Habitat Selection and Movement of Adult Humpback Chub in the Colorado River in Grand Canyon, Arizona during an Experimental Steady Flow Release

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ABSTRACT

Effective conservation and restoration programs for many native riverine fish communities are highly dependent on regulated river operations developed by water managers. Successfully implementing river flows to meet human needs and minimize ecosystem impacts requires understanding the linkages between hydrology, physical habitat, and fish ecology. In the Colorado River within Grand Canyon, Arizona, altered river conditions following the construction of Glen Canyon Dam have contributed to the decline of Humpback Chub, *Gila cypha*. In 2010, a management experiment was implemented to contrast the modified low fluctuating flow policy with an experimental steady flow release. We assessed habitat selection and movement of 30 adult Humpback Chub implanted with acoustic telemetry tags during two months of fluctuating flow followed by two months of steady flow. We found that telemetered Humpback Chub used eddies extensively while avoiding runs and were associated with intermediate depths and larger substrates. During both flow treatments, Humpback Chub exhibited small daily movements of about 100 m per day. No effect of the flow experiment was observed on Humpback Chub habitat selection or movement. However, nearshore habitat use by Humpback Chub increased with turbidity fluxes caused by tributary floods. Overall our results suggest that adult Humpback Chub habitat selection and movement may not be impacted by the current hydropower operations but habitat use and spatial distribution are influenced by changes in turbidity which has changed greatly in the Colorado River since the completion of Glen Canyon Dam.
Habitat protection and restoration actions are commonly used in the USA and Canada (i.e., Magnuson-Stevens Fisheries Conservation and Management Act, Endangered Species Act, Species at Risk Act) as a primary means to conserve fish communities and promote biodiversity (Minns et al. 1996). Many habitat restoration efforts focus on increasing habitat heterogeneity and assume that with sufficient habitat diversity the target species or community will respond favorably to the restoration action (Bond and Lake 2003; Palmer et al. 2009). However, habitat restoration projects are rarely evaluated experimentally and often produce counterintuitive responses in part because of the spatial scale and time frame in which biological responses are monitored (Palmer et al. 2009). Thus, restoration actions are often unable to assess whether habitat use, demographic parameters, or species diversity change following restoration (Rosenfeld 2003).

Widespread habitat loss caused by large dams has led to the decline of native fish in many river systems, including the Colorado River in the western USA (Tyus and Karp 1991; Minckley and Marsh 2009). The completion of Glen Canyon Dam (GCD) led to dramatic changes in the hydrology and ecology of the Colorado River ecosystem in Grand Canyon, Arizona (Topping et al. 2003; Cross et al. 2011). The pre-dam riverine environment was characterized by large seasonal changes in discharge, turbidity, and temperature while the post-dam river exhibits elevated base-flows, loss of seasonal floods, daily fluctuation in discharge, reduction in sediment inputs, and a stabilized thermal regime (Topping et al. 2003; Voichick and Wright 2007). The trophic structure shifted from allochthonous to autochthonous production along with reduced aquatic invertebrate diversity and production (Cross et al. 2011). Native fish populations also
declined from changes to physical habitat and the proliferation of exotic species (Yard et al. 2011). Current restoration efforts on the Colorado River have targeted elements of the historic flow regime to improve physical conditions within the river to benefit native fish populations (Schmidt et al. 1998).

The Glen Canyon Dam Adaptive Management Program (GCDAMP) was formalized in 1996 to address uncertainty in policy actions regarding the effects of GCD on the Colorado River ecosystem. Conservation of the endangered Humpback Chub, *Gila cypha*, is one of the primary goals of the program (Melis et al. 2006). As part of the GCDAMP, a variety of flow experiments have been conducted to assess the physical and biological responses of the Colorado River ecosystem to contrasting flow policies (Melis et al. 2006; USFWS 2008, 2011; Melis 2011). Despite these tests, uncertainty remains regarding how dam operations affect physical and biological resources.

To help address this uncertainty, experimental steady flow releases from GCD were conducted during September and October of 2008-2012 and contrasted with the existing modified low fluctuating flow (MLFF) policy. MLFF operates similarly to hydropower peaking flows following electrical load demand. Daily discharges under MLFF range from 140 m$^3$/sec to 850 m$^3$/sec with a maximum daily fluctuation of 141 m$^3$/sec to 226 m$^3$/sec depending on monthly release volumes (USDOI 1996). During the experimental steady flow releases, discharge from the dam was held constant at 250 m$^3$/sec for 8 weeks each year. Diel fluctuations in discharge have been hypothesized to negatively influence survival of native fish by destabilizing habitats and altering habitat use patterns (Scrutan et al. 2005; Murchie et al. 2008; USFWS 2008).
In this study, we compared adult Humpback Chub habitat selection and movement between MLFF and the experimental steady flow release in 2010. We also evaluated the influence of turbidity on the spatial distribution and habitat use patterns of adult Humpback Chub. Past research on Humpback Chub habitat use in the mainstem Colorado River has primarily focused on inferring habitat relationships for large adult fish via radio telemetry (Kaeding et. al. 1990; Valdez and Ryel 1995) and catch per effort indices (Converse et al. 1998). However, no studies have quantified Humpback Chub habitat selection and no studies have compared habitat selection and movement during MLFF and experimental steady flow releases.

METHODS

Study Site. —A section of the mainstem Colorado River in Grand Canyon, Arizona (river km (rkm) 102-106) was sampled during four, 16 d river trips in July-October of 2010. The largest aggregation of Humpback Chub in Grand Canyon occurs within the study area (Valdez and Ryel 1995). The MLFF period (discharges ranging from 250 m$^3$/sec to 500 m$^3$/sec) was sampled during July and August and the experimental steady flow release (constant 250 m$^3$/sec) was sampled during September and October (Figure 1). Discharge and formazin turbidity units (FTU) were continuously monitored (15-min intervals) using an acoustic doppler profiler at USGS gauge 093402500 (rkm 145). The Colorado River Flow, Sediment, and Stage model was used to back-calculate the difference in average water travel time between USGS gauge 093402500 and the study location (Wiele and Griffin 1997). Tributary flooding during August and September
caused spikes in turbidity and discharge that were unrelated to dam operations (Figure 1).

Fish handling and surgery methods. —Thirty-two adult Humpback Chub between 180-245 mm total length (TL) were surgically implanted with acoustic telemetry tags (model PT-3: 8-mm diameter, 19-mm length, 1.5 g, 45-60-d battery life; Sonotronics, Tuscon, Arizona, USA). We selected this size class for study to bridge the gap between previous research on subadult (100-199 mm TL) and large adult Humpback Chub (> 375 mm TL) habitat use (Valdez and Ryel 1995; Valdez and Ryel 1997; Converse et al. 1998), as well as to minimize the influence of tagging on the survival of smaller fish (Jepsen et al. 2002). All fish implanted with telemetry tags were captured via hoop netting and anesthetized with sodium bicarbonate prior to surgery. During surgery, aerated river water was passed continuously over the gills using a gravity fed tank. Tags were implanted by making a small incision (~8-mm) into the abdominal cavity. The incision was closed with 2-3 interrupted stitches using absorbable suture material and sealed with cyanoacrylate. Following surgery, fish were retained for recovery until able to maintain equilibrium and exhibit normal fin movements. All tagged fish were released at the original site of capture. A staggered-entry tagging design was used to increase the temporal resolution of the study (Pollock et al. 1989). All fish were implanted with tags between July-September and tag life was expected to last two months. No fish were implanted during the October trip as viable tags were still active from prior trips.

Tracking telemetered Humpback Chub. —Fish tracking began 24 h post-surgery and continued through October. Relocations (e.g. telemetered fish detections) recorded within 3 d of surgery were omitted from all analyses to account for recovery. Generally,
fish were tracked twice per day during the morning (between 0500 and 0700 h) and afternoon (between 1400 and 1800 h). Tracking efforts were confined to the study area due to permitting constraints. Tag performance was assessed across a range of flow conditions and depths during pilot sampling in 2009 and signal attenuation was observed at distances greater than 100 m. We implemented a systematic tracking framework to search for telemetered individuals by stopping at fixed locations approximately 100 m apart. Each location was searched for 3-4 min with the boat moving as slowly as possible. Telemetry surveys were discontinued in rapids because of poor signal reception and unsafe boating conditions. Following detection of a tagged fish, the receiver gain was reduced to find the precise location. Once a fish was located, the position was entered into a mobile Geographic Information System (GIS) database and attributes of the location including time, depth, distance from shore and XY coordinates were recorded. In addition, stationary hydrophones were placed at the top and bottom of the study site to monitor emigration. **Habitat mapping.**—Relocations of tagged fish were related to GIS data layers consisting of hydraulic type, habitat type, water depth, and substrate size using existing information collected by USGS Grand Canyon Monitoring and Research Center (GCMRC) and field measurements (Table 1). The hydraulic type was mapped in the field and split into either eddy or run categories (Table 1). Following field mapping, hydraulic type was digitized in GIS. Habitat type was delineated into six classes including backwater, cliff, debris fan, offshore, sand and talus using existing GIS imagery (Table 1). GIS based habitat classifications were verified in the field. Water depth was determined in GIS as surface water elevation minus the elevation of the river.
bottom for a given discharge. For the selection ratio analysis, water depth was grouped into six discrete categories including: 0-2 m, 2-4 m, 4-6 m, 6-8 m, 8-10 m, and > 10 m.

Water depth was considered a continuous variable in the mixed model analysis. Existing bathymetric and channel coarseness maps were used to classify substrate type into 12 discrete sizes using a modified Wentworth scale. Substrates sizes were grouped into three classes: small, medium and large substrates for the selection ratio analysis (Table 1) and the 12 substrate classes were treated as a continuous variable in the mixed model analysis.

Habitat availability was determined by generating random locations within the study site using the ArcGIS extension Hawth’s Tools. The number of random locations generated to quantify habitat availability was equal to the number of fish relocations during each flow release. Habitat characteristics were related to available locations in ArcGIS.

Statistical Analysis of Habitat Selection. – Following Rosenfeld (2003), habitat selection was inferred as differential use of a habitat given habitat availability. We used two statistical approaches to assess habitat selection including selection ratios and logistic regression mixed models. Univariate selection ratios were calculated following a type II study design (Thomas and Taylor 1990; Manly et al. 2002). This design compared the frequency of habitat use in a discrete habitat class to the availability of the habitat class. Habitat classes included hydraulic type, habitat type, water depth category and substrate size class. Prior to constructing selection ratios, two different chi-square tests were used to test if Humpback Chub were uniformly distributed across habitat classes and determine if habitat selection was occurring. Once selection was established,
selection ratios ($W_i$) and Bonferroni adjusted 95% confidence intervals were constructed to determine which habitats were being selected (Manly et al. 2002; Rogers and White 2007). Selection was indicated by values greater than one while avoidance is indicated by values less than one (Rogers and White 2007). Selection ratios equal to one indicated that use is proportional to available habitat (i.e. no selection). Log-likelihood chi-square tests and selection ratios were calculated using the adehabitat package in Program R (R Development Core Team 2012).

Mixed effects logistic regression models were implemented to compare used versus available locations as a function of habitat attributes for tagged Humpback Chub. Nine different a priori models were developed to propose mathematical descriptions of covariates that influence habitat selection. In this analysis, the tagged fish was considered a random effect while hydraulic type, habitat type, water depth, substrate size and flow (e.g. MLFF versus steady flow release) were fixed effects (Rogers and White 2007). The mixed model framework accommodates non-normal (e.g. binomial) error structure and controls for autocorrelation associated with repeatedly sampling the same fish (Gillies et al. 2006). Model fit was compared using Akaike Information Criterion (AIC, Burnham and Anderson 2002). The model with the lowest AIC value was chosen for interpretation of habitat selection. Mixed effects logistic regression models were implemented using lme4 package in R.

Statistical Analysis of Movement. —To describe the movement patterns of Humpback Chub, mean daily displacement and extent of movement were calculated for both flow releases. We calculated mean daily displacement as the linear distance moved between successive relocations during daily morning tracking events and extent of
movement as the linear distance between the farthest upstream and downstream relocations. A linear mixed model was used to determine if mean daily displacement varied as a function of flow (e.g. MLFF, steady flow release). An individual tagged fish was considered the random effect while flow regime was the fixed effect (Rogers and White 2007). Wald’s chi-square statistic was used to assess model significance and a non-parametric bootstrap procedure was used to determine 95% confidence intervals around mean daily displacement. A one-way Kruskal-Wallis test was used to determine if there were differences in extent of movement between flow releases and a bootstrap procedure was used to determine confidence intervals. To assess the influence of changing discharge on the spatial distribution of tagged fish a linear mixed-model was used to compare distance to shore to discharge level.

Statistical Analysis of Turbidity. —The influence of turbidity on the spatial distribution of Humpback Chub was assessed with a linear mixed model to determine if distance from shore varied as a function of turbidity category and a non-parametric bootstrapping procedure was used to assess uncertainty. Three turbidity categories were considered. Low turbidity ranged from 0-30 FTU, medium turbidity levels ranged from 31-300 FTU and high turbidity levels ranged from 301-10,000 FTU. A Pierson chi-square test was used to evaluate if tagged fish habitat use changed with increased turbidity.

RESULTS

Thirty-tagged Humpback Chub were relocated 1,034 times from July to October 2010. Thirty-two fish were originally implanted with tags but only 30 individuals were known to have remained in the study site and included in subsequent analyses.
Fourteen fish were relocated a total 344 times during MLFF and 25 fish were detected a total of 690 times during the experimental steady flow release. Tagged fish were relocated on average 25 (SD=12.7) times and observed for 46 (SD=16.2) days. The mean size of tagged Humpback Chub was 199 mm (SD=19.2) and ranged between 180 mm to 245 mm TL.

During both flow releases, locations used by tagged fish differed significantly (P-value <0.05) from availability for all habitat characteristics except for substrate category during MLFF (Table 2). The largest selection ratios were for hydraulic type, habitat type, and depth class (Figure 2). Adult fish strongly selected eddy hydraulic types and these areas were used in proportions greater than three times their availability. Tagged fish avoided runs during both flow releases. Habitat types including cliff and debris fan shorelines were positively selected for during both flows while selection for backwaters was highly uncertain in part due to the limited availability of this habitat type. Fish demonstrated no selection or avoidance for talus during MLFF while positively selecting this habitat type during the steady flow release. Tagged fish selected intermediate water depths of 4-6 m during both flows and did not exhibit strong substrate selection patterns (Figure 2).

The most highly supported mixed model describing Humpback Chub habitat selection included hydraulic type, water depth, substrate size and an interaction between hydraulic type and substrate size (Table 3). These variables best explained the probability of habitat selection by tagged fish. Hydraulic type was the strongest predictor of habitat selection causing the largest improvement in model fit (Table 3). Similar to the selection ratio analysis, eddies were selected for while runs were avoided.
Telemetered fish used shallower depths and larger substrate than would be expected based on availability. The significant interaction effect between substrate category and hydraulic type indicated that tagged fish used a wide variety of substrate categories in eddies while being negatively associated with small substrates and positively associated with larger substrates in runs. Including a parameter that represented the contrasting flow releases did not improve model fit, suggesting that habitat selection did not change markedly between flows (Table 3, $\Delta$ AIC = 2 between competing models).

Mean daily linear movements of adult Humpback Chub were not significantly different between MLFF and the experimental steady flow release ($\chi^2 = 0.16$, $P = 0.6867$). During MLFF, tagged fish moved a mean distance of 92 m/d (95% confidence interval, 67-123 m; Figure 3) while during the steady flow, fish moved 106 m/d (95% confidence interval, 91-123 m; Figure 3). In both flows, long distance daily movements (> 500 m) were rare. The extent of movement by tagged fish was not significantly different ($\chi^2 = 0.14$, $P = 0.7015$) between MLFF and the steady flow release. The mean extent of movement was 414 m (95% confidence interval, 258-595 m) during MLFF and 515 m (95% confidence interval, 333-743 m) during the steady flow (Figure 3). No relationship was found between distance from shore and discharge level ($\chi^2 = 1.56$, $P = 0.20$) suggesting that tagged fish did not alter their spatial distribution in response to the discharge levels observed. During low turbidity conditions, tagged fish were located significantly farther offshore ($\chi^2 = 77.869$, $P < 0.01$) than during high turbidity conditions (Figure 3). Similarly, the frequency of nearshore habitat use for all nearshore habitat types increased significantly ($\chi^2 = 77.869$, $P < 0.01$) with higher turbidity levels (Table 5).
DISCUSSION

We found that adult Humpback Chub habitat selection and movement patterns did not differ between MLFF and the experimental steady flow release. This is an important finding because of concerns that fluctuating flows may destabilize habitats and alter habitat use patterns. Our results demonstrate that tagged fish exhibit strong selection for eddy hydraulic types across the observed river flows and that fish greater than 180 mm TL have transitioned from occupying nearshore habitats to residing in eddy complexes while making occasional nearshore movements. Kaeding et al. (1990) suggested that Humpback Chub rely on channel obstructions such as debris fans which create velocity refuges via eddy complexes and Valdez and Ryel (1995) postulated that the distribution of adult Humpback Chub may be related in part to the presence of large eddies (Valdez and Ryel 1995; Valdez et al. 2001). In Grand Canyon, eddies generally occur below rapids caused by channel constricting debris fans. Eddies create areas of recirculating flow adjacent to the main current and increase material retention time as a function of slower average water velocities when compared to runs (Schmidt 1990). Our results agree with previous research on adult Humpback Chub and suggest that the observed strong selection of eddy habitats maybe related to food availability and reduced energetic expenditure (Valdez et al. 1997; Valdez et al. 2001). Residing in depositional environments adjacent to turbulent runs may allow Humpback Chub to maintain position in lower velocity water while making foraging attempts at entrained organic matter and invertebrates in the water column. Similar patterns have been observed for cyprinids in small stream systems in the southeastern and southwestern
United States (Rinne 1991; Freeman and Grossman 1993) but observations for large-bodied cyprinids in big rivers such as the Colorado are less well known. We observed that adult Humpback Chub make small daily movements and exhibit a restricted distribution. Most movements of tagged fish were made within large eddy complexes. However, movements between eddy complexes, up and down small rapids, and from runs to eddies were also observed. Previous studies using telemetry and passive tags over short and long temporal scales (i.e. weeks to several years) suggest that Humpback Chub exhibit strong patterns of site fidelity (Valdez and Ryel 1995; Valdez et al. 2001; Paukert et al. 2006). Seasonal movements of adult Humpback Chub in Grand Canyon are characterized by potadromous spawning migrations between the mainstem Colorado River and the Little Colorado River between March and May (Gorman and Stone 1999; Coggins et al. 2006). Our sampling period did not overlap with the timing of this migration and no evidence of movement between the mainstem and Little Colorado River was documented. Long distance movements in excess of 50 km by Humpback Chub have been observed through long-term tagging studies (Paukert et al. 2006). However, given the limited movements observed, it appears that long distance dispersal may be rare during the late summer and fall. This result is important in planning mark-recapture studies where knowledge of limited movement is important in assessing whether or not the population is closed to immigration or emigration during the study time period (Gwinn et al. 2011).

Overriding turbidity conditions appeared to have a stronger influence on the spatial distribution of tagged fish than the experimental steady flow release. Spikes in turbidity cause behavioral responses in many fish species (Gregory 1993; Sweka and
Hartman 2001) including loss of visual acuity, decreased reliance on cover, and changes to foraging mode (Stone 2010). Turbidity has been observed to strongly influence native fish catch rates in the Little Colorado River (Stone 2010), and Valdez and Ryel (1995) observed a greater frequency of nearshore habitat use by Humpback Chub during turbidity fluxes. In this study, fewer tagged fish were relocated during low turbidities, yet emigration outside of the study area was not observed. We posit that during low turbidities, tagged fish used cover in areas with irregular bathymetry which would impede detection with acoustic telemetry. Changes in habitat use under differing turbidity levels may correspond to a change in foraging mode. Under low turbidity conditions Humpback Chub forage on material entrained in eddies (Valdez and Ryel 1995). As turbidity increases, nearshore habitats are increasingly used and Humpback Chub may become opportunistically piscivorous (Stone and Gorman 2006). In support, predation risk experiments which occurred concurrently to this study found that predation risk for juvenile fish in nearshore habitats was highest under moderate turbidity (mean 165; range 34 – 594 FTU) conditions (Dodrill 2012) and on two occasions, Humpback Chub were observed foraging on tethered fish (M. Dodrill, personal observation). This study contributes to the body of knowledge suggesting that turbidity is an important factor influencing behavior and spatial distribution of fish within the mainstem Colorado River. Given that sediment inputs and turbidity have declined in this reach of the Colorado River following construction of GCD (Topping et al. 2003) our findings suggest Humpback Chub movements and habitat use may also have changed with altered sediment inputs.
Our results are similar to Valdez et al. (2001) who examined the response of 10 adult, radio tagged, Humpback Chub to the 1996 experimental flood from GCD. They found that habitat use and movement of tagged fish was largely unaffected by the test flood (Valdez et al. 2001). The lack of a response by Humpback Chub to these flow experiments may have been affected by numerous factors. First, the range of flows observed in this study were within the operational constraints of the MLFF policy (USDOI 1996). Given that the historical range of flows in Grand Canyon ranged from summer flows of less than 85 m$^3$/s to spring floods greater than 2,400 m$^3$/s, flows greater than 1,274 m$^3$/s (e.g. typical test flood discharge) or lower than 141 m$^3$/s (e.g. lowest allowable discharge prescribed under MLFF) may be required to elicit a change in Humpback Chub habitat selection and movement patterns (Topping et al. 2003). Secondly, the river reach in this study and Valdez and Ryel (1995) is primarily comprised of large eddy complexes adjacent to complex high angle shoreline habitat such as debris fans and talus slopes. These habitats are relatively invariant to discharge fluctuations, likely contributing to why habitat selection patterns were robust to changes in discharge (Valdez et al. 2001; Korman et al. 2004). Lastly, smaller size classes (< 180 mm) of Humpback Chub may be more reliant on nearshore habitats (Stone and Gorman 2006) and more affected by daily fluctuations in river stage. However, concurrent research from 2009 to 2011 indicated no apparent change in the growth rate, survival, and habitat selection of juvenile native fish in response to the steady flow release (Dodrill 2012; Finch 2012; Gerig 2012).

Since 1996, experimental floods and steady flows have been implemented in Grand Canyon as part of an adaptive management program tasked in part with the
recovery of Humpback Chub (Valdez et al. 2001; Trammel et al. 2002; Ralston 2011).

To date, native fish have exhibited a much smaller response to flow related
management actions than anticipated given the expected positive response (Pine et al.
2009). This may be partly due to unrealistic expectations of how rapidly fish respond to
a management treatment with respect to the magnitude and scale of the treatment
being applied to the system. We suggest that substantial learning can take place when
managers contrast observed versus expected responses to management actions and
seek to understand why the system or species did not respond as anticipated (Walters
and Holling 1990; Walters 2004). This type of iterative assessment should help
managers develop more effective policies to aid in informing future flow related
management actions by more clearly identifying shortcomings and successes in
predicting Humpback Chub responses to river regulation in the Colorado River.
ACKNOWLEDGMENTS

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REFERENCES


Figure 1. Mean, maximum and minimum daily discharge (m³/sec) during modified low fluctuating flow (MLFF) and the experimental steady flow releases and daily turbidity (FTU) measurements from July to October 2010 in the Colorado River in Grand Canyon. In the lower panel, the solid line represents mean daily discharge and dashed lines represent minimum and maximum daily discharges. In the upper panel, the solid line represents mean daily turbidity (FTU).
Figure 2. Selection Ratios with 95% Bonferroni confidence intervals of (A) habitat type, (B) hydraulic type, (C) depth category (m) and (D) substrate class. Closed data points represent the modified low fluctuating flow while open data points represent steady flow releases. Habitat type abbreviations include: BW (Backwater), CL (Cliff), DF (Debris fan), OF (Offshore), SD (Sand), and TL (Talus). Substrate classes include 1-4 (small substrates), 5-8 (medium substrates), and 9-12 (large substrates).
Figure 3. Movement and spatial distribution of telemetered Humpback Chub during contrasting flow releases and turbidity levels. (A) Daily movement and (B) spatial extent during contrasting flow releases. (C) Observed distance from shore of Humpback Chub during low, medium and high turbidity levels.
Table 1. Description of habitat covariates used in selection ratio and mixed model analysis of telemetered humpback chub habitat selection during contrasting flow releases.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydraulic Type</td>
<td>Eddy</td>
<td>Areas of recirculating flow; generally occur downstream of debris fans.</td>
</tr>
<tr>
<td></td>
<td>Run</td>
<td>Areas of downstream flow.</td>
</tr>
<tr>
<td>Habitat Type</td>
<td>Backwater</td>
<td>Areas of low velocity water that are partially isolated from the main channel.</td>
</tr>
<tr>
<td></td>
<td>Cliff</td>
<td>Sheer walls rising vertically and laterally over the river.</td>
</tr>
<tr>
<td></td>
<td>Debris Fan</td>
<td>Large cobble and boulder that were transported into the river by tributary flooding.</td>
</tr>
<tr>
<td></td>
<td>Offshore</td>
<td>Any area that was greater than 15 m from shore.</td>
</tr>
<tr>
<td></td>
<td>Sand</td>
<td>Areas of predominantly exposed sand.</td>
</tr>
<tr>
<td></td>
<td>Talus</td>
<td>Boulder and larger material deposited by and rock fall along shoreline.</td>
</tr>
<tr>
<td>Water Depth</td>
<td>1-4</td>
<td>2-m water depth classes : 0-2 m, 2-4 m, 4-6 m, 6-8 m, 8-10 m, and &gt;10 m.</td>
</tr>
<tr>
<td>Substrate Class</td>
<td>5-8</td>
<td>Medium substrates; small gravel to medium cobble.</td>
</tr>
<tr>
<td></td>
<td>9-12</td>
<td>Large substrates; large cobble to large boulder.</td>
</tr>
</tbody>
</table>
Table 2. Chi-square statistics testing (1) the distribution and (2) selection of habitat characteristics of Humpback Chub during contrasting flow releases.

<table>
<thead>
<tr>
<th>Habitat Characteristic</th>
<th>Flow Type</th>
<th>Distribution</th>
<th>Selection</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>χ²</td>
<td>df</td>
<td>P</td>
</tr>
<tr>
<td>Habitat Type</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fluctuating</td>
<td>83.87</td>
<td>60</td>
<td>0.02</td>
</tr>
<tr>
<td>Steady</td>
<td>164.07</td>
<td>105</td>
<td>&lt;0.001</td>
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<tr>
<td>Hydraulic Type</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Fluctuating</td>
<td>30.32</td>
<td>12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Steady</td>
<td>32.4</td>
<td>21</td>
<td>0.05</td>
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<td>Depth Class</td>
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<td></td>
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<tr>
<td>Fluctuating</td>
<td>190.81</td>
<td>60</td>
<td>&lt;0.001</td>
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<tr>
<td>Steady</td>
<td>220.08</td>
<td>105</td>
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<tr>
<td>Substrate Class</td>
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<td></td>
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<tr>
<td>Fluctuating</td>
<td>26.2</td>
<td>24</td>
<td>0.32</td>
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<tr>
<td>Steady</td>
<td>64.27</td>
<td>42</td>
<td>0.015</td>
</tr>
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Table 3. AIC ranking of mixed model logistic regression models used to determine habitat selection of telemetered Humpback Chub.

<table>
<thead>
<tr>
<th>Model</th>
<th>LL&lt;sup&gt;a&lt;/sup&gt;</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>K&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth+ Substrate Size+ Hydraulic Type+ (Substrate Size*Hydraulic Type)</td>
<td>-1073</td>
<td>2157</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Depth+ Substrate Size+ Hydraulic Type+ Flow Release+(Substrate Size*Hydraulic Type)</td>
<td>-1072</td>
<td>2159</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Depth+ Substrate Size+ Hydraulic Type+ (Depth*Hydraulic Type)</td>
<td>-1076</td>
<td>2163</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Depth+ Substrate Size+ Hydraulic Type+ Flow Release+ (Depth*Hydraulic Type)</td>
<td>-1074</td>
<td>2165</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Depth+Depth²+Substrate Size+Hydraulic Type</td>
<td>-1080</td>
<td>2171</td>
<td>14</td>
<td>5</td>
</tr>
<tr>
<td>Depth+Substrate Size +Hydraulic Type</td>
<td>-1081</td>
<td>2172</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Hydraulic Type</td>
<td>-1111</td>
<td>2228</td>
<td>71</td>
<td>2</td>
</tr>
<tr>
<td>Habitat Type</td>
<td>-1296</td>
<td>2607</td>
<td>450</td>
<td>6</td>
</tr>
<tr>
<td>Depth+Substrate Size</td>
<td>-1364</td>
<td>2736</td>
<td>579</td>
<td>3</td>
</tr>
</tbody>
</table>

<sup>a</sup> = Log Likelihood;  <sup>b</sup> = # of parameters
Table 4. Coefficient estimates from top AIC ranked mixed model logistic regression for telemetered Humpback Chub during contrasting flow releases.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>z value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.05</td>
<td>0.190</td>
<td>-10.67</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Depth</td>
<td>-0.07</td>
<td>0.015</td>
<td>-4.68</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Substrate</td>
<td>0.37</td>
<td>0.050</td>
<td>6.93</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Hydraulic Type</td>
<td>3.20</td>
<td>0.230</td>
<td>13.62</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Substrate * Hydraulic Type</td>
<td>-0.27</td>
<td>0.070</td>
<td>-4.10</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>
Table 5. Frequency of habitat use during contrasting turbidity conditions for telemetered Humpback Chub. Low turbidity ranged between 0-30 FTU, medium turbidity was between 31-300 FTU, and high turbidity ranged from 301-10,000 FTU.

<table>
<thead>
<tr>
<th></th>
<th>Backwater</th>
<th>Cliff</th>
<th>Debris Fan</th>
<th>Offshore</th>
<th>Sand</th>
<th>Talus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>0</td>
<td>13</td>
<td>17</td>
<td>90</td>
<td>6</td>
<td>41</td>
</tr>
<tr>
<td>Medium</td>
<td>16</td>
<td>57</td>
<td>65</td>
<td>189</td>
<td>4</td>
<td>88</td>
</tr>
<tr>
<td>High</td>
<td>35</td>
<td>101</td>
<td>80</td>
<td>169</td>
<td>8</td>
<td>62</td>
</tr>
</tbody>
</table>
Acceptance notification from journal

---------- Forwarded message ----------

From: <rick.eades@nebraska.gov>
Date: Wed, Aug 28, 2013 at 4:45 PM
Subject: North American Journal of Fisheries Management - Decision on Manuscript ID UJFM-2013-0101.R1
To: bgerig@nd.edu

28-Aug-2013

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Ref: Habitat Selection and Movement of Adult Humpback Chub in the Colorado River in Grand Canyon, Arizona during an Experimental Steady Flow Release

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rick.eades@nebraska.gov