

Suitable habitat

We computed the amount of total suitable habitat by summing the total wetted area of each study reach where velocity was less than or equal to a critical value of 0.25 m/s. The amount of suitable shoreline habitat was computed by placing an additional constraint that depth was less than or equal to 1 m. The amount of total suitable habitat and suitable shoreline habitat was computed for each study reach for nine discharges (Table II).

Table II. Significance of nine discharge levels used to develop habitat–discharge relationships

Discharge (m^3/s)	Significance
84	Annual average minimum pre-dam flow
141	Nightime minimum under current operations
226	Daytime minimum under current operations
425	Approximate average post-dam flow
566	Typical high operating flows
907	Approximate powerplant capacity Glen Canyon Dam
1272	March–April 1996 experimental flood
2123	Exceeded in 28% of years between 1922 and 2000
2830	Exceeded in 13% of years between 1922 and 2000

The maximum velocity criterion we used to define suitable habitat is consistent with numerous field observations and laboratory studies on humpback chub. Average and maximum velocities used by YOY chub (21–74 mm TL) in the upper Colorado River were 0.06, and 0.30 m/s, respectively (Valdez *et al.*, 1990). Laboratory studies of 30–100 mm YOY chub at 14°C, a near-maximum summertime temperature in the mainstem downstream of the LCR (Valdez and Ryel, 1995), measured sustained swimming speeds of 0.2–0.4 m/s and cruising speeds of 0.1–0.2 m/s (Bulkley *et al.*, 1982). YOY and juvenile chub in Grand Canyon have been sampled in velocities of up to 0.1 m/s in talus habitats, 0.2 m/s in debris fan, sand beach, and vegetated bank habitats, and 0.6 and 0.3 m/s in cobble bar and bedrock habitats, respectively (Converse *et al.*, 1998). The 0.25 m/s criterion we used is slightly above the maximum juvenile humpback chub cruising speed measured in the laboratory and the typical velocity from which fish were sampled in their preferred habitats. We examined the sensitivity of the habitat availability–discharge curves predicted by the model to changes in the velocity criterion by recomputing the habitat indices under a series of velocity criteria from 0.05 to 0.25 m/s. Within-site correlations in habitat availability based on the different criteria were then examined.

To compute historical changes in suitable shoreline habitat, we used the 1921–2000 continuous discharge record computed from stage records and stage–discharge relations from the US Geological Survey (USGS) Colorado River at Lees Ferry gauging station (09380000) located 99 km upstream from the LCR confluence (digitized 1922–1986 records supplied by D. Topping, USGS, written communication, 2000; the 1921–1986 data are available from ftp.gcmrc.gov; the 1987–2000 data were provided by the USGS Arizona District office). The continuous Lees Ferry record is ideal for assessing habitat change in a system where power-load following causes large variation in discharge over the course of a day. A corresponding habitat value for each discharge observation was computed by linear interpolation using the site-specific suitable shoreline habitat–discharge relations. A daily mean habitat value was then computed as a time-weighted average of the instantaneous values. Mean monthly habitat values and 95% confidence limits, based on the variation in monthly averages among years, were computed for the pre-dam (1922–February 1963) and post-dam (March 1963–2000) periods. One-way analysis of variance (ANOVA) was used to test for significant differences among monthly means between pre- and post-impoundment periods. In addition, we computed mean monthly habitat values for particular periods of the post-dam record to assess specific operating regimes (Table III).

Historical changes in GCD operations have resulted in dramatic differences in the extent of daily variation in discharge. There is evidence that the persistence of low-velocity habitats over short time scales affects survival rates of young fish (Bowen *et al.*, 1998; Freeman *et al.*, 2001). Valdez and Ryel (1995) hypothesized that hourly

Table III. Summary of Glen Canyon Dam (GCD) operating regime characteristics compared in our analysis. The pre-dam period of record used was from 1922 to February 1963. Note that the maximum daily flow fluctuation under 'Interim' and MLFF operating regimes is dependent on the monthly release volume from GCD

Operating regime	Period	Years of Lees Ferry record used for analysis	Minimum flow (m^3/s)	Maximum flow (m^3/s)	Maximum daily flow fluctuation, m^3/s (GCD monthly release volume, $m^3 \times 10^6$)	Ramping rate ($m^3/s/h$)
No action	1963–1990	1987–1989	25 (winter) 28 (summer)	892	<864	Unlimited
Interim flows	1991–1995	1993	141 (day) 226 (night)	566	141 (<740) 170 (740–987) 226 (>987)	42 (downramp) 71 (upramp)
Modified low fluctuation flows (MLFF)	1996–present	1997–1999	141 (day) 226 (night)	708	141 (<740) 170 (740–987) 226 (>987)	42 (downramp) 113 (upramp)
Low summer steady flow experiment (LSSF)	May–Sept. 2000	May–Sept. 2000	226	226	0	0

variation in discharge below Glen Canyon Dam results in 'destabilization' of nearshore habitats used by native fish that could have a negative effect on mainstem survival. We quantified the relative extent of this destabilization between reaches by determining the area of suitable habitat that was stable across typical daily ranges in discharge. To do this, we first computed the average minimum and maximum monthly discharges under specific operating regimes (Table III) as measures of the daily variation in discharge. We then computed the locations of suitable habitat in each study reach that were present at both the average minimum and maximum monthly discharges. The total area of this common habitat is referred to as the amount of 'persistent suitable habitat'.

To evaluate the effects of discharge-driven changes in suitable habitat area on CPE data, we queried the Grand Canyon Monitoring and Research Center fisheries database (GCMRC, Flagstaff, Arizona, unpublished data) to return the dates and times of all electrofishing sampling events that occurred in 1993 within the upstream and downstream range of our modelling sites (river km 99–107). We selected 1993 because it was a year of intensive study when many samples were collected during a period when hourly variation in discharge was relatively small (Table III). Our analysis, therefore, provides a near-minimum estimate of the additional bias and variation in CPE data resulting from changes in discharge. To estimate the discharge during each of the 190 unique date–time sampling events that were returned from the database, we routed the relevant portions of the 1993 Lees Ferry discharge record to the upstream limit of sample sites (river km 99) using a one-dimensional model of diurnal discharge wave propagation (Wiele and Griffin, 1997). The one-dimensional model computed the length of time for a discharge wave measured at the Lees Ferry gauge to travel downstream to the LCR confluence, a requirement to determine the discharge at the time of each sampling event. We then generated a frequency histogram of the number of sampling events by discharge interval and compared it to the predicted changes in suitable shoreline habitat area over the same intervals. The potential for large, discharge-driven variation in CPE data was identified by the presence of a significant number of CPE measurements collected across a discharge range where the predicted change in suitable shoreline area was large.

Dispersal

A particle-tracking algorithm was used to simulate the dispersal of fish out of each study reach under a range of discharges. We began each simulation by randomly placing 500 particles within the wetted perimeter of each reach. The movement of each particle, predicted on a 0.5 s timestep, was predicted from the cross-stream and downstream velocity vectors generated from the hydrodynamic model. A bilinear interpolation program (Press *et al.*, 1992) was used to compute the velocity vectors at the particles' positions at each timestep on the basis of their distance to the four nearest surrounding nodes of the hydrodynamic model grid. Particles were given a swimming behaviour and speed (Table IV) to evaluate the effects of swimming ability on downstream dispersal. The passive behaviour simulated the dispersal of larval fish while the active behaviours simulated the movement of young-of-the-year and juvenile fish. The distance and direction of movement for each timestep were calculated as the vector sum of current velocities and swimming speeds in cross-stream and downstream directions.

To quantify the ability of a reach to retain fish at a specific discharge, we computed the percentage of 500 particles that remained in the study reach after 100 min of simulation time had elapsed. Retention rates were computed for all swimming speeds and behaviours (Table IV) in each of the seven study reaches across nine discharges (Table II).

Table IV. Summary of swimming behaviours and speeds used for simulating dispersal of larval, young-of-year, and juvenile humback chub

Behaviour	Description	Swimming speed (m/s)
Passive	Drifting particle, no behaviour	0
Rheotactic	Particle attempts to move in cross-stream direction towards slower current	0.1 and 0.2
Geotactic	Particle attempts to move in cross-stream direction towards closest bank	0.2
Upstream	Particle attempts to move in upstream direction	0.2

RESULTS

Response of habitat availability to discharge

Total suitable shoreline habitat typically declined with increasing discharge; however, the response varied among reaches and depended on local morphology (Figure 3). Reaches ALC, R1, and R4 showed the greatest declines between 226 and 425 m^3/s, while R2 and R5 showed the greatest declines at a lower discharge range of 84–141 m^3/s. Some reaches were relatively insensitive to changes in flow (e.g. R3, R5), whereas others (ALC, R1, and R4) were very sensitive. The morphology of the insensitive reaches is dominated by large fans creating large eddies downstream. These fans have a steep profile that maintains the eddies, and therefore the availability of low-velocity habitat, as discharge is increased. At very high discharges (e.g. 2830 m^3/s), however, the fans eventually are overtopped leading to the loss of habitat with suitable velocities. In contrast, a very sensitive reach such as R4 has a relatively low profile fan that is overtopped at discharges of 425 m^3/s and higher. ALC has a morphology that is not dominated by debris fans. Low discharges expose a large mid-channel cobble bar creating low-velocity habitat upstream and downstream from the bar and in the side channel created by the bar. As discharge increases, this low-velocity area is progressively reduced until all that remains is a thin ribbon of suitable habitat adjacent to the banks. As a result, ALC had a consistent decline in suitable habitat availability with increasing discharge.

The Palisades (PAL) reach showed a unique bimodal response where total suitable shoreline habitat was highest when discharges were either low or high, with the lowest habitat values occurring at intermediate discharges of 907–1272 m^3/s. This bimodal response is a result of the channel shape, which differs from the shape of other study reaches in several key attributes. Unlike the banks in the other reaches that tend to be steep on both sides of the channel, the bank along river left in the PAL reach flattens to a low angle above the stage associated with 1272 m^3/s. As a result, the flow at discharges above 1272 m^3/s expands into this area creating a large amount of suitable habitat. Below 1272 m^3/s, the flow is relatively confined resulting in a smaller area of suitable habitat than at higher discharges down to about 907 m^3/s. Below 907 m^3/s, discharge is low enough to create a considerable area of suitable habitat along the banks of the main channel.

The effect of discharge on the availability of suitable shoreline habitat, when stratified by substrate type, also was highly variable among reaches (Figure 3). In the ALC reach, the availability of suitable shoreline habitat decreased with increasing discharge, yet debris fan and talus habitat stayed relatively constant, and the amount of vegetated shoreline habitat increased considerably, reaching a maximum at 1272 m^3/s. R2 and R5 showed relatively large changes in total suitable shoreline habitat between 84 and 141 m^3/s, yet the amount of suitable habitat over debris fans or talus increased or was constant across these discharges.

The relative change in total suitable habitat due to increasing discharge was remarkably similar across reaches, with near-minimum values reached at 425 m^3/s (Figure 4a). The large gain in habitat at the lowest discharges reflects a typical cross-sectional response where the largest decreases in velocity occur at the low end of the discharge range. In contrast, change in the area of suitable shoreline habitat to variations in discharge was much more variable across reaches (Figure 4b), suggesting it was much more sensitive to local differences in morphology.

The shape of the response of habitat availability to discharge was insensitive to the value of the velocity criterion used to quantify suitable habitat. Reducing the value of the velocity criterion from the base value of 0.25 m/s reduced the amount of suitable habitat predicted at a given discharge, but the relative pattern across discharges remained unchanged. On average, the trend in habitat availability with discharge based on one velocity criterion could explain 95% of the habitat trend based on a different criterion.

Effects of Glen Canyon Dam on discharge and habitat availability

Construction and operation of GCD caused considerable changes in the magnitude and shape of the hydrograph of the Colorado River in Grand Canyon (Figure 5a). Impoundment has reduced average flows in the months of May and June from about 1500 to 400 m^3/s and has increased the annual minimum flows (based on monthly averages) from 226 to 300 m^3/s. Seasonal variation in discharge since impoundment has been greatly reduced. Impoundment has resulted in a large increase in base flows; in the pre-dam era, flows in excess of 226 m^3/s occurred 50% of the time, whereas in the post-dam era, they occur at a frequency of greater than 70% (Figure 5b).

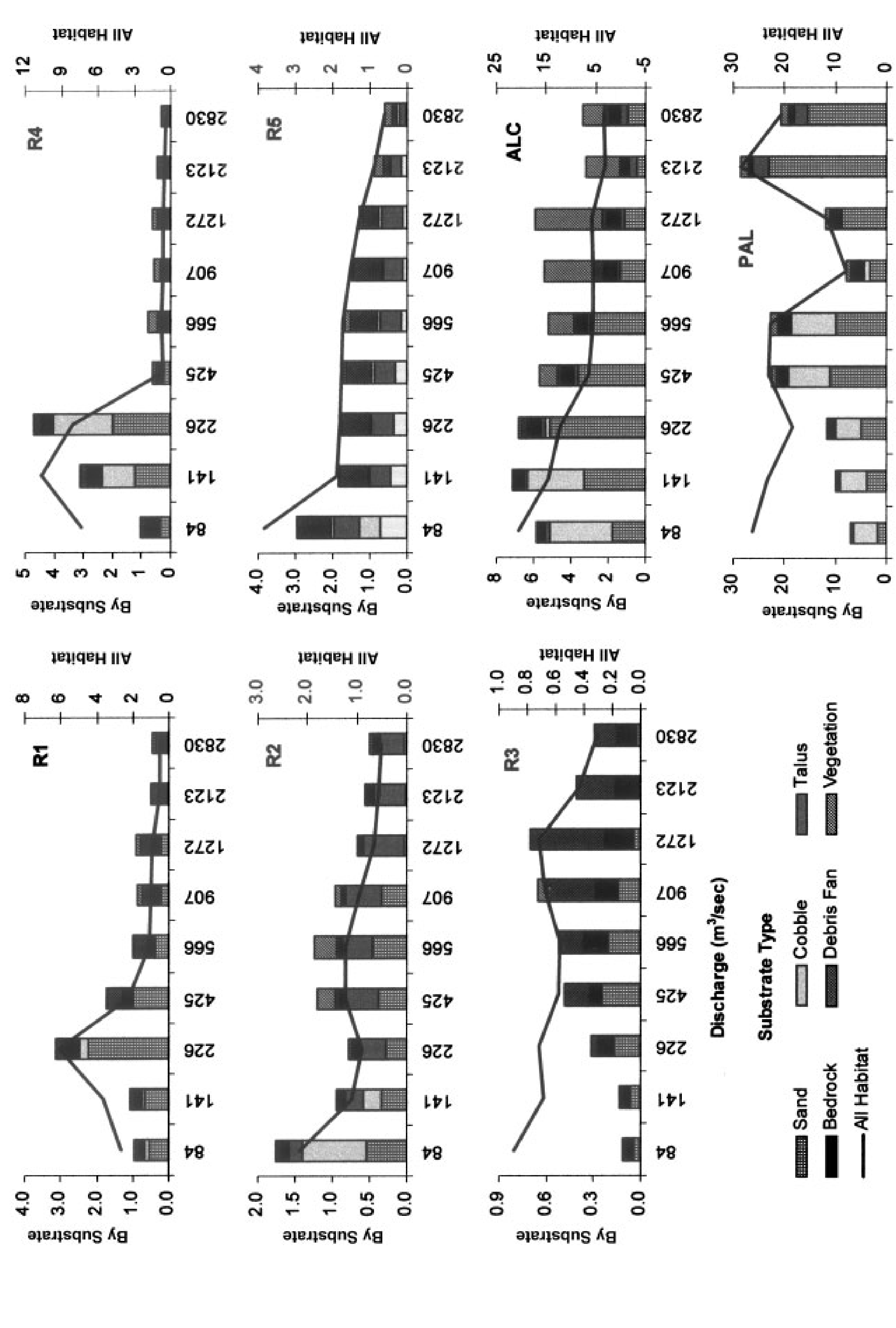

Figure 3. Effect of discharge on availability of suitable shoreline habitat ($m^2 \times 10^3$). Solid lines show total amount of shoreline habitat (right-hand y-axis) and bars show amount of shoreline habitat stratified by substrate type (left-hand y-axis). Note that total habitat includes the unmapped substrate type and is therefore greater than the sum of habitat across the types shown

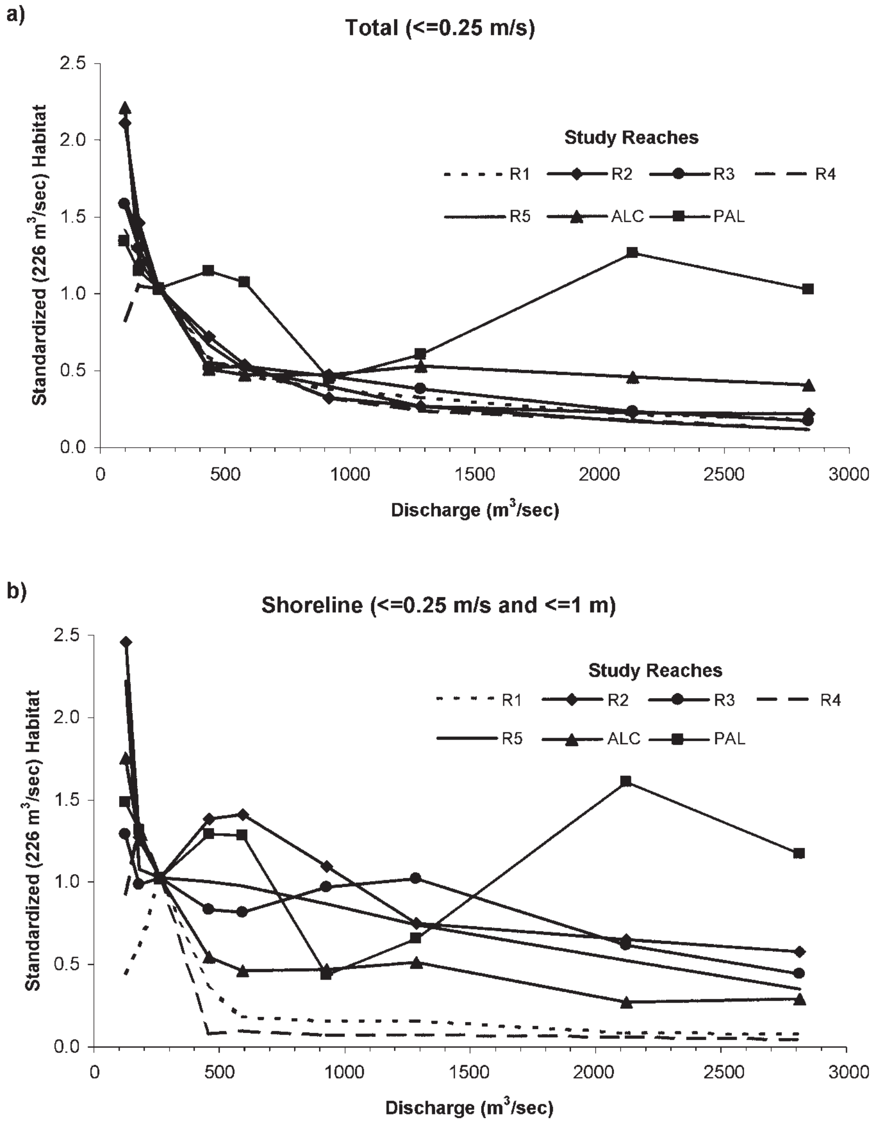

Figure 4. Effect of discharge on relative change in availability of suitable total (a) and shoreline (b) habitat. Units are standardized by reach-specific values at 226 m^3/s to facilitate comparison among study reaches

Seasonal trends in the availability of shoreline habitat in the pre-dam era were highly variable among reaches (Figure 6). There were large seasonal fluctuations among sensitive reaches (e.g. ALC, R1, and R4) but relatively little fluctuation at insensitive ones (e.g. PAL, R2, R3, and R5). These differences were driven by the site-specific sensitivity of suitable shoreline habitat availability to discharge (Figure 4b). The alteration of the hydrograph caused by impoundment (Figure 5) resulted in considerable change in the seasonal pattern of shoreline habitat availability, but again, this response was highly variable among reaches (Figure 6, Table V). In general, dam operations have decreased the availability of suitable shoreline habitat relative to the pre-dam era during low-flow months (August–February) but have increased habitat availability in the spring (May–June). When averaged across sites, impoundment significantly ($\alpha \leqslant 0.05$) decreased suitable shoreline habitat for about six months of the year and increased it for three months. Significant differences between pre- and post-dam suitable habitat availability by month were more common at the sensitive sites. At R2, most of the significant impoundment effects were positive (Table V) because of the presence of a secondary peak in suitable habitat availability at 425–566 m^3/s (Figure 4b), a discharge range that has become more prevalent since impoundment.

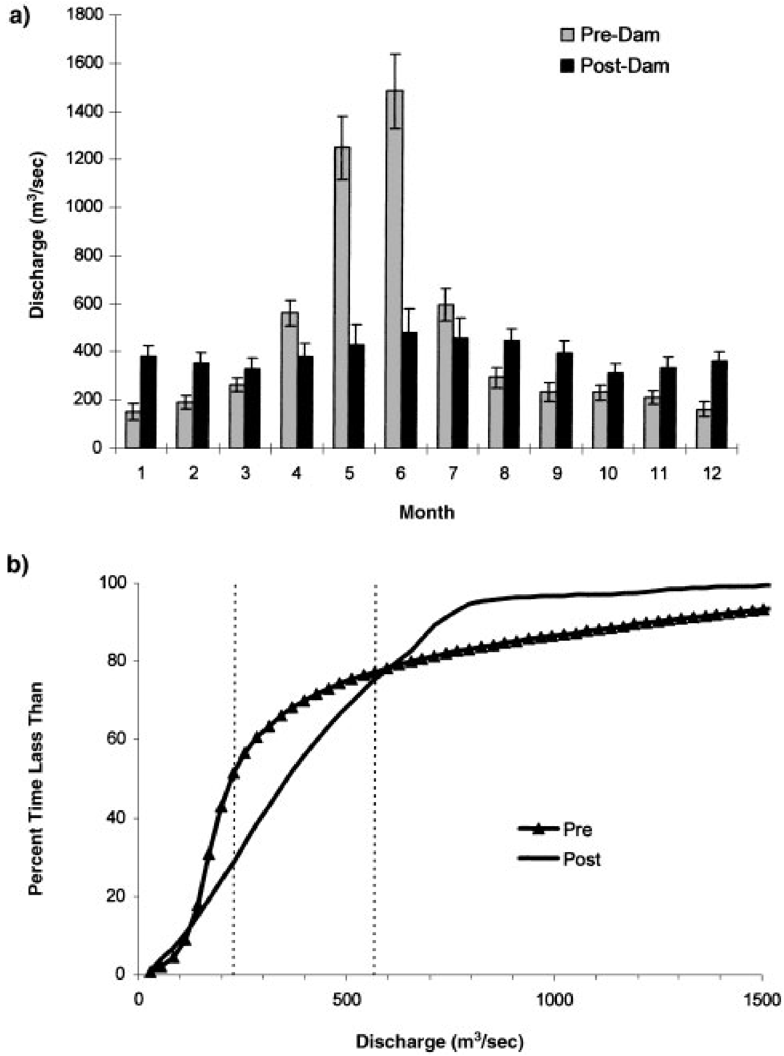

Figure 5. Mean monthly discharge and 95% confidence limits for pre- and post-dam periods (a) and flow exceedance curves (b) measured at the Lees Ferry gauge. Dashed vertical lines highlight discharges of 226 and 566 m^3/s

Historical changes in dam operations have influenced seasonal patterns in suitable shoreline habitat (Figure 7). Differences in daily average suitable shoreline habitat area across operating regimes were greatest at the sensitive sites (ALC, R1, R4). The modified low fluctuating flow (MLFF) alternative restricted the diurnal range of discharge from GCD (Table III, Figure 8). This in turn reduced both the frequency of low flows and the monthly variation in low-flow frequency relative to the ‘no action’ alternative, resulting in lower but consistent suitable shoreline habitat availability. Greater suitable shoreline habitat availability under the ‘no action’ alternative relative to MLFF could also be caused by higher discharge in the years used to assess the latter regime (1996–1999). A comparison of the two regimes in months with similar average discharges (e.g. January), however, still showed that the ‘no action’ alternative produced more suitable shoreline habitat. The effects of the LSSF experimental steady flow in the spring and summer of 2000 (May–September) on suitable shoreline habitat availability is evident at the sensitive sites. The reduced flow resulted in a large improvement in suitable shoreline habitat availability in June, July, and August relative to other operating regimes and the pre-dam period. The LSSF experiment did not produce a ‘natural’ seasonal pattern in suitable shoreline habitat availability that mimicked the pre-dam era. Instead, it generated high suitable shoreline habitat availability in June and July, which, in the pre-dam period, were months when suitable shoreline habitat availability was lowest.

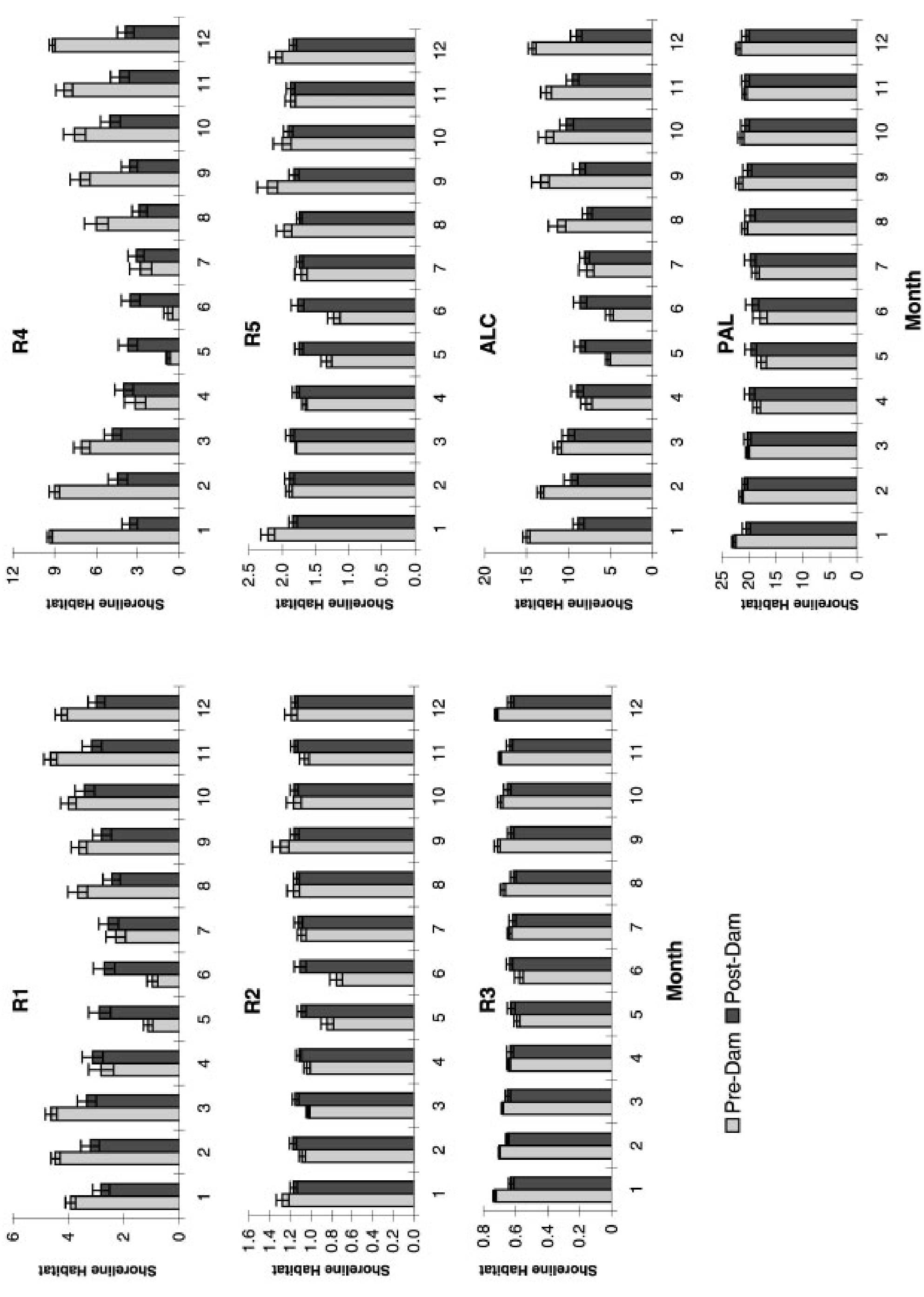

Figure 6. Mean monthly suitable shoreline habitat availability ($m^2 \times 10^3$) and 95% confidence limits for pre- and post-dam periods computed from reach-specific suitable shoreline habitat–discharge relations (solid lines of Figure 3) and discharge measured at the Lees Ferry gauge

Table V. Effects of dam operations on the availability of suitable shoreline habitat for the seven study reaches. Plus and minus signs denote whether operations have increased or decreased suitable shoreline habitat availability relative to pre-dam conditions. The number of symbols denotes the significance level of the operations effect[a]

	R1	R2	R3	R4	R5	ALC	PAL
January	−−−	−−	−−−	−−−	−−−	−−−	−−−
February	−−−	+++	−−−	−−−		−−−	
March	−−−	+++	−−−	−−−	++	−−	
April		+++			+++	+	+
May	+++	+++	+	+++	+++	+++	++
June	+++	+++	++	+++	+++	+++	
July							
August	−−−		−−−	−−−	−−−	−−−	
September	−−−	−−	−−−	−−−	−−−	−−−	−−
October	−		−−	−−−		−−−	
November	−−−	++	−−−	−−−		−−−	
December	−−−		−−−	−−−	−−−	−−−	−−
No. positive effects	2	6	2	2	4	3	2
No. negative effects	8	2	8	8	4	8	3

[a] +, −, $p \leqslant 0.05$; ++, −−, $p \leqslant 0.01$; +++, −−−, $p \leqslant 0.001$.

The large changes in the extent of daily variation in discharge under different operating periods (Figure 8) had a strong effect on the amount of suitable habitat area that persisted across typical daily discharge ranges (Table VI). We used September as an index month for this analysis because the average daily discharge range was well represented by the discharges that we modelled in this study (Table II), and with discharge ranges seen in other months. During the pre-dam period, the daily range in discharge for September was minimal, increased to 226–566 m^3/s during the 'no action' period, and was reduced to 425–566 m^3/s under the current operating regime (MLFF). Persistent suitable shoreline habitat was almost completely eliminated in the post-dam period under the 'no action' regime at all sites. The reduction in daily variation in discharge under the MLFF regime resulted in the persistence of small amounts of suitable habitat at all reaches except PAL, where the increase was much larger. The amount of persistent total suitable habitat in the pre-dam period was reduced by 60–90% under the 'no action' regime at all study reaches and by 50–70% under the MLFF regime for all reaches except PAL, where the reduction was only 20%.

Effects of discharge and catch per unit effort indexing

The potential for discharge changes to increase variation in CPE data was highly variable among reaches. The 190 electrofishing samples taken in 1993 between river km 99 and 107 were collected over a discharge range of 175 to 550 m^3/s, but more than 80% were collected over a narrower range of 200 and 400 m^3/s (Figure 9). In the worst case (R4), the amount of suitable shoreline habitat area decreased fourfold over the 200–400 m^3/s range. Under the assumption of an inverse linear relationship between suitable habitat area and catchability (Equation 1), this change implies that CPE densities taken at 400 m^3/s could be fourfold greater than those taken at 200 m^3/s. Reaches R1 and ALC showed potential for variations in CPE densities as high as two- and 1.5-fold, respectively, over this same discharge range, whereas R3 and R5, where suitable shoreline habitat area was relatively insensitive to changes in discharge, showed little potential for increased variability even at the extreme ends of the discharge range where sampling was conducted. Reaches R2 and PAL showed a limited potential for CPE estimates to decrease at higher discharges because of increases in suitable shoreline habitat area.

Dispersal

The ability of a reach to retain particles tended to decline with increasing discharge, but the pattern varied considerably owing to differences in the morphology among reaches and the swimming behaviours that were modelled (Figure 10). In general, the more effective the behaviour at moving a particle to the low-velocity area near the banks, the higher the retention rate. Thus, a geotactic behaviour, where all the swimming velocity is focused in

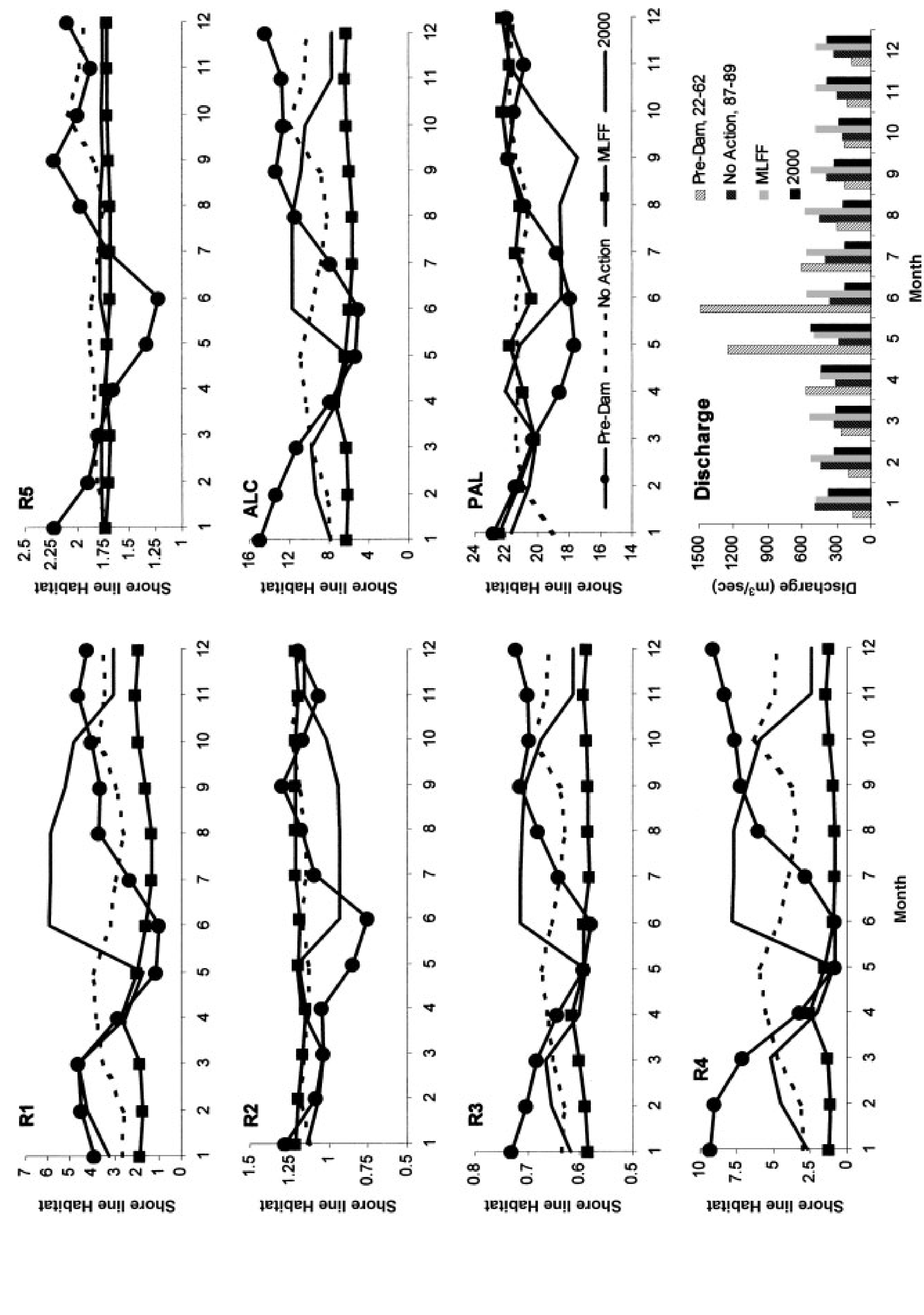

Figure 7. Effects of changes in flow regimes from Glen Canyon Dam on the mean monthly suitable shoreline habitat availability ($m^2 \times 10^3$). See Table III for a description of flow regime characteristics

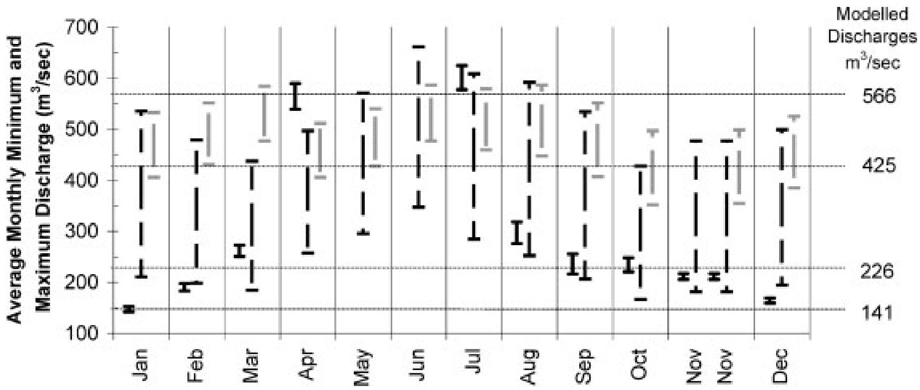

Figure 8. Average minimum and maximum monthly discharges during the pre-dam period (black solid lines) and under the 'no action' (black dashed lines) and MLFF (grey dashed lines) operating regimes. See Table III for a description of flow regime characteristics. Horizontal gridlines show the extent of overlap between discharges modelled in this study and daily discharge ranges. Note that the flow ranges for the pre-dam period in May (1200–1300 m^3/s) and June (1430–1530 m^3/s) occur above the y-axis maximum

Table VI. Persistent suitable habitat area ($m^2 \times 10^3$) at daily discharge ranges typical of three historical GCD operating regimes

Reach	Pre-dam (2000 LSSF) (226 m^3/s)	Post-dam	
		No action (566–226 m^3/s)	MLFF (566–425 m^3/s)
Shoreline ($\leqslant$1 m and $\leqslant$0.25 m/s)			
R1	6.1	0.0	0.2
R2	0.9	0.0	0.4
R3	0.7	0.0	0.1
R4	8.1	0.0	0.1
R5	1.8	0.0	0.4
ALC	12.0	0.2	2.4
PAL	18.4	0.5	16.8
Total ($\leqslant$0.25 m/s)			
R1	14.0	4.1	5.4
R2	10.0	3.4	4.4
R3	13.4	5.9	4.4
R4	15.8	4.8	6.3
R5	39.0	16.6	18.2
ALC	18.7	2.0	5.6
PAL	26.7	4.7	20.7

the cross-stream direction towards the closest bank, had the highest retention rates. The rheotactic behaviour was the next most effective, and the higher the swimming speed, the higher the retention rate. There was considerable reach-to-reach variation on the effectiveness of swimming behaviour at maintaining high retention rates. At longer reaches (e.g. ALC, R1; Table I), particles starting near the centre of the channel with a bank-seeking behaviour had sufficient time to move into low-velocity water near the banks, and hence remain in the reach. In contrast, reaches that were relatively short had low retention rates even under the geotactic behaviour because the particles passed through the reach before entering low-velocity water near the banks.

Retention rates under the passive behaviour were the least sensitive to discharge and very dependent on local morphology (Figure 10). Reaches R3 and R4 had considerably higher retention rates compared to other sites at lower discharges. Large eddies take up a large proportion of the total wetted area of these reaches, and most particles that were randomly assigned starting positions in the eddies were retained. Retention rates were highest in reaches where eddies make up a large proportion of the wetted area.

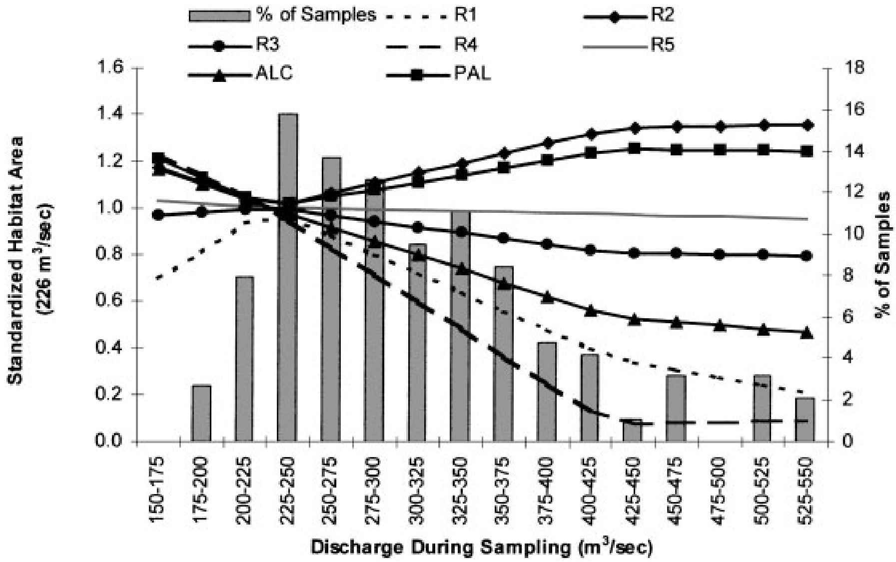

Figure 9. Effects of discharge on relative suitable shoreline habitat availability (standardized to 226 m^3/s) compared to percentage of 190 electrofishing samples collected in 1993 between river km 99 and 107

DISCUSSION

Converse *et al.* (1998) concluded that the effect of artificially elevated base flows due to impoundment on native fish habitat has not received adequate attention in studies related to GCD, and our simulation study is the first effort to address this deficiency. Researchers working in Grand Canyon have hypothesized that reductions in the frequency of low-flow periods, coupled with reduced water temperature, have resulted in reduced habitat quality and an extremely detrimental post-dam environment for juvenile humpback chub (Valdez and Ryel, 1995; Converse *et al.*, 1998). While we cannot comment on the effects of temperature, on the basis of our results, the effect of dam operations on suitable fish habitat is extremely variable across seasons and reaches, and the effect is not always negative. Dam operations have decreased suitable habitat availability in the pre-dam low-flow months by increasing discharge, but have increased it in the spring (April–June) by attenuating the freshet (Figure 6, Table V). Furthermore, pre- and post-impoundment suitable habitat differences were highly variable among reaches, and one questions whether there are any meaningful biological effects of impoundment on habitat availability in the less-sensitive reaches (e.g. PAL, R3, R5) even though the differences were often statistically significant. Because many years of habitat estimates were computed in pre-impoundment and post-impoundment periods, the number of degrees of freedom in the ANOVAs was high. This resulted in statistically significant differences among means even when some of these differences were quite small.

Conclusions on the overall effect of flow-driven changes in habitat availability on juvenile humpback chub survival in the mainstem are difficult to make because we do not have an adequate model to integrate the seasonal and spatial variation documented in our study and, more importantly, to translate the overall habitat effect into a population response. Dam operations have increased suitable shoreline habitat availability in the spring but reduced it in most reaches from August to February. Is the overall impact therefore negative because operations have reduced suitable shoreline habitat in more months than they have increased it, or has increased suitable shoreline habitat availability during the period of dispersal from the LCR (early to mid-summer) resulted in a net beneficial effect? Similar questions can be asked in a spatial context. Are potentially negative effects of the decreased frequency of low-flow periods on suitable habitat availability in highly sensitive reaches compensated, or at least minimized, by relatively constant suitable shoreline habitat availability at insensitive reaches? Further refinement of our numerical habitat model, by adding more details to the biological component of the calculations, or by increasing the spatial extent of the study area, will not address these questions. The interaction between habitat and ecosystem processes like competition and predation are highly uncertain. Ultimately, questions regarding the effects of dam

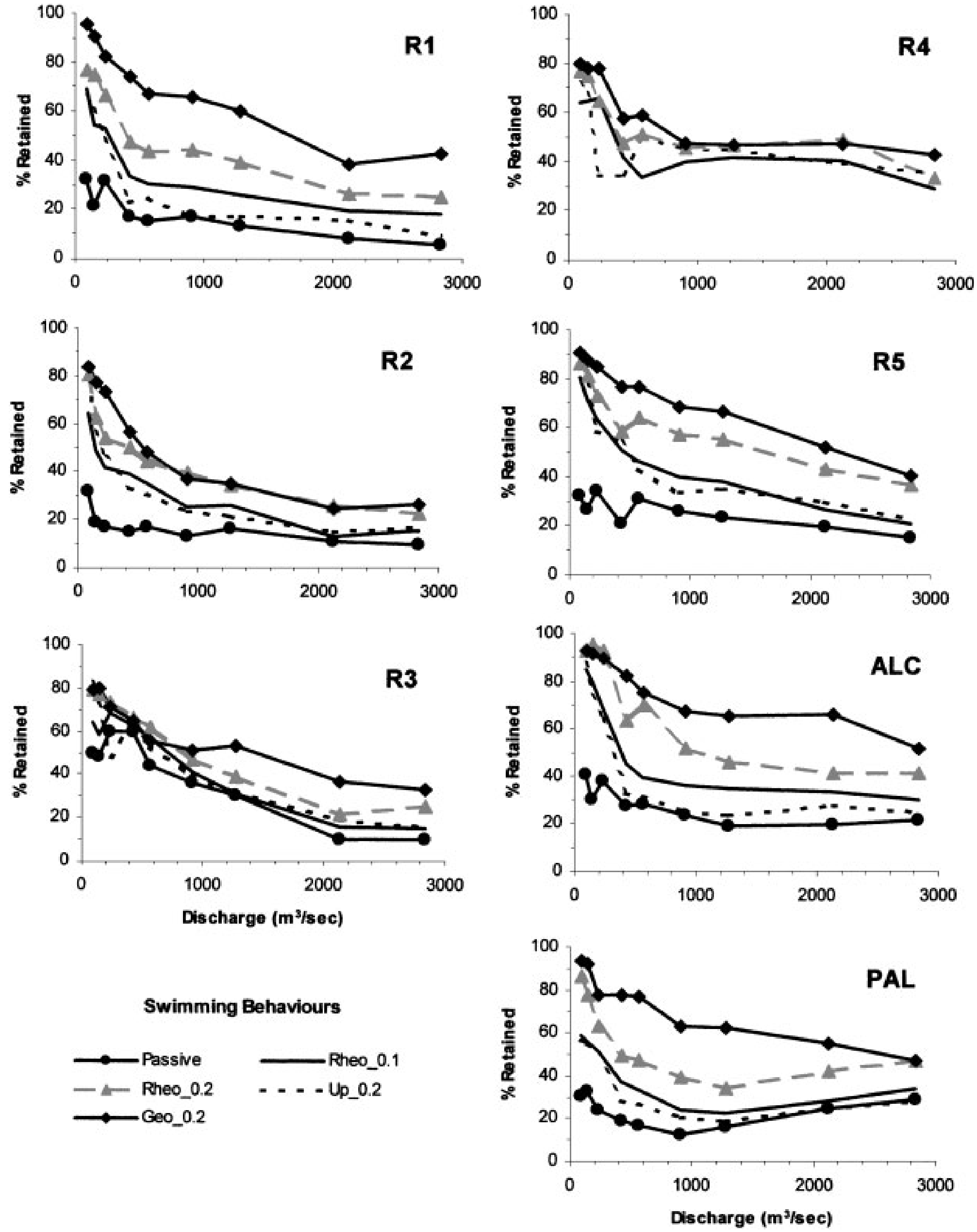

Figure 10. Effects of discharge on retention rate of simulated particles moving under different assumptions of swimming behaviour and speed. 'Geo,' 'Rheo,' 'Up,' and 'Passive' denote geotactic, rheotactic, upstream, and passive swimming behaviours, respectively (see Table IV for details). Non-passive behaviours were simulated using swimming speeds of 0.2 and 0.1 m/s

operations on juvenile humpback chub must be addressed by monitoring the response of critical population parameters to flow manipulations conducted within a sound experimental design.

The reduction in diurnal-flow variation from GCD through the implementation of the MLFF regime reduced the average daily suitable habitat availability relative to the 'no action' regime that maximized hydropower revenues (Figure 7). This occurred because the MLFF regime, which reduced power-load following (Table III), also reduced the frequency of low-flow periods when habitat availability was highest. On the other hand, our analysis based on the typical minimum and maximum daily flows (Figure 8) showed that the MLFF regime resulted in the creation of small amounts of persistent suitable shoreline habitat that did not exist during the 'no action' period (Table VI). The relative importance of changes in the average amount of suitable habitat versus changes in the amount of persistent suitable habitat to native fish populations is unknown. Bowen *et al.* (1998) and Freemen *et al.* (2001) showed that abundance of YOY native fish populations in the Tallapoosa River in the southeastern USA was correlated with the amount of persistent shallow water habitat. Valdez and Ryel (1995) hypothesized that hourly variation in discharge results in 'destabilization' of nearshore habitats used by native fish that could have a negative effect on mainstem survival. In Grand Canyon, there are no data to quantify or test this assertion for native fish, but there has been a well documented and dramatic increase in the rainbow trout population in the clear-water reach upstream of Lees Ferry since the early 1990s when hourly flow variation was first reduced (McKinney *et al.*, 2001). More recent sampling shows what looks like a large increase in rainbow trout throughout the canyon (L. Coggins, Grand Canyon Monitoring and Research Center (GCMRC), Flagstaff, AZ, personal communication, 2001). While there is a reasonable consensus among Grand Canyon researchers that reduced flow variation has caused an increase in the trout population, the overall effect on humpback chub and other native fish remains to be seen. It may be that the exotic response to reduced flow variation outweighs the direct habitat benefits for native fish and results in an overall negative effect on the resources of most concern.

A common theme in our results was the relatively high variation among reaches in the response of suitable habitat availability to changes in discharge (Figures 3 and 4). We modelled more than 3.6 km (19%) of the mainstem habitat used by the LCR/mainstem humpback chub aggregation, yet in spite of this relatively comprehensive coverage, it was difficult to make conclusive statements about the overall effect of impoundment on habitat availability. For example, reductions of flow from 425 to 226 m^3/s, a change achieved during the LSSF experiment in 2000, improved habitat availability at four reaches, reduced it at two reaches, and had no effect on the remaining reach (Figure 3). Extensive reach-to-reach variation was a dominant characteristic of our results, so extrapolation to sections that were not modelled is tenuous. Interestingly, Schmidt *et al.* (1999) documented high spatial variation in the erosion and deposition of sand in eddies after the 1996 experimental flood in this same section of river. Strong spatial variation in responses driven by flow fields affected by local morphology may be a dominant theme in Grand Canyon, and perhaps more caution must be exercised here than for other rivers when trying to make inferences about system-wide responses on the basis of site-specific results.

Restoring elements of the natural hydrograph has been identified as a cornerstone in restoration of riverine ecosystems (National Research Council, 1992; Poff *et al.*, 1997) and the approach has been recommended for restoration of the Colorado River in Grand Canyon (National Research Council, 1996). The seasonally adjusted low steady flow regime identified in the Biological Opinion of 1994 was designed to mimic parts of the historical seasonal discharge pattern with high, steady flows in May–June and low steady flows through the summer and fall (Valdez and Carothers, 1998). Low summer steady flows were hypothesized to increase growth and survival of young native fish in the mainstem through a combination of stabilizing nearshore and backwater habitats and increasing water temperatures downstream from the LCR (Valdez *et al.*, 1999). Habitat stabilization (Table VI) and temperature increases were achieved during the LSSF experiment, but it is worth noting that the seasonal pattern in habitat availability documented in our analysis was anything but natural. The 226 m^3/s steady discharge from June to August 2000 resulted in greatly improved suitable shoreline habitat availability during months when suitable habitat availability was at minimum or near-minimum values prior to impoundment (Figure 6). It may be that this 'unnatural' strategy will be more effective than a more 'natural' one in a post-impoundment era that is characterized by several new and unnatural elements, such as fluctuating daily discharge, abundant piscivorous exotic fish populations, and colder water temperatures.

Changes in discharge from GCD have the potential to affect our ability to monitor fish populations as well as affecting the populations directly through habitat effects. The range of discharges over which the 1993 electrofishing samples were collected was relatively small, yet at reaches where the amount of suitable shoreline habitat area was sensitive to changes in discharge, these discharge differences could result in significant (twofold to fourfold) variation in CPE estimates (Figure 9). Our estimates of the amount of discharge-driven variation in CPE estimates is probably lower than what would be expected under the current sampling programme because diurnal flow variation under the MLFF regime is slightly larger relative to a year like 1993 when interim flows were in effect (Table III). It is worth examining the sensitivity of suitable shoreline habitat area to changes in discharge at fish sampling sites whenever possible to identify the sites where differences in discharge between sampling periods should be minimized.

Our simulation of movement and dispersal of young fish in sites downstream from the LCR demonstrates that even moderate swimming abilities result in a large improvement in the ability of fish to move into low-velocity habitats and to not be displaced downstream (Figure 10). A 100 mm fish swimming at 2 body lengths/s (Bainbridge, 1958) can maintain a cruising speed of approximately 0.2 m/s, consistent with speeds measured by Bulkley *et al.* (1982) for humpback chub. In our simulations, this swimming speed typically resulted in retention rates 1.6 (rheotactic) to 2.9 (geotactic) times larger than those for passively drifting particles. This suggests that discharge is likely to have a significant effect only on retention rates of larvae and small YOY fish entering relatively early in the dispersal period (May–June) from the LCR. If reduced retention leads to decreases in mainstem survival rates, our simulation results provide a mechanism for the hypothesis that larval and smaller YOY humpback chub (<52 mm TL) dispersing from the LCR do not survive (Valdez and Ryel, 1995; Robinson *et al.*, 1998).

There is great uncertainty in the reliability of numerical habitat models to predict the responses of fish populations to changes in flow because the responses depend on a complex series of interactions between habitat and ecological processes (Walters and Korman, 1999). This is especially true in Grand Canyon where exotic species are present in high numbers. Why then, did we pursue our analysis? Habitat models have the potential to provide some guidance about designing flow experiments. For example, if simulation results showed a dramatic improvement in suitable shoreline habitat availability at 350 m^3/s, it could be argued that this would be a more appropriate discharge for LSSF experiments. Similarly, breakpoints in the relationship between daily discharge variation and the amount of persistent suitable habitat could be used to design experiments testing the effects of fluctuating flows. The potential effect of discharge-driven changes in suitable shoreline habitat availability on CPE data highlights the importance of considering the interactions between flow treatments and our ability to monitor population responses to these treatments, an issue that is probably applicable to adaptive management experiments on other regulated rivers.

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