SITE OCCUPANCY AND HABITAT SELECTION OF ENDANGERED HUMPBACK CHUB DURING EXPERIMENTAL FLOW RELEASES FROM GLEN CANYON DAM IN THE COLORADO RIVER IN GRAND CANYON, ARIZONA

By

BRANDON GERIG

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To my family and friends

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By

Brandon Scott Gerig

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Conserving native riverine fish communities is in part dependent on how regulated river corridors are managed. In order for dams and hydropower operations to be managed optimally with respect to ecosystem integrity, an understanding of the ecological linkages between stream flow conditions, physical habitat and fish community structure is essential. In the Colorado River within Grand Canyon altered river conditions caused by the installation of Glen Canyon Dam have been implicated in the decline of the humpback chub. Specifically, hydropeaking flow schedules or fluctuating flow regimes have caused diel destabilization of nearshore habitats that are thought to be important for humpback chub. Beginning in 2009 a multi-year adaptive management experiment was implemented to contrast the current fluctuating flow management policy with an experimental steady flow regime. We examined the habitat use patterns of humpback chub using a patch occupancy approach during 2009-2011 to assess the influence of this experimental steady flow regime on habitat use. Additionally, in 2010 I assessed habitat selection for a 30 newly recruited humpback chub implanted with acoustic telemetry tags. Four river trips occurred yearly during July through October 2009 and

2010. River sampling surveys were conducted in July and August were during fluctuating flows whereas trips conducted in September and October occurred during steady flows. During this study, I found that site occupancy was most related to time varying (e.g. sampling survey, year + flow regime) and size specific covariates for hoop net and electrofishing gears. Habitat covariates received little model support and robust relationships between occupancy and habitat were not observed. For telemetered humpback chub I found that they extensively select eddy hydraulic types while avoiding runs. Tagged fish were also associated with intermediate depths and larger substrates. No effect of the flow experiment was observed. My research suggests that for both passive and active gears humpback chub did not respond to the steady flow regime. Future research assessing the influence of flow on humpback chub should carefully consider the magnitude and timing of discharge releases while also considering the spatial area in which sampling will occur.

CHAPTER 1
BACKGROUND

This thesis evaluated the effects of a series of steady flow releases from Glen Canyon Dam on humpback chub in the Colorado River in Grand Canyon, AZ. The completion of Glen Canyon Dam caused a suite of abiotic changes that influenced the ecology of the Colorado River ecosystem (Topping 2003, Gloss and Coggins 2005, Kennedy and Gloss 2005). Prior to Glen Canyon Dam the Colorado River in Grand Canyon exhibited large seasonal changes in discharge, turbidity and temperature. In post-dam environment, the river has been characterized by elevated base-flow, elimination of seasonal floods, daily fluctuation of discharge for hydropower production, reduction of sediment inputs, and stabilized thermal regime (Topping 2003). The changes to the hydrology have had cascading effects on biota. There have been changes to the food base, shifts in the aquatic invertebrate community, increases in the abundance of non-native fishes and reductions in the native fish community.

The original Grand Canyon fish community consisted of eight native species and exhibited a high degree of endemism (Minckley and Marsh 2009). Habitat alterations caused by mainstem hydroelectric dams and the widespread introduction of non-native species led to the extirpation of 4 native species (bonytail chub (*Gila elegans*), Colorado pikeminnow (*Ptychocheilus lucius*), razorback sucker (*Xyrauchen texanus*)) and roundtail chub (*Gila robusta*), reductions in native fish populations, and increased population sizes of non-native fishes in Grand Canyon (Minckley and Marsh 2009). The current Grand Canyon fish community consists primarily of a mixture of native: bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (Catastomous latipinnis), humpback chub (Gila cypha), speckled dace (*Rhinichthys osculus*), and non-native: rainbow trout (*Onchorychus mykiss*), brown trout (*Salmo trutta*), black bullhead (*Ameiurus melas*), common carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*), plains killifish (*Fundulus zebrinus*) fishes (Gloss and Coggins 2005). The focal species of Colorado River management actions in Grand Canyon is the humpback chub (Coggins et al. 2006; Coggins et al. 2011). The humpback chub was listed as a federally endangered species in 1967 and became federally protected in 1973 under the Endangered Species Act. Currently, humpback chub exist in six fragmented populations within the Colorado River Basin and the largest population occurs in Grand Canyon near the confluence of the Little Colorado River and Colorado River (Coggins et al. 2006).

The Glen Canyon Dam Adaptive Management Program was formed following the 1996 Record of Decision from the Environmental Impact Statement on the operation of Glen Canyon Dam (Melis et al. 2006). Conservation of native Colorado River Basin fishes, particularly the endangered humpback chub was one of the primary goals of this program. The Glen Canyon Dam Adaptive Management Program consists of federal, state, tribal and public stakeholders that work together to implement management strategies designed to improve the understanding and management of resources within the Colorado River corridor in Grand Canyon. Given that resource response to management is highly uncertain an active adaptive management approach is used to couple resource management with research (Melis et al. 2006).

This study resulted from formal consultation between the Bureau of Reclamation and U.S. Fish and Wildlife Service to address the implementation of modified low fluctuating flow and the effect of this policy action on the endangered humpback chub population in Grand Canyon. Within the Glen Canyon Dam Adaptive Management Program stakeholders felt that the continued implementation of modified low fluctuating flow negatively influenced native fish and that steady flow releases during certain times of the year would benefit humpback chub and the other members of the extant native fish community. In this study, I utilized a series of experimental steady flow releases from 2009 to 2011 from Glen Canyon Dam to relate f dam operations to endangered humpback chub populations in the Colorado River in Grand Canyon. As part of this experiment, flow operations from Glen Canyon Dam were changed from the typical operating policy of modified low fluctuating flow to steady discharge rates for eight weeks. I utilized the manipulation of Glen Canyon Dam operations to assess the difference between flow regimes (modified low fluctuating flow and steady flow) on habitat use and movement of humpback chub in the Colorado River in Grand Canyon. Specifically, the research objectives are: 1.) assess nearshore habitat use of humpback chub using site occupancy models during contrasting flow regimes, and 2.) determine the habitat selection and movement patterns of newly-recruited adult humpback chub during contrasting flow regimes using acoustic telemetry.

CHAPTER 2
SITE OCCUPANCY OF HUMPBACK CHUB IN THE COLORADO RIVER IN GRAND CANYON, AZ

Introduction

Fish habitat use in rivers is a complex trade-off between numerous abiotic and biotic factors such as thermal environment, flow regime, food availability, competition (Werner and Hall 1979; Butler 1980), predation risk (Werner et al. 1983; Walters and Martell 2004), and shifts between foraging and resting areas. Habitat use and selection often varies with life-stage for many organisms and ontogenetic habitat shifts are commonly adopted by fish to utilize specific spawning, nursery and foraging areas (Werner et al. 1988; Walters and Juanes 1993; Faush et al. 2002; Walters and Martell 2004). Understanding the temporal and spatial patterns of habitat use is a critical need in ecology (Johnson 1980; Morrison et al. 2006).

Observations of animal habitat use are often used to inform decisions about habitat requirements thus informing management policies designed to protect specific habitat types and species (Van Horne 1983). Increasingly, efforts to manage aquatic resources have emphasized habitat protection as an approach to manage ecosystems versus traditional approaches of managing single species (Minns et al.1996; Minns et al. 1999). Habitat protection and restoration measures have been mandated in the United States (Magnuson-Stevens Fisheries Conservation and Management Act, Endangered Species Act) as a primary means to conserve fish populations from decline. However, many of these efforts are not well informed and habitat mitigation and restoration efforts are rarely assessed experimentally thus they often fail to assess whether habitat use and population vital rates change following protection or restoration efforts (Van Horne 1983, Quinn and Kwak 2000, Gunn and Sein 2000, Rosenfeld 2003).

Riverine ecosystems have been significantly altered by anthropogenic changes to flow regime through the widespread construction of dams or other control structures (Dynesius and Nilsson 1994; Poff et al. 1997; Richter et al. 1997; Bunn and Arthington 2002). Large dams often change the timing, magnitude, frequency, duration and rate of change in hydrologic conditions within rivers (Poff et al. 1997) and these hydrologic changes are thought to alter riverine processes including ecosystem productivity, sediment transport and temperature all of which are thought to have had negative effects on riverine ecosystems including fish populations (Nilsson et al. 2005; Poff et al. 2007).

The completion of Glen Canyon Dam led to dramatic changes in the hydrology and ecology of the Colorado River ecosystem in Grand Canyon (Topping 2003; Gloss and Coggins 2005; Kennedy and Gloss 2005). The pre-dam environment in Grand Canyon exhibited large seasonal changes in discharge, turbidity and temperature. The post-dam environment has been characterized by elevated base-flow, elimination of seasonal floods, daily fluctuation of discharge for hydropower production, reduction of sediment inputs, and stabilized thermal regime (Topping 2003). Along with changes to the physical environment there were large scale changes to the biotic community. Trophic structure shifted from allochthonous to autochthonous production and reduced aquatic invertebrate diversity and abundance (Kennedy and Gloss 2005; Gloss and Coggins 2005). Native fish populations declined as a result of changes to physical habitat and the proliferation of exotic species (e.g. cold-water salmonids) (Yard et al.

2011). Because of the scientific consensus on the negative consequences of Glen Canyon Dam on the aquatic ecosystem of the Colorado River in Grand Canyon there has been an increase in restoration efforts designed to manage the dam in a way that mimics elements of the historic flow regime with the intent of positively influencing native fish populations while preserving ecological integrity (Schmidt et al. 1998).

The Glen Canyon Dam Adaptive Management program was implemented in 1996 to address uncertainty in policy actions on the operation of Glen Canyon Dam on resources within the Colorado River ecosystem. Conservation of native Colorado River Basin fishes, particularly the endangered humpback chub was one of the primary goals of the program (Melis et al. 2006). In 2008 an adaptive management experiment was implemented to assess fish population responses to a series of planned steady flow releases from Glen Canyon Dam. Glen Canyon Dam is typically operated as a peak power facility under the modified low fluctuating flow regime in which the dam is peaked daily between 140 (m^3/sec) to 850 (m^3/sec) to produce hydroelectric power. Dam operations during September and October were scheduled to operate under a steady flow regime allowing humpback chub populations to be monitored during contrasting flow regimes. It was hypothesized that diel fluctuations in discharge could influence survival of native fish by destabilizing nearshore habitats that are thought to be important to juvenile humpback chub. Further, it was hypothesized that the steady flow regimes would raise temperature of nearshore areas and improve growth rates.

Despite long term monitoring programs which track native fish populations in Grand Canyon most research efforts have focused on humpback chub population status and trend (Coggins et al. 2003) with less attention on habitat use and requirements

(Gorman and Stone 1999; Stone and Gorman 2005). To date, there is only one published study on patterns of habitat use in humpback chub in the Colorado River in Grand Canyon (Converse et al. 1998) and a little information exists on the role dam operations play in structuring habitat use patterns.

The goal of this study is to assess habitat use of humpback chub using site occupancy models in the Colorado River in Grand Canyon during contrasting flow regimes to evaluate the impact of a steady flow regime from Glen Canyon Dam on humpback chub. This approach allows the estimation of un-biased habitat use or occupancy probabilities by explicitly accounting for heterogeneity in detection. Using this approach, I evaluated the importance of time varying, size specific, site specific and pass specific covariates on patterns of site occupancy while accounting for changes in detectability. This information on habitat use of humpback chub will help guide the management of the Colorado River in Grand Canyon by providing managers with insight into the influence of experimental flows, importance of habitat features and evaluation of sampling methodologies.

Methods

Study Area

This study was conducted within the Little Colorado River inflow area of the Colorado River in Grand Canyon (Figure 1-1). My study area was 4.5 km in total length and located between Heart Island (RM 125 RKM) and Lava Chuar Rapid (RKM 131.2). The study area was subdivided into three reaches approximately 1500 m in length (3,000 m total shoreline). Each of the study reaches was separated by small (~1.5-m height) rapids. Within each reach the shoreline was further broken up into adjacent 50-m nearshore sites using aerial photographs in a geographic information system (Figure

2-5). I sampled each reach during 12 river surveys in July, August, September, and October of 2009 through 2011.

Discharge Patterns

Discharge patterns were continuously monitored at 15-min intervals remotely at USGS gauge 09383100 (RKM 165). The Colorado River Flow Sediment and Stage model was used to back-calculate the difference in average water travel time between USGS gauge 0983100 and the study location (RKM 125-131.2) using an unsteady flow model (Wiele and Griffin 1997). As part of this study, July and August surveys during 2009 and 2010 sampling surveys occurred during the modified low fluctuating flow regime (MLFF, diel discharges of 250 to 500 m^3 sec in 2009; 300 to 500 m^3 sec in 2010), and September and October sampling surveys were sampled during the low steady flow regime (constant flows of 250 m^3 sec in 2009; 300 m^3 sec in 2010; Figure 1-2 and Figure 1-3). Due to increases in upper basin water inputs to Lake Powell in 2011 and record low reservoir levels in Lake Mead, discharge patterns in 2011 from GCD were a high steady flow regime (HSF) during July and August (constant flows of 715 m^3 sec) and a medium steady flow regime (MSF) during September and October (constant flows of 460 m^3 sec; Figure 1-4). Extensive tributary flooding during August and September 2010 caused increases in discharge that were unrelated to dam operations (Figure 1-3). Daily turbidity measurements were continuously monitored in 15-minute intervals remotely from an acoustic Doppler profiler at USGS gauge 09383100 (RKM 165). An unsteady flow model was used to back calculate water travel time to the study area (Wiele and Griffin 1997). Spikes in turbidity were caused by tributary floods.

Sampling Procedures

Hoop nets and boat electrofishing were used to sample humpback chub during this study to evaluate patterns of site occupancy. Eighty hoop nets were set within designated sites in the first and second sampling reach. The hoop net sites were fished during each of the four yearly sampling surveys during 2009 to 2011. Hoop nets were fished for 24 hour passes over 12 consecutive nights during each sampling survey. Boat electrofishing was conducted in sampling reaches one, two and three. The effective sampling area of hoop nets boat electrofishing was estimated to be a 50-m site within 4 m of shore. Sampling reach one had 58 sites, sampling reach two had 49 sites and sampling reach three had 52 sites. This sampling design allowed for all shoreline areas excluding rapids in my sampling area to be sampled completely. During 2009, each site within a reach was repeatedly sampled three times over a five day period for reaches one and two (48 hours between passes) and over successive nights in reach 3 (24 hours between passes). During 2010 and 2011, each site within a reach was repeatedly sampled three times over successive nights (24 hours between passes). Electrofishing surveys were conducted using two-6 m Osprey boats outfitted with either a Smith-Root Type 12b or Coffelt CPS system powered by a Honda 4500 watt generator to apply a complex pattern of pulsed DC (Speas et al. 2001, Korman et al. 2009). During each electrofishing pass, nearshore sites were shocked slowly (10 m^{-1} sec). All electrofishing sampling began at dark between 1800 hours and 2000 hours depending on season. All surveys were finished by 0300 hours. All fish captured during hoop net and electrofishing sampling were processed and returned to the site from which they were captured following standard sampling protocols (Persons et al. 2011).

Catch data for humpback chub were stratified by size class and converted to a binary encounter history of presence-absence observations. Hoop net catches by pass were stratified into three size classes: 40-80 mm, 81-150 mm, and 150-250 mm. Electrofishing catches by pass were stratified into 40-80 mm and 81-150 mm size classes. Size classes were determined by visually analyzing length-frequency histograms. Humpback chub greater than 150 mm in electrofishing and 250 mm in hoop net surveys were captured too infrequently to be used in occupancy models and excluded from analysis.

Habitat Classification and Covariates

A suite of site specific categorical and continuous habitat covariates were used for modeling humpback chub detection and occupancy probabilities (Table 2-1). Categorical habitat covariates used included habitat type and hydraulic type. Continuous habitat covariates included substrate proportion, mean depth and mean site depth^2 (Table 2-1). Habitat type in each site was classified in field into four discrete habitat types: cliff, debris fan, talus slope and sandbar following Converse (et al. 1998). Cliff habitats were characterized as shear walls rising vertically and laterally over the river. Debris fans were characterized as shorelines of large cobble and boulder that were transported into the river corridor by tributaries during flooding. Sandbar habitats were classified as shorelines of contiguous beach and exposed sand. Talus habitats were classified as shorelines consisting mainly of boulders deposited by rockslides and rockfall. The hydraulic type of a site was mapped in the field and split into two discrete types: eddy flow and downstream flow. Eddies represent areas of recirculating flow that generally occur downstream of channel constricting debris fans. The downstream category represents any portion of the river where the water is traveling downstream.

Substrate classes were grouped into three classes: small, medium and large substrates using a modified Wentworth scale. In GIS, a 4 m (electrofishing sites) and 10 m (hoop net sites) buffer was applied to the river edge and the proportion of each substrate category in the site was calculated. Substrates classified as small ranged from silt to course sand. Substrates classified as medium represented small gravel to small cobble. Substrates classified as large ranged in size from large cobble to boulder. A bathymetry map of the study reach was used to determine the mean elevation of each hoop net and electrofishing site along the river edge. Similar to the substrate classification a 4 m and 10 m buffer were applied to electrofishing and hoop net sites. Depth was determined as the average shoreline elevation minus the average elevation of the river bottom within each site.

Description of Occupancy Models

The estimation of occupancy and detection probabilities required the use of presence absence data from repeated hoop net and electrofishing passes. Multi-season occupancy models estimated probabilities of site occupancy and detection probability using the encounter histories (h_i) within a given site for a given survey (MacKenzie et al. 2006, Donovan and Hines 2007). As an example, an observed h_i =010 represents a site that was sampled for 3 passes in a survey. Given incomplete detection, the species was observed only during the second pass. The probability of the following h_i is:

$$\mathrm{p(hi)} = \Psi(1-\mathrm{p1})(\mathrm{p2})(1-\mathrm{p3})$$

where Ψ is the probability of site occupancy, p_i is the probability that a species in detected in pass $_i$. 1-p_i is equal to the probability that the species in not detected during pass $_i$. An observed detection history, h_i = 000 indicates that during each of the 3 passes the species of interest was not detected. Given that detection probability is less than one this detection history can arise two ways: the species is truly absent or the species is occupying the site yet undetected. The probability of h_i=000 is:

$$p(hi) = \Psi(1 - p1)(1 - p2)(1 - p3)(1 - \Psi)$$

where $\Psi(1\text{-}p_1)(1\text{-}p_2)(1\text{-}p_3)$ is the probability that the species of interest was present at the site but undetected and (1-Ψ) represents the probability that the species of interest does not occupy the site of interest. Detection (p) and occupancy (Ψ) were estimated by maximizing the following model likelihood:

$$L(p, \Psi|h_i) = \Pi \, Pr(h_i),$$

which represents the product of each encounter histories (h_i) probability (MacKenzie et al. 2002, MacKenzie et al. 2006, Donovon and Hines 2007) .   A logit link function was used to model the effect of covariates on occupancy and detection probabilities. The logit link function is specified as:

$$\ln[\theta/1 - \theta i] \; = \; \beta_0 + \beta_1 * x_i + \cdots + \beta_j x_{ij},$$

where θ is the parameter of interest (occupancy or detection), β_j is the effect of the given covariate x_{ij}. β_o is the intercept of the model.

Assumptions of multi-season occupancy models included: (1) Detectability and occupancy probability of humpback chub is constant among sites or heterogeneity in detection and occupancy can be modeled completely with the inclusion of covariates, (2) detection of humpback chub are independent at each site, and (3) sites are closed to changes in occupancy by humpback chub during the course of a sampling survey (season). I further assumed that assumption three could be relaxed if movement in and out of a site occured randomly (Kendall 1999; MacKenzie et al. 2006).   When random localized movement occurs it is appropriate to restrict our interpretation of occupancy models to the proportion of sites used rather than the proportion of sites occupied (MacKenzie et al. 2006).

Model Structure (p and Ψ)

A priori models were developed to propose mathematical descriptions of factors that influenced site occupancy and detection probability of humpback chub (Table 1-1). Following the recommendation of MacKenzie et al. (2006), models were fit for detection probability first and the best model for detection was selected to model site occupancy. Covariates included in models were presumed to be biologically important to occupancy and detection probabilities. Time varying, size specific, site specific and pass specific covariates were considered. Time varying covariates included survey (e.g. 1-12), flow regime (e.g. MLFF, LSF, MSF, HSF), year (e.g. 2009, 2010, 2011) and year + flow regime (e.g. unique parameter for each year-flow regime combination). Size specific covariates included humpback chub size class. Site specific covariates included sampling reach (electrofishing only), mean site depth, substrate proportion (e.g. small, medium, large), site habitat type and site hydraulic type. Mean site depth^2 was also considered to determine if site occupancy and detection exhibited a non-linear response to this covariate. Turbidity was considered a pass specific covariate and was only modeled for detection probability (Table 1-1).

Competing detection and occupancy models were compared using Akaike's information criteria (AIC, hereafter; Burnham and Anderson 2002). AIC ranks competing models by comparing maximized log-likehoods while applying a penalty for the number of model parameters. ΔAIC was used to visualize the top model. Model weights (w_i) were calculated to determine the support each model received given the data. Because of model uncertainty models with AIC w_i greater than 0.05 were also used to draw inference from. All occupancy models were fit using Program Presence 3.1 (Hines 2011).

Results

Catch Composition

Eighty hoop net sites were sampled over the course of 12 sampling surveys in 2009 to 2011. Because of inconsistency in site location and increased number of sites in 2010 and 2011 only 57 sites were included in subsequent analyses for fish captured in hoop nets. A total of twelve fish species were collected in hoop net surveys while 15 species were sampled during electrofishing surveys. During hoop net surveys humpback chub (HBC) were the numerically dominate catch in 2009-2011 accounting for 74%, 72.5% and 76% of the total catch (Table 2-2). A total of 158 electrofishing sites were sampled a total of 36 times over 12 surveys in 2009 to 2011. Humpback chub (HBC) accounted for 16% and 10% of the catch in 2009 and 2010 while increasing to 24% of the total catch in 2011.

Detection Probabilities

Hoop net

A total of fourteen models were constructed to assess heterogeneity in detection across a range of physical, temporal and biological attributes (Table 2-1). The best fitting model estimated a range of detection probabilities between 0.05-0.33 and included sampling survey, fish size, and a quadratic form depth (including mean depth + mean depth squared in model statement) as covariates (Figure 2-6, Table 2-2). Detection probabilities were lowest for humpback chub 150-250 mm and highest for chub 40-80 mm and 81-150 mm. Humpback chub 150-250 mm were detected significantly less than chub between 40-80 mm and 81-150 mm across all sampling surveys with the exception of October of 2009 (Figure 2-6). The best fitting model also indicated that the probability of detection was highest at intermediate depths (Figure 2-7). Detection models that included other habitat covariates (Table 2-1) were not supported by the data (Table 2-2). Models that did not include sampling survey and fish size as covariates performed poorly (Table 2-2). There was no support for models that modeled heterogeneity of detection as a function of year of sampling or flow regime.

Electrofishing

A total of sixteen models were constructed to model heterogeneity in detection probability of humpback chub captured during electrofishing surveys (Table 2-3). The top detection model included sampling survey, sampling reach, humpback chub size class and substrate heterogeneity (proportion of medium sized substrate within the site sampled) as important covariates (Table 2-3). Detection probability estimates for this model ranged by time and fish size from the highest values in September of 2011 (range=0.18-0.54) to lowest in October of 2009 (range=0.05-0.22) (Figure 2-8; Figure 2-10). Detection probabilities for humpback chub between 40-80 mm captured during electrofishing surveys were always higher than detection probabilities for fish between 81-150 mm across all sampling surveys and sampling reaches. Detection probabilities for both 40-80mm and 81-150 mm humpback chub exhibited a monotonic decline from sampling reach one to reach three in 2009 through 2011 (Figure 2-8; Figure 2-9, Figure 2-10). The best fitting model also indicated that there was a positive relationship between the probability of detection and substrate heterogeneity (proportion of medium substrate within a habitat sampling unit) (Figure 1-11). The second best fitting model, ranked by AIC was parameterized similarly to the top model except that a negative relationship between detection probability and substrate homogeneity (proportion small substrate within a site) was observed (Table 2-3, Figure 2-12). Detection models that included other habitat covariates (Table 2-3) were not supported by the data. Models that did not include survey, reach and size as covariates fit the data poorly (Table 2-3). There was no support for models that modeled heterogeneity of detection as a function of year of sampling or flow regime.

Occupancy Probabilities

Hoop net

A total of thirteen models were constructed to model heterogeneity in occupancy (habitat use) probability of humpback chub captured in hoop nets as a function of habitat, temporal and biological attributes. The best fitting model indicated that occupancy probability varied as a function of survey of sampling and size category of humpback chub (Table 2-4). Estimated occupancy probabilities were relatively consistent among surveys and size class with a mean occupancy probability of 0.80 (Figure 2-13). During all surveys chub 151-250 mm exhibited the lowest occupancy probability but this result was not statistically significant. The inclusion of habitat covariates to explain occupancy did not result in a significant improvement in model fit or significant habitat relationships (Table 2-4).

Electrofishing

A total of eighteen models were constructed to model occupancy (use) probability of humpback chub observed in electrofishing surveys. The model best supported by the data indicated that occupancy probability varied as a function of year, flow regime and size category. Overall occupancy probabilities ranged from 0.72 -0.90 for chub 40-80 mm and 0.28-0.59 for fish 81-150 mm (Figure 2-12). Occupancy probabilities for humpback 40-80 mm and 81-150 mm declined slightly through time

(Figure 2-12). Eight additional models were within a Δ AIC of 5 of the top model (Table 1-5). Each of these models were parameterized identically to the top model except that they each had a habitat covariate included. The inclusion of habitat covariates in occupancy models did not significantly improve model fit and exhibited weak insignificant habitat relationships (Table 1-5). Models that included survey as a covariate provided poor model fit (Table 1-5).

Discussion

During this study, occupancy probabilities were observed to be consistently high and there was no marked change in occupancy state between the fluctuating flow regime and experimental steady flow regimes. This is interesting because it had been hypothesized that stabilized steady flow would elicit a population level response causing occupancy patterns to change between flow regimes. Because estimates of occupancy probabilities were high, robust relationships between habitat covariates and humpback occurrence were not able to be estimated. Detection probabilities exhibited considerable heterogeneity reflecting differences among survey, size class and habitat covariates.

The magnitude of discharge releases from Glen Canyon Dam between the fluctuating flow regime and steady flow regimes may not have been sufficient to elicit a response in humpback chub populations. The implementation of modified low fluctuating flow in 1996 reduced the diel range in discharge and reduced the frequency of low flow events (Gloss et al. 2006) effectively minimizing large daily contrasts in discharge from GCD. Despite differences in discharge during field surveys from 2009 to 2011 the ranges of flows observed in this study were within the operational constraints of modified low fluctuating flow. If the contrasts in flow regimes had been greater humpback chub responses to steady flow experiment may have been observed.

The spatial location of the study area may have contributed to the lack of a response to flow variation by humpback chub. Korman (et al. 2004) modeled humpback chub habitat use over a range of discharges and found that areas which were comprised of steep angle shoreline such as talus and debris fan habitat types were more robust to changes in discharge than low-angle homogenous shorelines such as sandbars. About 60% of my study area was comprised of talus and debris fan shorelines and geomorphically defined by eddy-fan complexes. The high structural complexity of shorelines in my study area may act as a refuge from discharge fluctuations which allowed humpback chub to be resistant to changing river stage (Korman et al. 2004). I postulate that the general habitat attributes available to juvenile humpback chub likely did not change enough between the fluctuating flow and the steady flow regimes to necessitate a shift in habitat use. While there is no natural analog in river systems to a fluctuating flow regime, minor peaking operations such as modified low fluctuating flow operations from Glen Canyon Dam may not influence how chub use habitat significantly. However, this could vary spatially and temporally.

The timing of the steady flow experiment may have influenced the lack of response by humpback chub to the steady flow regimes. The steady flow regimes prescribed by the Bureau of Reclamation were designed to take place in the fall of each year. Different experimental designs that alternated the timing of the steady flows (e.g. Fall Steady Flow 2009, Summer Steady Flow 2010, Fall Steady Flow 2011) were not considered. Thus, I was unable to assess how flow regime and season interact to influence occupancy. The potential benefits of steady flows to humpback chub vary based on the timing and size of discharge releases. During this study measured differences in nearshore temperatures between the fluctuating and steady flow during the 2010 field season were negligible (Ross and Grams 2011) suggesting that the hypothesis of differential warming of nearshore areas was not achieved given the implemented experimental design. A previous steady flow experiment implemented in the summer of 2000 demonstrated that nearshore water temperatures do warm considerably if the discharge releases are low and the timing allows for maximum absorption of solar radiation (i.e. summer) (Trammel et al. 2002). To better understand the interaction between Glen Canyon Dam operations and humpback chub populations, future flow experiments should give careful consideration to the magnitude of discharge released from Glen Canyon Dam, the spatial location where fish monitoring will occur and the timing of discharge releases.

In this study no strong relationships between habitat covariates and site occupancy were established. This suggests that given the parameters measured and modeled, no single variable was a strong predictor of whether a habitat will be occupied by humpback chub. Past research by Converse (et al. 1998) suggested that juvenile humpback chub selected vegetated, talus and debris fan habitat attributes while generally avoiding cobble, bedrock and sandy habitats attributes. Differences in observed habitat relationships between this study and prior research may be a result of multiple factors. Abundances of humpback chub have increased substantially in recent years (Coggins et al. 2011). Given the high abundances of chub, habitat relationships may not be apparent using occurrence data because most available nearshore habitats within my study area were being used. Inference from this research is restricted to a 4.5 km section of the Colorado River that has the highest abundances of chub of any location in Grand Canyon. Factors governing humpback chub occupancy may occur at a scale larger than was considered in this study and future research on humpback chub habitat use should increase the spatial extent of the study site to improve on the strength of inference. In the future, the use of occupancy models as an analytical technique may be most useful when combined with a generalized linear modeling approach that estimates habitat covariate influence on humpback chub abundance. This nested approach would allow occupancy models to determine the scale at which chub occurrence varies and the generalized linear model would identify factors that are related to fish density.

Previous assessments of habitat use of humpback chub in Grand Canyon did not incorporate an estimation of detectability; therefore, it is uncertain if the observed patterns of catch are in fact differences in habitat use or whether sampling was more effective in particular habitats (Valdez and Ryal 1995, Converse et al. 1998, Hubert and Fabrizio 2007). Detection probabilities in this study varied among humpback chub size category and survey suggesting size selectivity of the gear and temporal variation in humpback chub available for capture. Habitat characteristics including mean site depth and substrate heterogeneity were also observed to influence detection probability depending on the gear type used for sampling. Understanding how detection changes temporally, with fish size and site habitat characteristics will be useful for future and research and monitoring activities.

As humpback chub grow they undergo an ontogenetic habitat shift from using nearshore habitats as juveniles to large recirculating eddies as adults (Stone and Gorman 1999, Gerig 2012). Hoop net detectability was increased at intermediate depths 5-10 m from shore and most effectively sampled humpback chub size classes between 40-80 mm and 81- 150 mm. Larger humpback chub having undergone their ontogenesis may move in and out of the effective sampling area of an individual hoop net while occupying an area larger than an individual habitat site. Juvenile chub between 40-80 mm which reside in nearshore habitats exhibited higher detection probabilities when sampled using boat electrofishing and habitat sub-units with increased substrate heterogeneity had higher detection probabilities. Sites of increased substrate heterogeneity may offer increased interstitial space for small fish and may act as a refuge from discharge fluctuations and predators. In general, to maximize detection probability for humpback chub boat electrofishing should be considered for to sample fish under 80 mm while hoop netting is most effective for fish between 81-150 mm.

Temporal variation in detection probabilities of humpback chub were observed between sampling surveys within and between years (Figures 1-4, 1-6, 1-7). Considering sampling survey as a covariate likely integrates important biotic and physical factors such as season, overriding turbidity and humpback chub abundance that can act in concert to influence detection probability. The large reduction in detection probability in October of 2009 may be related to turbidity conditions. Turbidity conditions during the October survey of 2009 were the lowest observed during the course of the study (mean=4 NTU). In response to low turbidity conditions, humpback chub may reduce movement and seek physical cover in talus or debris fan shorelines, move to deep locations outside of the effective sampling area or emigrate from the sampling universe due to a perceived increase in predation risk caused by clear water (Stone 2011). In contrast to Stone (2011), humpback chub in the mainstem Colorado River may not seek hoop nets as cover during periods of extremely low turbidity. In 2010 and 2011, detection probabilities increased consistently from July to September and plateaued or decreased from September to October. Detectability is influenced by increases or decreases in abundance (MacKenzie and Royale 2005). Timing of emigration of humpback chub from the Little Colorado River varies through time and by fish size (Gorman and Stone 1999) and is likely influenced by timing of monsoonal floods which cause small to large flood pulses. Floods of sufficient size likely elicit an emigration event of juvenile and newly recruited humpback chub rearing in the Little Colorado River to move to the mainstem Colorado River. An active flood year in the LCR basin in 2010 and smaller events in 2011 may have been responsible for the increase in detection probability that was observed between surveys.

Table 2-1. Covariates thought to influence probability of occupancy and probability of detection of fish in Colorado River in Grand Canyon.

Predictor	Inference to Occupancy (Ψ)	Inference to Detection (p)
Depth	Ψ varies with mean depth of site	p varies with mean depth of site
Substrate small	Ψ varies with proportion small subs.in site	p varies with proportion small subs. in site
Substrate medium	Ψ varies with proportion medium subs. in site	P varies with proportion medium subs. in site
Substrate large	Ψ varies with proportion large subs. in site	p varies with proportion large subs. in site
Turbidity (NTU)	Does not influence Ψ	p is influenced by turbidity level
Habitat type	Ψ varies by habitat type of site	p varies with habitat type of site
Hydraulic type	Ψ varies by hydraulic type	p varies with hydraulic type
Reach (EF)	Ψ varies spatially by reach for electrofishing	p varies spatially by reach for EF
Survey	Ψ varies temporally between surveys	p varies temporally between surveys
Year	Ψ varies with temporal variation in abundance	p varies with temporal variation in abundance
Flow Regime	Ψ varies with dam operations	p varies with dam operations

Table 2-2. Ranking of site occupancy models used to estimate detection probability of humpback chub captured in repeated hoop net surveys from 2009-2011.

Model	AIC	ΔAIC	AIC wt	K[a]
Ψ(.), p(Size+Survey+Depth+Depth^2)	20733	0	0.9998	18
Ψ(.), p(Size+Survey+Depth)	20751	17.13	0.0002	17
Ψ(.), p(Size+Survey+Large)	20755	21.58	0	17
Ψ(.), p(Size+Survey+Medium)	20772	38.66	0	17
Ψ(.), p(Size+Survey+Habitat)	20773	39.84	0	19
Ψ(.), p(Size+Survey+Small)	20775	41.17	0	17
Ψ(.), p(Size+Survey+Hydraulic Type)	20778	44.4	0	17
Ψ(.), p(Size+Survey)	20783	49.37	0	16
Ψ(.), p(Size+Survey+NTU)	20783	49.42	0	17
Ψ(.), p(Size+Year+Flow Regime)	20988	254.09	0	11
Ψ(.), p(Size+Flow Regime)	21058	324.71	0	9
Ψ(.), p(Size+Year)	21087	353.63	0	8
Ψ(.), p(Size)	21126	392.19	0	5
Ψ(.), p(.)	21202	468.54	0	3

[a] = # of parameters

Table 2-3. Ranking of site occupancy models used to estimate detection probability of humpback chub in repeated electrofishing surveys from 2009-2011.

Model	AIC	ΔAIC	AIC wt	K[a]
Ψ(.), p(Size+Reach+Survey+Medium)	9216.44	0	0.7837	18
Ψ(.), p(Size+Reach+Survey+Small)	9219.19	2.75	0.1981	18
Ψ(.), p(Size+Reach+Survey+Depth)	9225.49	9.05	0.0085	18
Ψ(.), p(Size+Reach+Survey +Habitat)	9226.01	9.57	0.0065	20
Ψ(.), p(Size+Reach+Survey+Depth+Depth2)	9227.47	11.03	0.0032	19
Ψ(.), p(Size+Reach+Survey+Hydraulic Type)	9237.83	21.39	0	18
Ψ(.), p(Size+Reach+Survey+Large)	9247.31	30.87	0	18
Ψ(.), p(Size+Reach+Survey+NTU)	9248.94	32.5	0	18
Ψ(.), p(Size+Reach+Survey)	9250.49	34.05	0	17
Ψ(.), p(Size+Season)	9329.09	112.65	0	15
Ψ(.), p(Size+Reach+Year+Flow Regime)	9339.02	122.58	0	12
Ψ(.), p(Size+Reach)	9353.4	136.96	0	6
Ψ(.), p(Size+Year)	9431.67	215.23	0	7
Ψ(.), p(Size+Flow Regime)	9433.62	217.18	0	8
Ψ(.), p(Size)	9434.05	217.61	0	4
Ψ(.), p(.)	9590.02	373.58	0	3

[a] = # of parameters

Table 2-4. Ranking of site occupancy models used to estimate occupancy probability of humpback chub in Grand Canyon.

Model	AIC	ΔAIC	AIC wt	K[a]
Ψ(Size+Survey), p(Best)	20703.45	0.00	0.5729	31
Ψ(Size+Survey+Hydraulic Type), p(Best)	20704.23	0.78	0.3879	32
Ψ(Survey), p(Best)	20708.88	5.43	0.0379	29
Ψ(Size+Survey+Small), ,p(Best)	20716.76	13.31	0.0013	26
Ψ(Size+Survey+Medium), p(Best)	20718.03	14.58	0.0007	26
Ψ(Year+Flow Regime+Size), p(Best)	20719.10	15.65	0.0002	26
Ψ(Size+Survey+Large),γ(.),p(Best)	20720.99	17.54	0.0002	26
Ψ(Size+Survey+Depth), p(Best)	20721.09	17.64	0.0001	26
Ψ(Year+Flow Regime), p(Best)	20723.71	20.26	0	23
Ψ(Flow Regime+Size), p(Best)	20724.12	20.67	0	23
Ψ(Flow Regime), p(Best)	20728.38	24.93	0	21
Ψ(Year+Size), p(Best)	20732.05	28.60	0	22
Ψ(.), p(Best)	20733.44	29.99	0	18
Ψ(Year), p(Best)	20736.16	32.71	0	20
Ψ(Size+Survey+Habitat), p(Best)*				
Ψ(Size+Survey+Depth+Depth^2), p(Best)*				

[a] = # of parameters, * model did not converge

Table 2-5. Ranking of site occupancy models used to estimate occupancy probability of humpback chub in Grand Canyon.

Model	AIC	ΔAIC	AIC wt	K[a]
Ψ(Year+Flow Regime+Size), p(Best)	9160.19	0	0.2189	24
Ψ(Year+Flow Regime+Size+Reach), p(Best)	9160.5	0.31	0.1875	26
Ψ(Year+Flow Regime+Size+Medium), p(Best)	9161.35	1.16	0.1226	25
Ψ(Year+Flow Regime+Size+Hydraulic Type), p(Best)	9161.92	1.73	0.0922	25
Ψ(Year+Flow Regime+Size+Large), p(Best)	9161.98	1.79	0.0894	25
Ψ(Year+Flow Regime+Size+Small), p(Best)	9162.07	1.88	0.0855	25
Ψ(Year+Flow Regime+Size+Habitat), p(Best)	9162.11	1.92	0.0838	27
Ψ(Year+Flow Regime+Size+Depth), p(Best)	9162.17	1.98	0.0813	25
Ψ(Year+Flow Regime+Size+Depth+Depth^2), p(Best)	9164.17	3.98	0.0299	26
Ψ(Year+Size), p(Best)	9166.61	6.42	0.0088	21
Ψ(Size+Reach), p(Best)	9181.92	21.73	0	21
Ψ(Size), p(Best)	9185.77	25.58	0	19
Ψ(Survey+Size), p(Best)	9201.95	41.76	0	30
Ψ(Year), p(Best)	9215.15	54.96	0	20
Ψ(.), p(Best)	9216.44	56.25	0	18
Ψ(Flow Regime), p(Best)	9216.84	56.65	0	21
Ψ(Reach), p(Best)	9218.93	58.74	0	20
Ψ(Year+Flow), p(Best)	9219.66	59.47	0	23
Ψ(Survey), p(Best)	9228.25	68.06	0	29

[a] = # of parameters

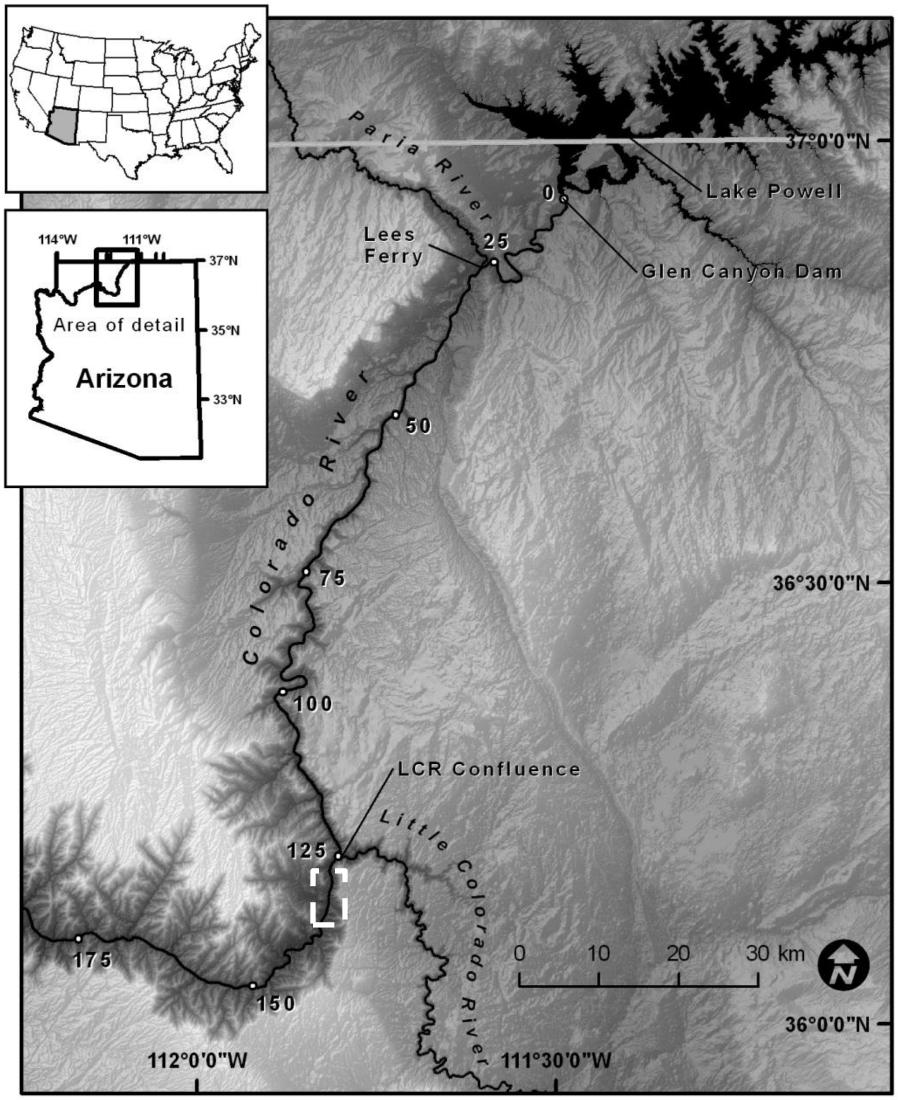

Figure 2-1. Map of the study site in the Colorado River in Grand Canyon, AZ. Study site was between Heart Island to Lava Chuar Rapid. White dashed box represents sampling area.

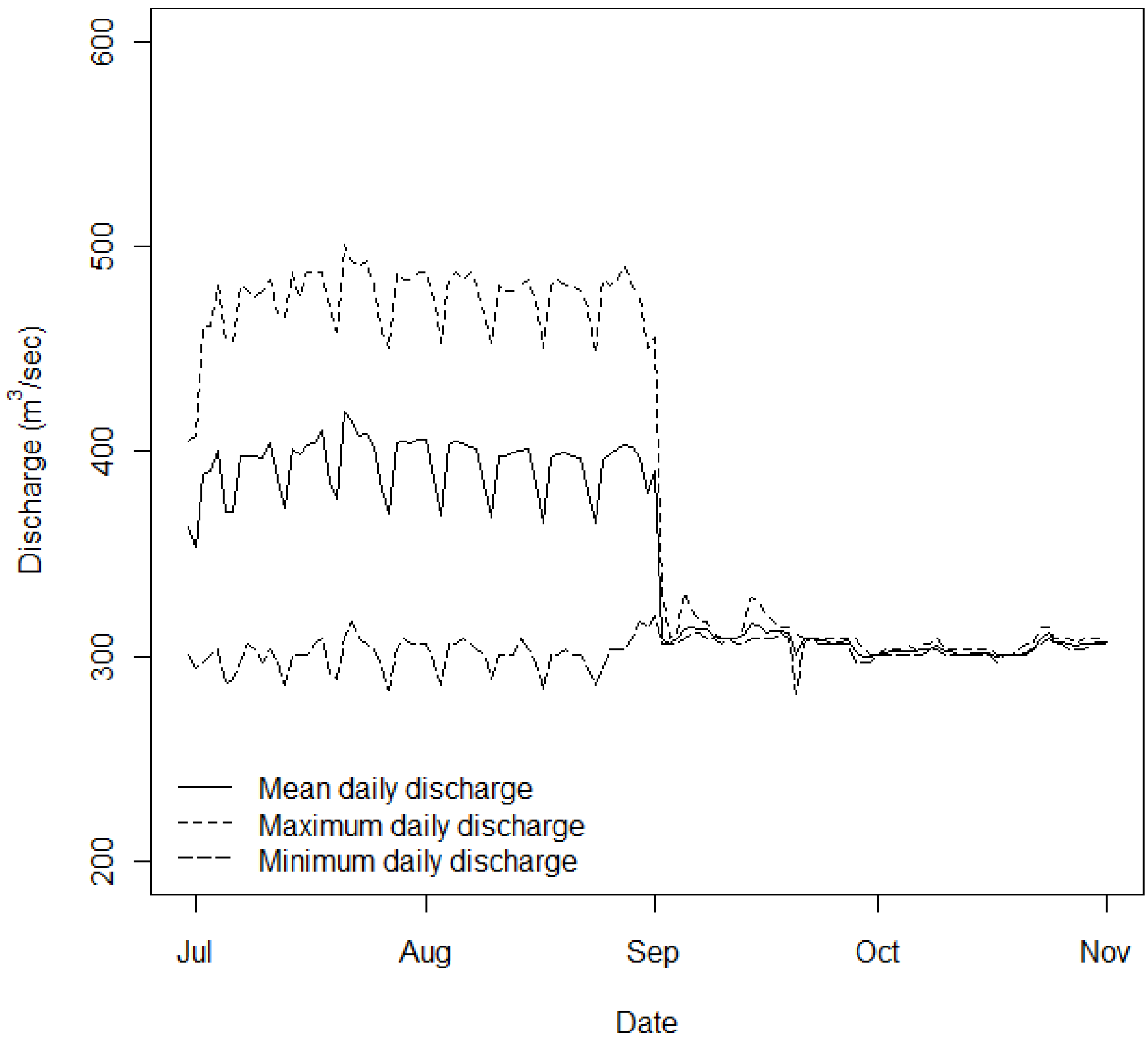

Figure 2-2. Discharge patterns during field sampling in 2009.

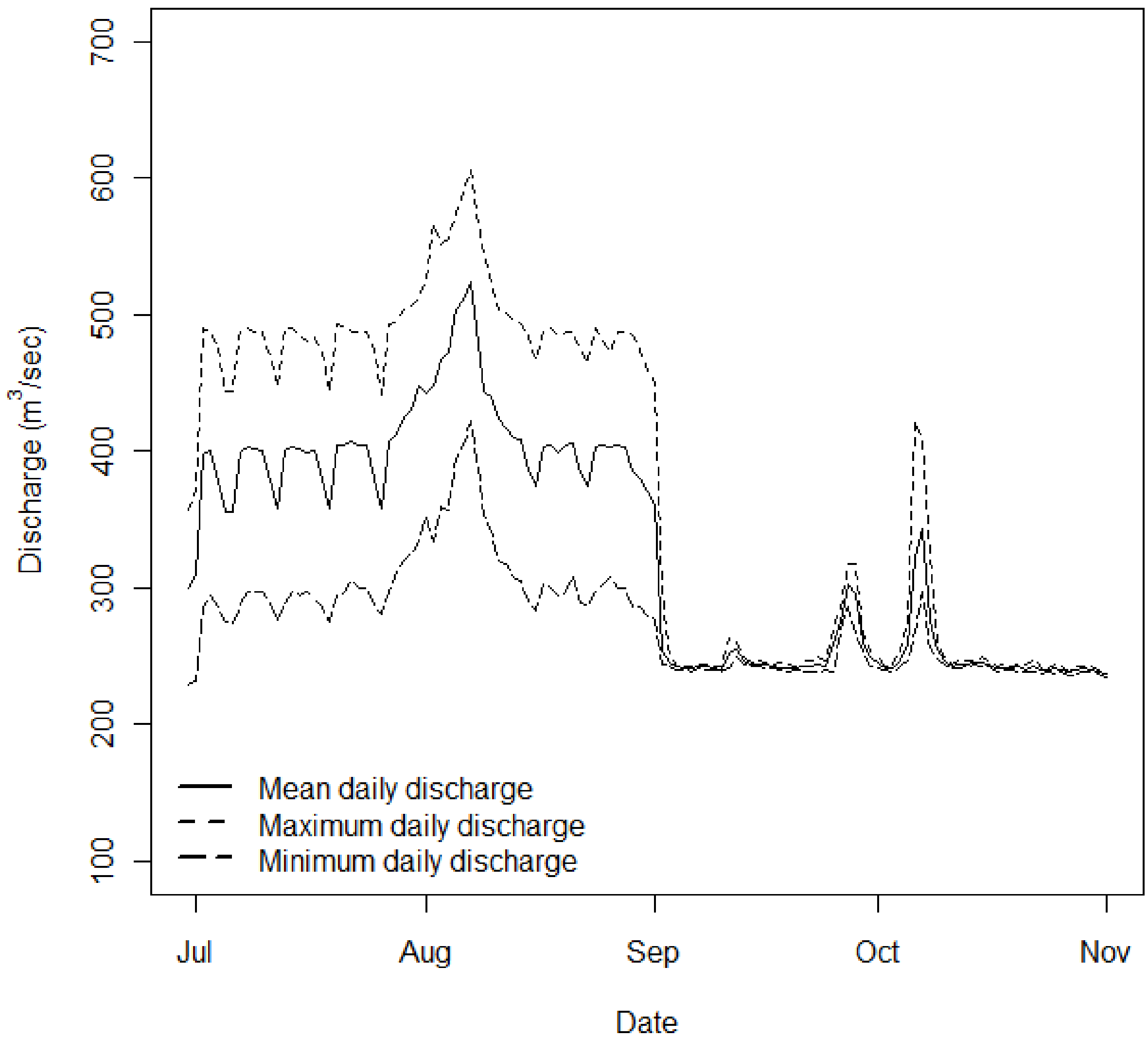

Figure 2-3. Discharge patterns during field sampling in 2010.

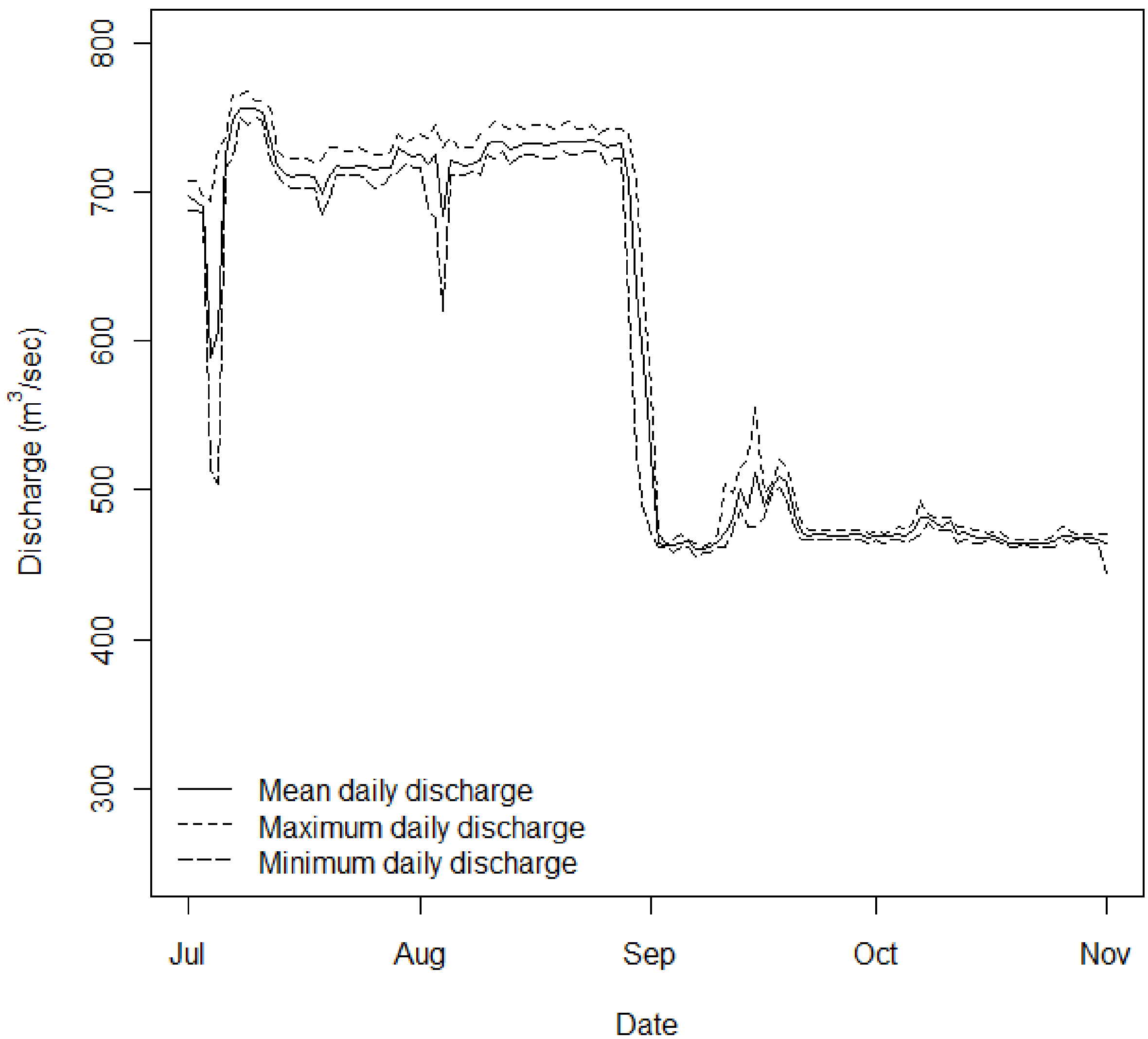

Figure 2-4. Discharge patterns during field sampling in 2011.

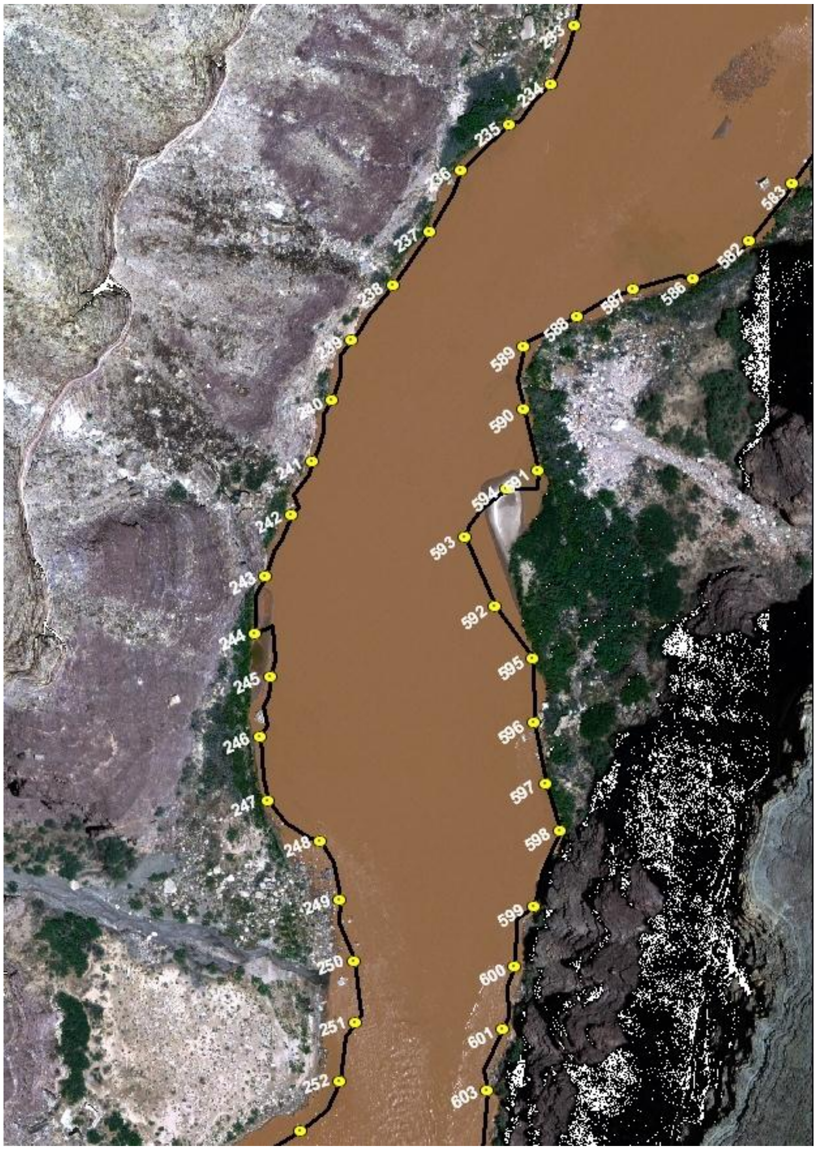

Figure 2-5. Aerial image from a GIS showing the typical arrangement of 50-m habitat sub units along shoreline habitats.

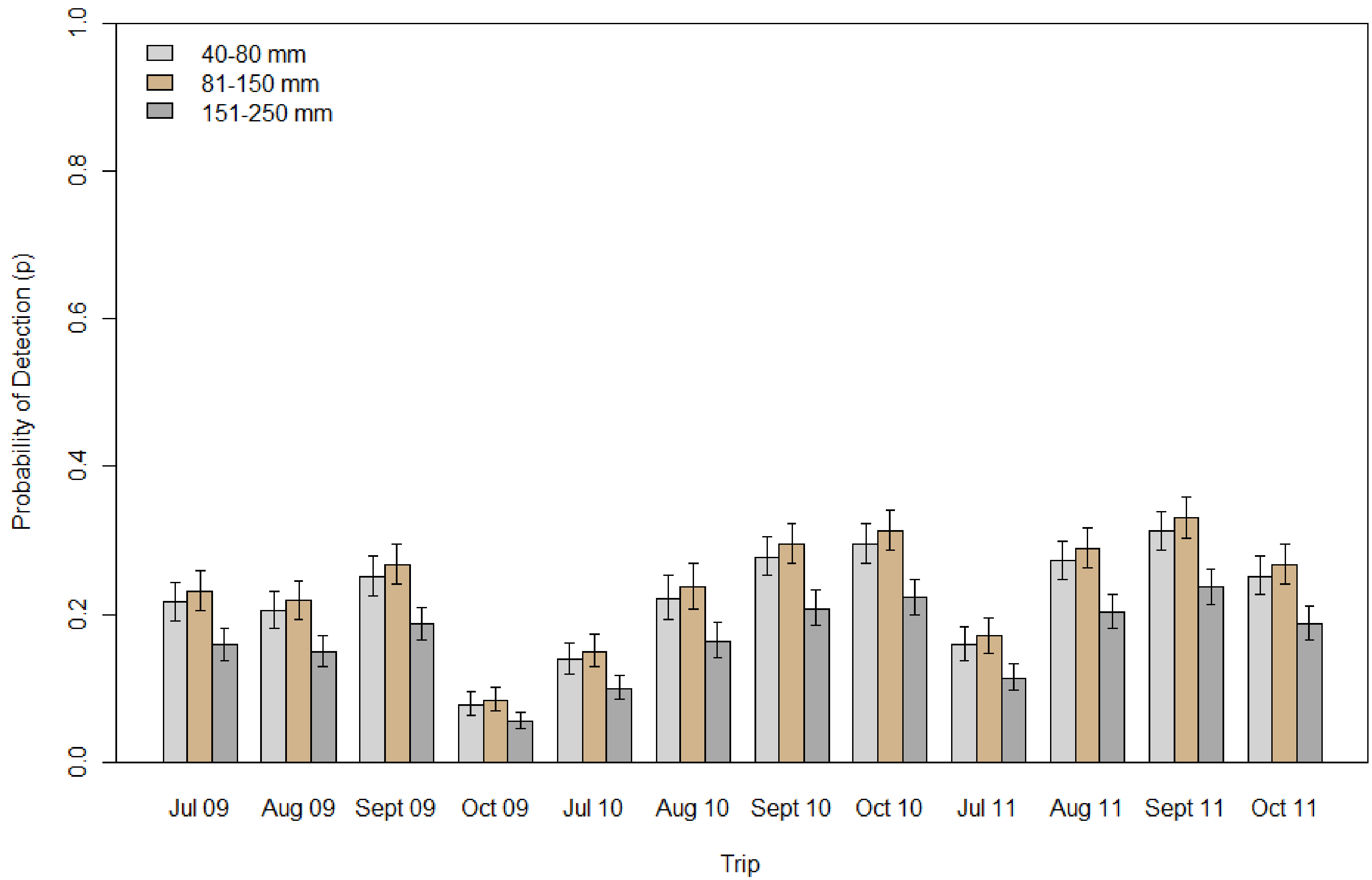

Figure 2-6. Patterns of detection probability for different size categories of humpback chub during repeated hoop net surveys in 2009-2011.

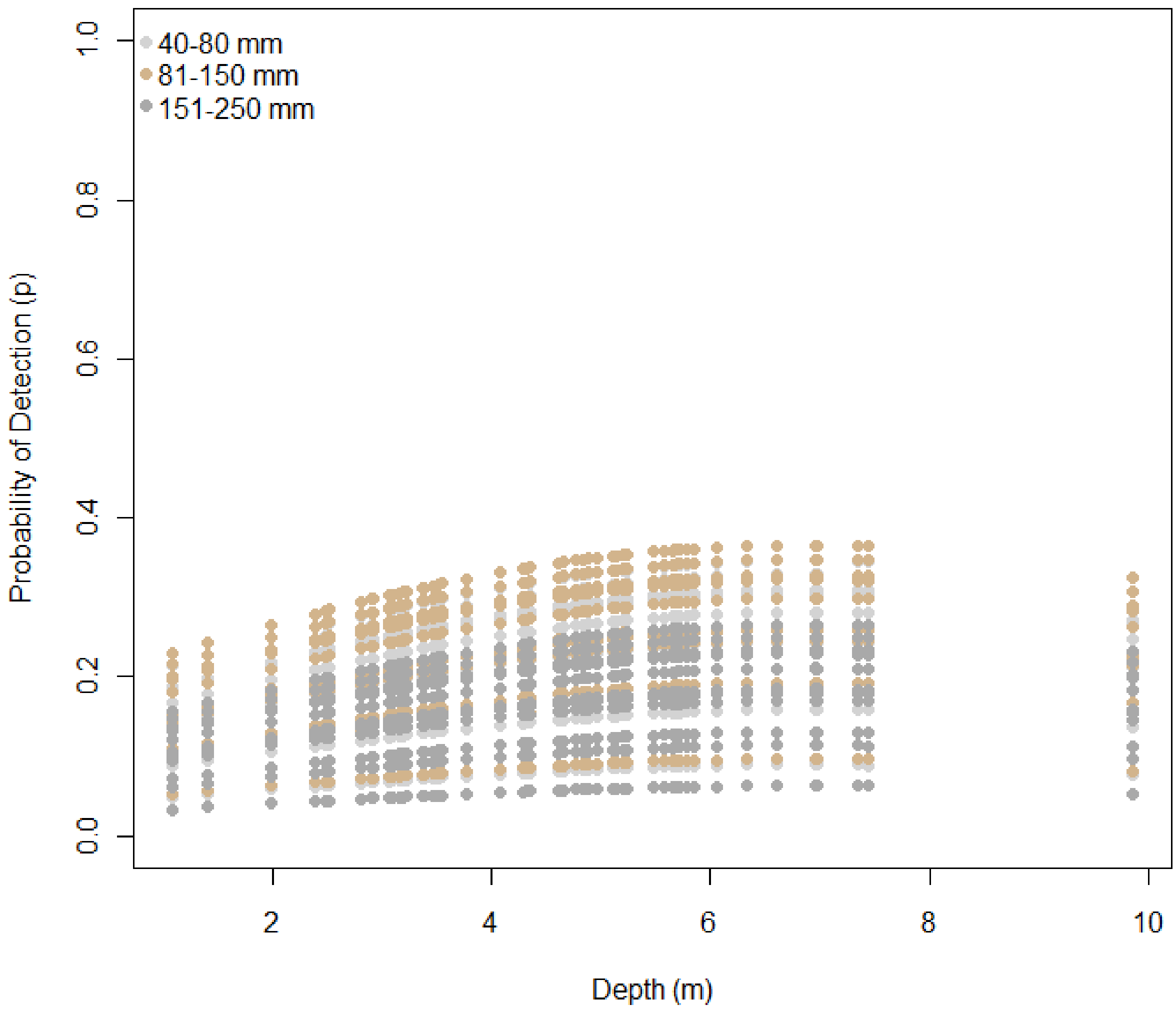

Figure 2-7. Relationship between probability of detection and mean depth of site during repeated hoop net surveys 2009 to 2011.

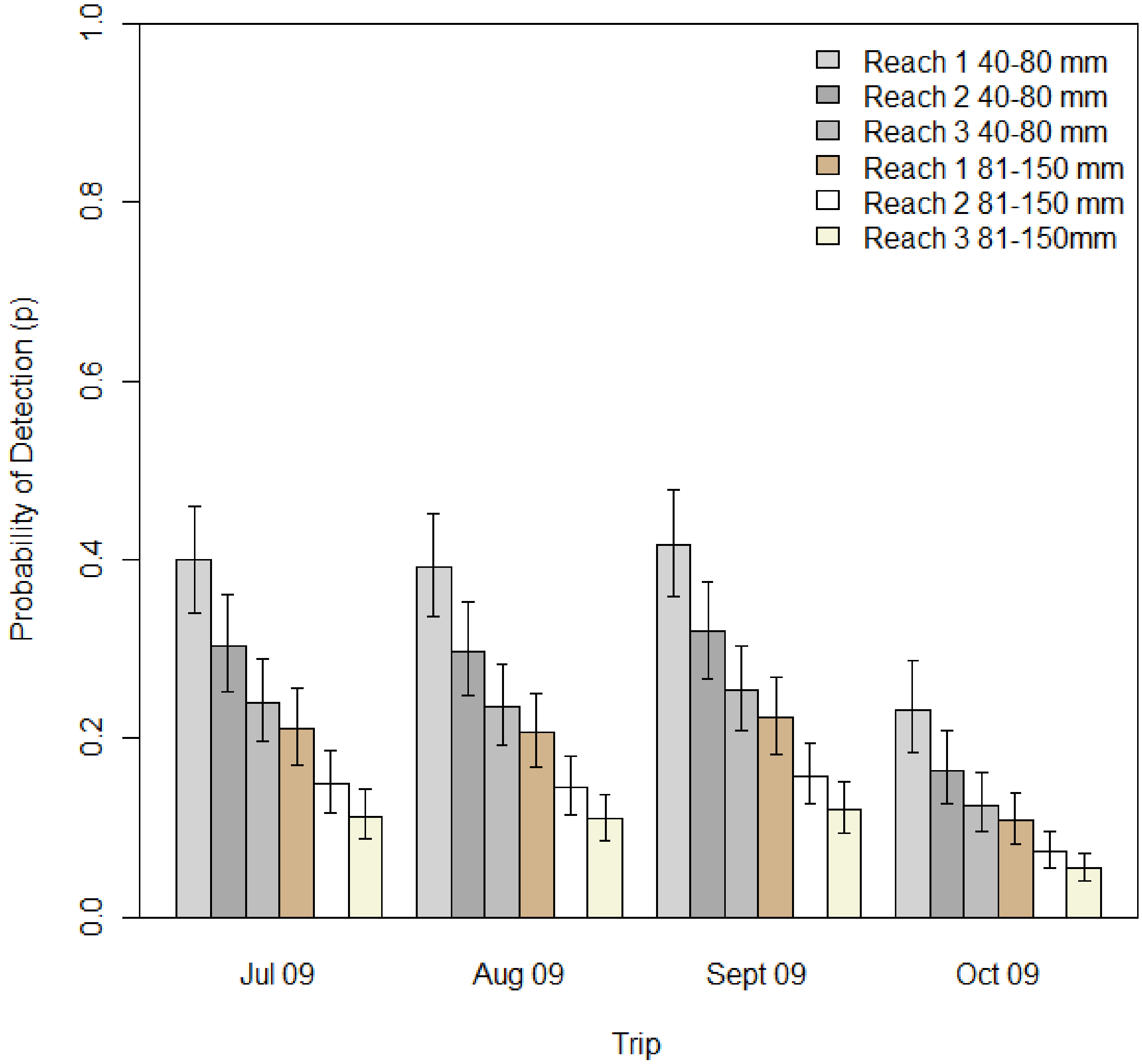

Figure 2-8. Patterns of detection probability for stratified by size category of HBC during repeated electrofishing surveys in 2009.

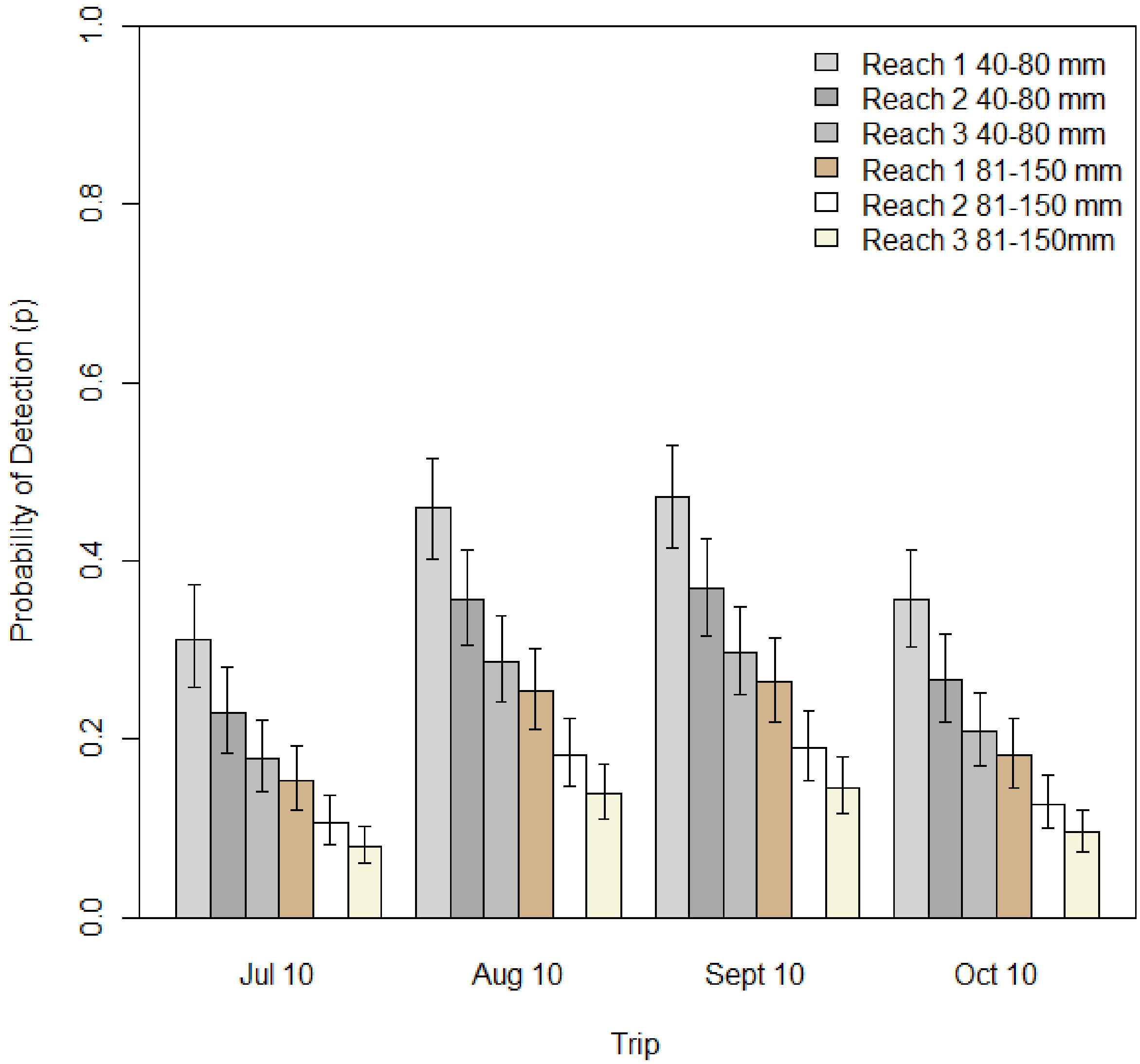

Figure 2-9. Patterns of detection probability for stratified by size category of HBC during repeated electrofishing surveys in 2010.

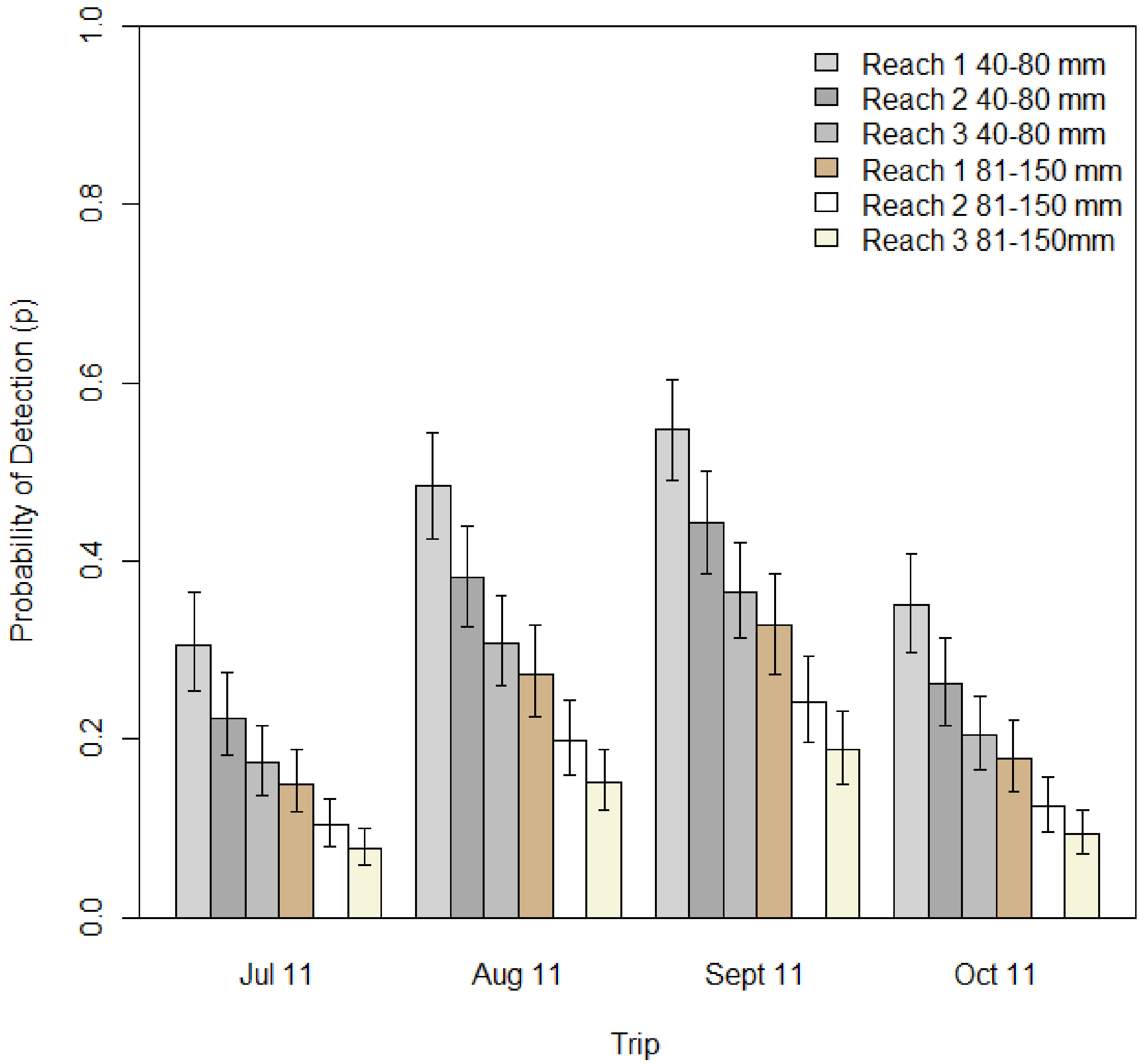

Figure 2-10. Patterns of detection probability for stratified by size category of HBC during repeated electrofishing surveys in 2011.

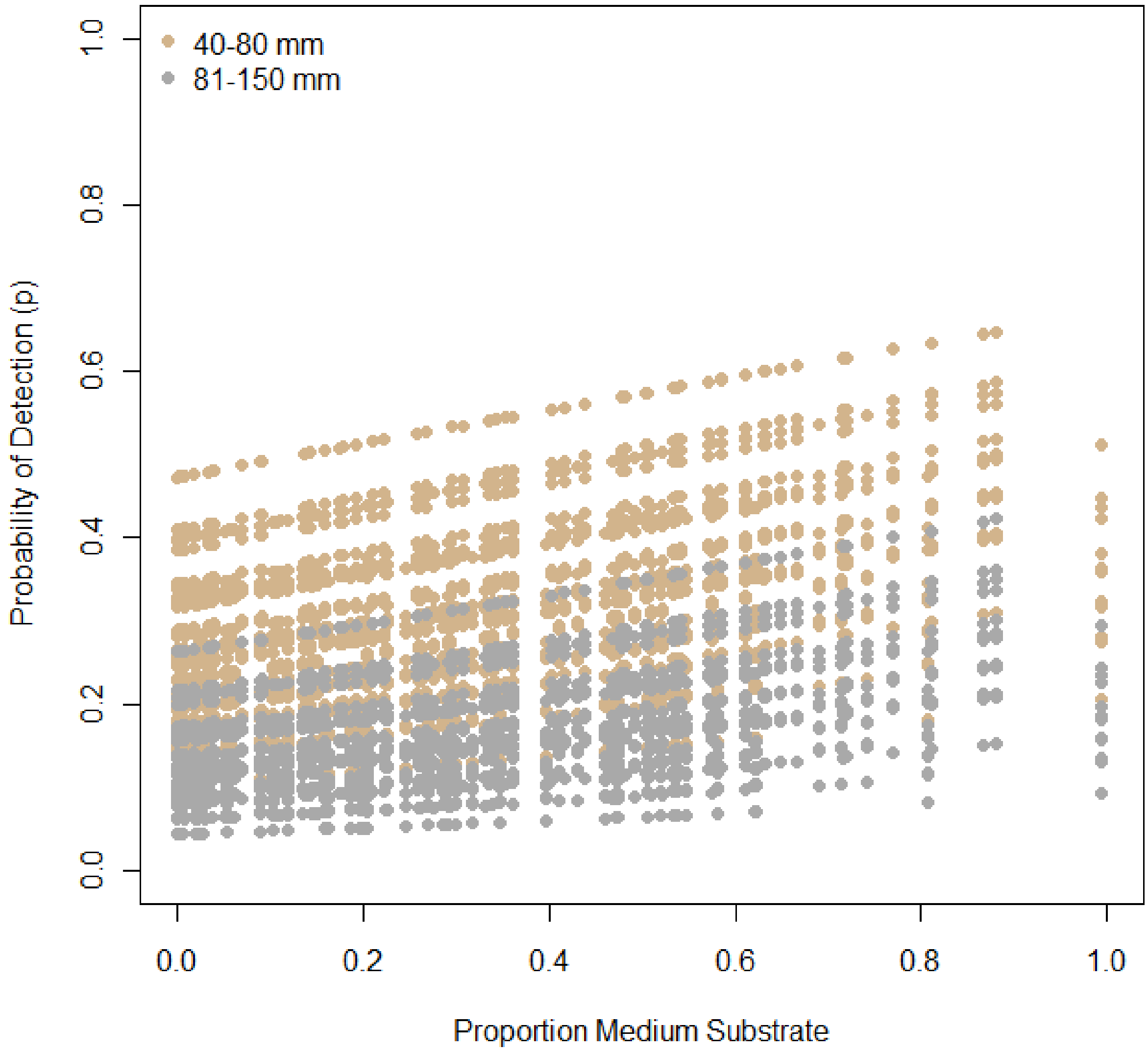

Figure 2-11. Relationship between probability of detection and proportion medium substrate in a site during repeated electrofishing surveys 2009 to 2011.

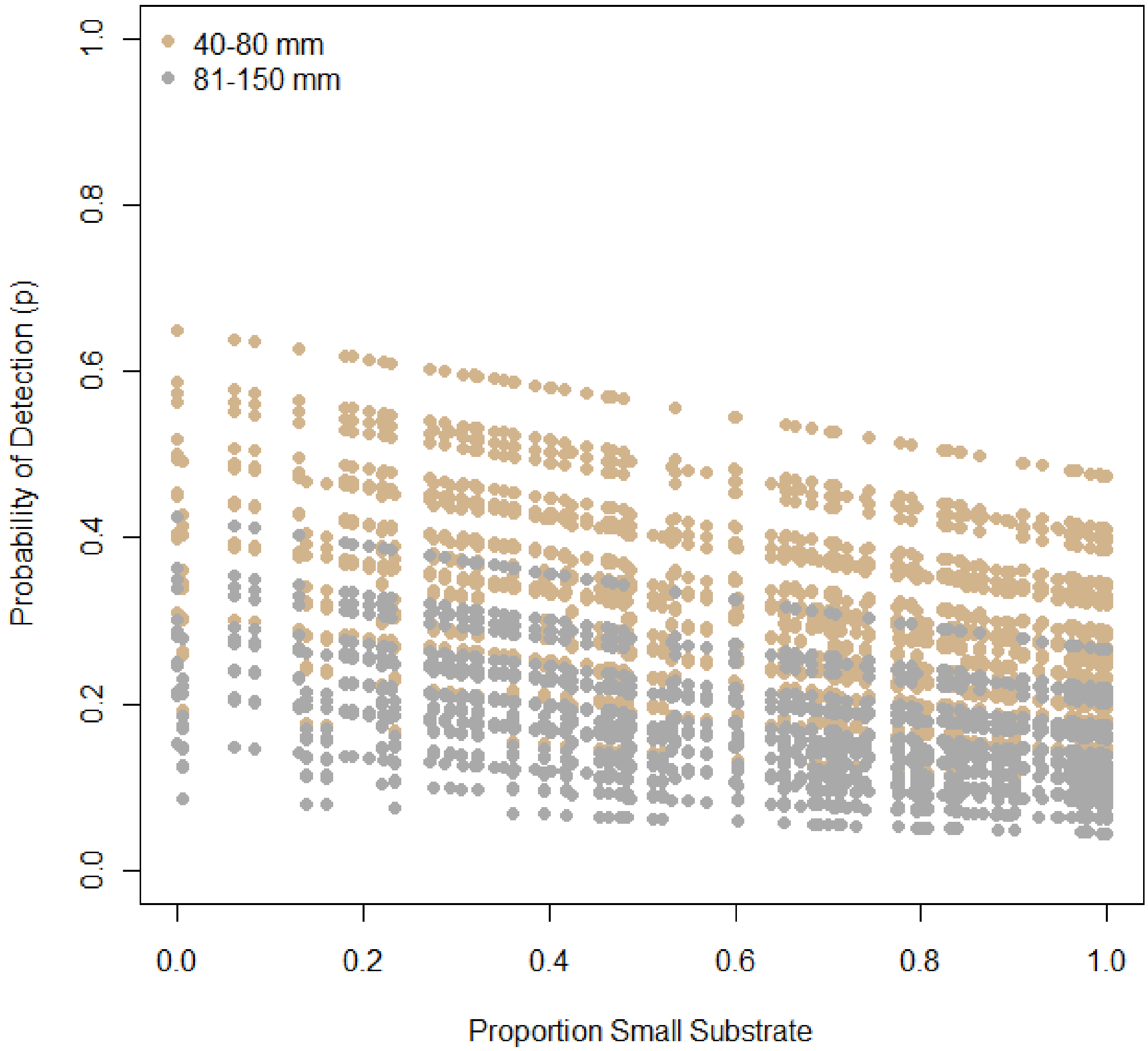

Figure 2-12. Relationship between probability of detection and proportion small substrate in a site during repeated electrofishing surveys 2009 to 2011.

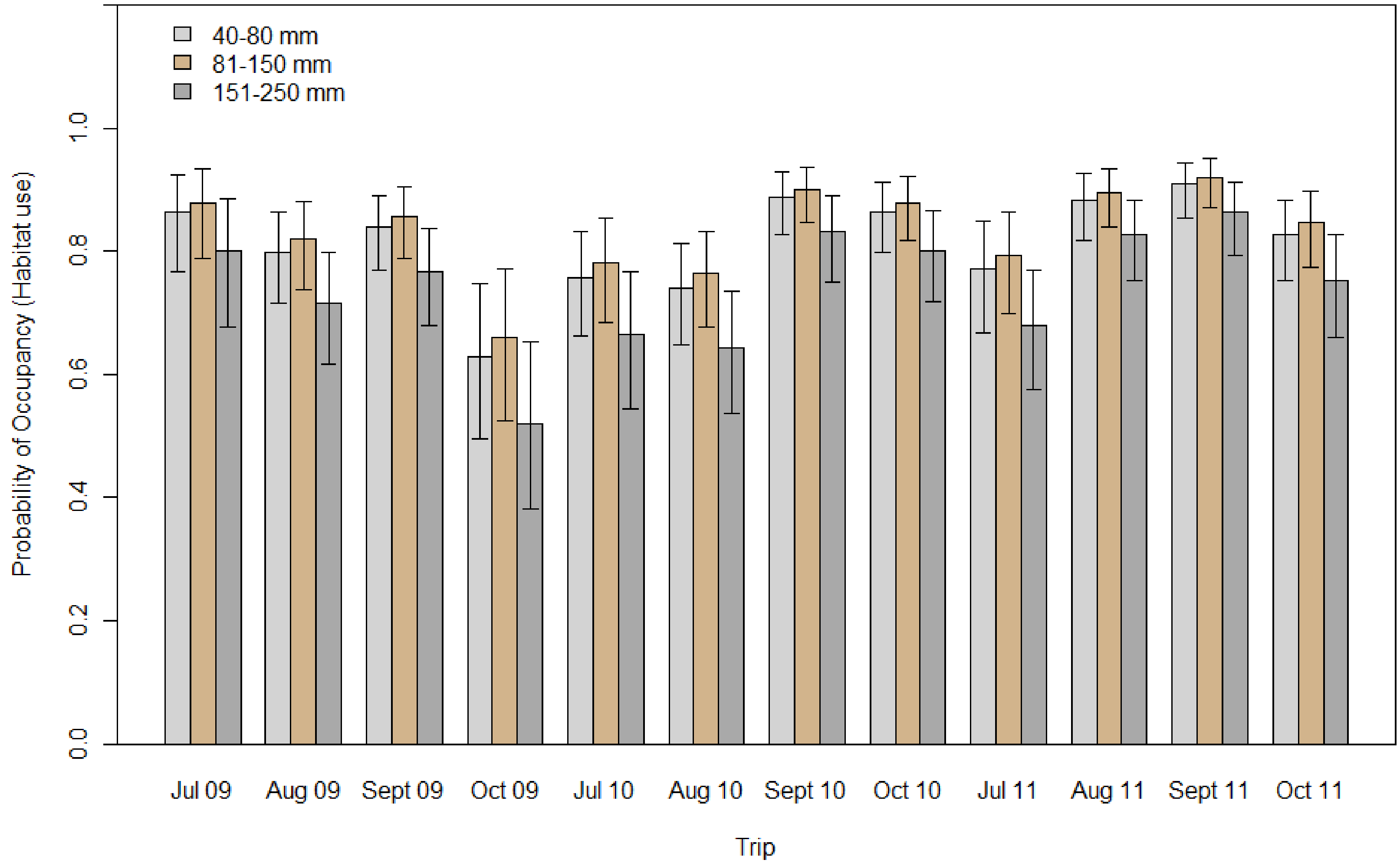

Figure 2-13. Patterns of occupancy probability stratified by size class and trip during repeated hoop net surveys from 2009 to 2011.

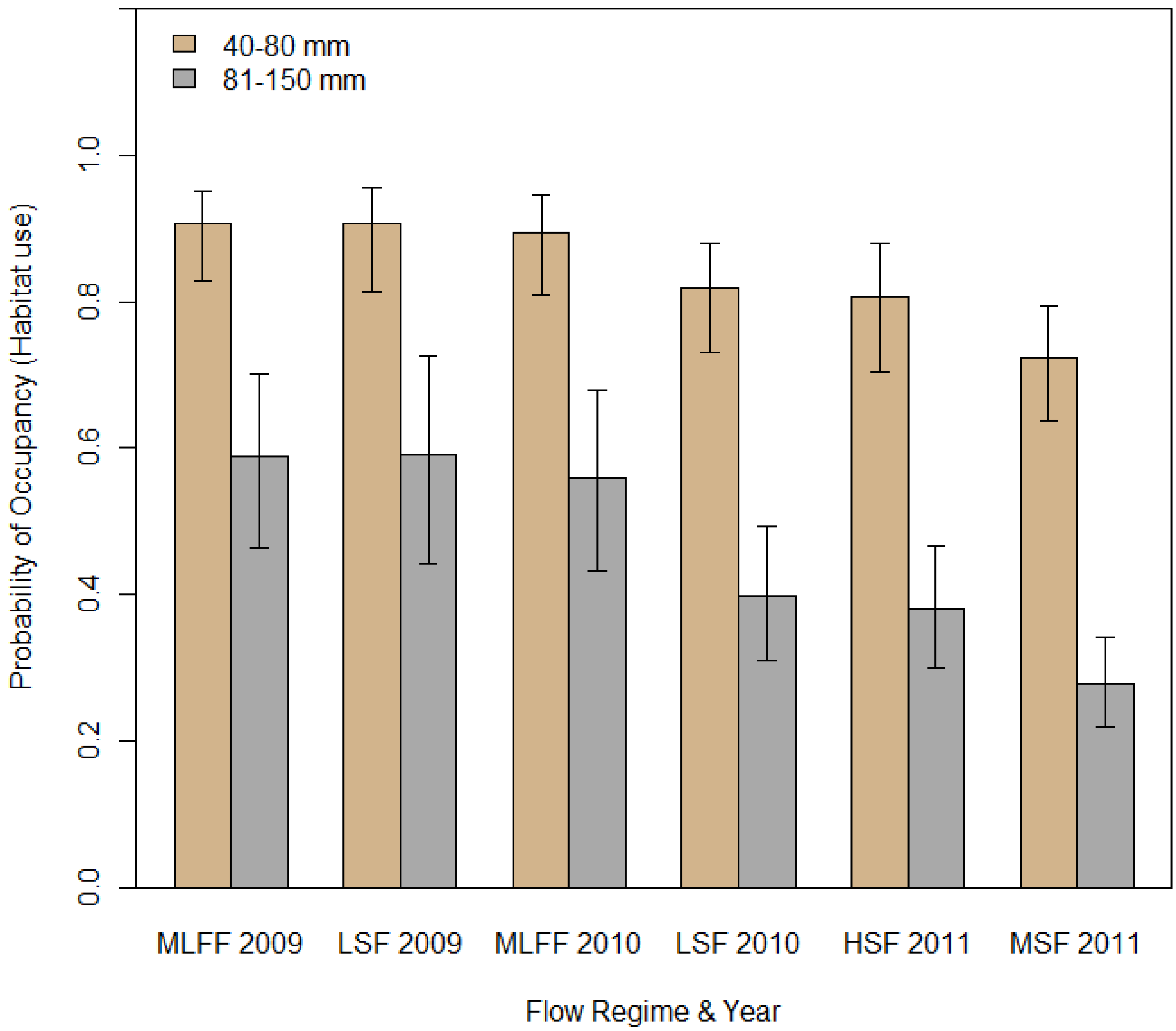

Figure 2-14. Patterns of occupancy probability from repeat electrofishing surveys stratified by size class, flow regime and year during 2009 to 2011.

CHAPTER 3
HABITAT SELECTION AND MOVEMENT OF HUMPBACK CHUB

Introduction

Globally, many populations of fish in rivers are endangered as a result of anthropogenic alteration of habitat (Minns et al. 1996; Rosenfeld 2003) and effective management of extant populations requires a clear understanding of the relationship between fish and their environment. In riverine systems it is essential to identify environmental or habitat characteristics that define the habitat requirements of river fishes. This information is required to identify and screen management and restoration policies to preserve or recover populations of individual species or restore in-stream habitats and flows to a desired state.

Widespread habitat loss and change caused by large dams has been implicated in the decline of native fish in the Colorado River Basin of the Western United States (Tyus 1991). Large dams disrupt the natural flow regime by changing the timing, magnitude, frequency, duration and rate of change in hydrologic conditions within rivers (Poff et al. 1997). Changes in flow regime alter riverine processes including ecosystem productivity, sediment transport and temperature which are thought to have negative effects on riverine ecosystems including fish populations. As an example, the installation of Glen Canyon Dam in 1963 significantly altered the hydrology of the Colorado River in Grand Canyon and has been implicated in the decline of the endangered humpback chub (Valdez and Ryal 1997; Stone and Gorman 1999).

The humpback chub is a large, long-lived cyprinid endemic to canyon reaches of the Colorado River Basin (Minckley and Marsh 2009). The humpback chub was one of the first species listed as federally endangered and became federally protected under the Endangered Species Act of 1973. Currently, six isolated populations of humpback chub exist within the Colorado River basin of which the largest population occurs in Grand Canyon (Stone and Gorman 1999; Coggins et al. 2006). Historically, the humpback chub was distributed widely throughout Grand Canyon and recruited successfully in both the Little Colorado and mainstem Colorado River (Valdez and Ryal 1995). Current populations of humpback chub in Grand Canyon are found in 9 aggregations, with the largest aggregation located near the confluence of the Little Colorado River and mainstem Colorado River (Valdez and Ryal 1995).

A large proportion of management and restoration efforts in Grand Canyon are directed at maintaining important river habitat (e.g. sandbars, backwaters) and mimicking natural flow patterns (e.g. artificial floods, seasonal steady flows) to positively benefit native fish, including humpback chub. While significant effort has been allocated to the monitoring of physical resources and native fish populations there has been little synthesis of the influence of habitat and flow regime on humpback chub (but see, Valdez and Ryal 1995, Valdez and Ryal 1997; Converse et al. 1998) in the Colorado River in Grand Canyon. Early investigations of humpback chub populations have primarily focused on inferring habitat relationships from catch per effort indices and radio telemetry (Kaeding et. al. 1990; Valdez and Ryel 1997; Converse et al. 1998). However, no studies to date have quantified humpback chub habitat use in relation to available habitat to determine if and how strongly humpback chub select particular habitats.

The objectives of this study were to determine the habitat selection and movement patterns of telemetered humpback chub in the Colorado River within Grand Canyon during contrasting flow regimes as part of an adaptive management experiment. Specifically, this study was designed to (1) determine if humpback chub select habitat features, (2) assess the influence of an experimental steady flow regime on habitat selection and movement patterns (3) evaluate the influence of overriding turbidity conditions to spatial distribution and habitat use and (4) provide insight into potential habitat requirements of humpback chub. This research will aid managers in evaluating the importance of habitat features to humpback chub population persistence in Grand Canyon and in informing Glen Canyon Dam flow operations and in designing future flow experiments.

Methods

Study Site

The Little Colorado River reach of the mainstem Colorado River in Grand Canyon, AZ was extensively sampled during 4 river trips in July, August, September and October of 2010 (Figure 3-1). July and August river trips occurred during the mean low fluctuating flow regime, and September and October river trips were sampled during an experimental steady flow regime. Current water releases from Glen Canyon Dam are tightly regulated and are typically operated under a hydropeaking flow schedule. The mean low fluctuating flow regime in this study was characterized by diel discharges ranging from 250 (m^3/sec) to 500 (m^3/sec) (Figure 3-2). During the experimental steady flow regime discharge from GCD was constant at 250 (m^3/sec) (Figure 3-2). Extensive tributary flooding during August and September caused spikes in the hydrograph that were unrelated to dam operations (Figure 3-2). Daily nephelometric turbidity units (NTU, hereafter) were continuously monitored in 15-minute intervals remotely from an acoustic doppler profiler at USGS gauge 09383100 (RKM 165). The Colorado River

Flow Sediment and Stage model was used to back-calculate the difference in average water travel time between USGS gauge 0983100 and the study location (RM 125-131.2) using an unsteady flow model (Wiele and Griffin 1997). Spikes in turbidity are the result of monsoonal rains which caused tributary flooding (Figure 3-3).

Fish handling and surgery methods

Thirty two humpback chub between 180-245 mm were surgically implanted with uniquely coded PT-3 Sonotronics® acoustic telemetry tags (Table 3-1) (PT-3: 8-mm diameter, 19-mm length, 1.5 grams, 45-60 day battery life; Sonotronics, Tuscon, AZ, USA). Humpback chub tagged with telemetry tags were captured via hoop netting. Given the size and body shape of humpback chub and guidelines on bodysize-tag size relationships from the literature, I chose 180-mm TL as the smallest size to implant humpback chub with an acoustic tag to minimize influence of tagging on survival of fish (Jepsen et al. 2002). All fish selected for surgery were anesthetized with sodium bicarbonate until equilibrium was lost and then non-anesthetic water was pumped across the gill membranes with a gravity pump. The tags were quickly implanted into the fish by making a small incision into the abdominal cavity and following insertion the incision was closed with 2-3 absorbable sutures and cyanoacrylate. Each tagged fish was observed for 2 hours until the immediate effects of anesthesia and surgery were no longer visible and the fish was able to remain upright with normal fin movements. Following recovery, fish were released into the same location they were collected. A staggered-entry tagging design was used to increase the temporal resolution of habitat selection and movement for telemetered humpback chub (Pollock et al. 1989). All fish were implanted with tags between July-September. No fish were implanted during the October trip as viable tags were still active from prior trips during October.

Tracking of telemetered humpback chub

Tracking of sonic tagged fish began 24 hours post-surgery and continued through October or tag failure; whichever occurred first. Relocations recorded within 3 days of surgery were censored from all analyses to allow for a recovery period following tag implantation. Telemetered fish were tracked twice daily. Generally, tracking event one occurred during the morning between 0500 and 0700 hours while tracking event two commenced in the afternoon between 1400 and 1600 hours. Tracking began at the upstream boundary of the study reach and ended at the bottom of the study reach (~RM 63.2-65.6). Tracking was restricted to this area because of operational constraints on our research from permitting agencies. Systematic sampling of telemetered individuals occurred by stopping at fixed locations approximately 100 m apart. Areas in swift water were floated multiple times to scan the area completely. Telemetry surveys were abandoned in rapids and turbulent areas for safety reasons and signal attenuation. As a telemetered fish position was approached, the gain on the telemetry unit was reduced until the telemetry signal was strong in all directions (omnidirectional). Fish locations were entered into a mobile GIS database and attributes of the location including time, depth, distance from shore, habitat type and hydraulic type were recorded.

Habitat mapping

Relocations of telemetered humpback chub during each tracking session were related to data layers of hydraulic type, habitat type, depth and substrate category using both existing information collected through the USGS Grand Canyon Monitoring and Research Center (GCMRC) physical science program and field measurements. The hydraulic type was mapped in the field and split into two discrete categories including eddies and runs. Eddies refer to areas of recirculating flow that generally occur downstream of channel constricting debris fans. Runs represent any portion of the river where the water was traveling downstream. Field measured hydraulic type was digitized in GIS for the entire study site and clipped to the river edge. Habitat type was delineated using existing GIS imagery and habitat classifications were verified in field. Habitat types were split into six discrete habitat types including backwater, cliff, debris fan, offshore, talus slope and sandbar by applying a 15-m buffer to wetted river perimeter in GIS. Backwater habitats are characterized as areas of sand deposition that are separated from the main river channel. Cliff habitats were characterized as shear walls rising vertically and laterally over the river. Debris fans were characterized as shorelines of large cobble and boulder that were transported into the river corridor by tributaries during flooding. Offshore habitat represented any area that was greater than 15-m from shore. Sandbar habitats were classified as shorelines of contiguous beach and exposed sand. Talus habitats were classified as shorelines consisting mainly of boulders deposited by rockslides and rockfall. Depth was determined in GIS as surface water elevation minus the elevation of the river bottom for a given discharge. Existing bathymetric and channel coarseness maps were used to classify substrate type into 12 discrete categories using a modified Wentworth scale. Substrates categories were grouped into three classes: small, medium and large substrates. Substrates classified 1-4 represented small substrates ranging from silt to course sand. Substrates classified 5-8 represented small gravel to medium cobble while substrates classified 9-12 represent large substrates including large cobble and boulder. Habitat availability was determined by generating random locations within the study site using the Arc GIS 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 regime. Habitat characteristics were related to available locations in Arc GIS.

Statistical Analysis Habitat Selection

Following Rosenfeld (2003), habitat selection was inferred as differential use of a habitat given the availability of the habitat. To assess habitat selection, I conducted my statistical analysis in two parts. First, univariate selection ratios were constructed to compare individual humpback chub relocation points to available locations within the study area (Thomas and Taylor 1990; Manly et al. 2002; Rodgers and White 2007). Secondly, I developed a resource selection function to investigate the influence of habitat characteristics on the relative probability of habitat use by humpback chub with a mixed effects logistic regression. These two approaches provide a complimentary approach to studying habitat selection. Univariate selection ratios allow for selection to be determined for specific habitat classes while the resource selection function allows a probability of use to be modeled as a function of habitat characteristics. Separate selection ratios were constructed to evaluate if selection differed between mean low fluctuating flow and the experimental steady flow regime. A single resources selection function was developed that allowed for the influence of the fluctuating and steady flow regime to be evaluated.

Univariate selection ratios were calculated following a type II study design (Thomas and Taylor 1990; Manly et al. 2002). A type II study design compared the frequency of habitat use in a discrete habitat class to the availability of the habitat class of interest within the study reach. Habitat classes included hydraulic type, habitat type, depth class and substrate 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 ratio (*Wi*) intervals were constructed to determine which habitats were being selected for (Manly et al. 2002; Rogers and White 2007). Selection was indicated by values greater than one while avoidance of habitats is indicated by values less than one (Rogers and White 2007). Selection ratios of one indicated that telemetered chub are not selecting for a particular habitat type (i.e. use is proportional to available habitat). I calculated Bonferroni 95% confidence intervals to determine if the selection ratio indicated positive, negative or neutral selection (Manly et al. 2002; Rogers and White 2007). Log-likelihood chi-square test and selection ratios were calculated using the function wides II in package adehabitat in Program R.

Mixed effects logistic regression models were implemented to compare used versus available locations as functions of habitat attributes for telemetered humpback chub. Nine different *a priori* models were developed to propose mathematical descriptions of covariates that influence habitat selection. In this analysis, the telemetered fish was considered a random effect while hydraulic type, habitat type, depth, substrate category and flow treatment were fixed effects (Rogers and White 2007). I choose a mixed model procedure because it accounts for non-normal distribution of residuals, autocorrelation associated with repeatedly sampling the same fish and uneven sample sizes (Gillies et al. 2006). I fit combinations of covariates and compared model fit using AIC (Burnham and Anderson 2002). The model with the lowest AIC was chosen for interpretation of habitat selection. Mixed effects logistic regression were implemented using the GLMER function from the lme4 library in program R.

Statistical Analysis of Movement

To describe the movement patterns of humpback chub mean daily displacement and extent of movement were calculated for the mean low fluctuating flow regime and the experimental steady flow regime. I calculated mean daily displacement as the linear distance moved between successive relocations during daily morning tracking events. A mixed model analysis of variance was used to determine if mean daily displacement varied as a function of flow regime. An individual telemetered humpback chub was considered the random effect while flow regime was the fixed effect (Rodgers and White 2007). Wald's chi-square statistic was used to assess model significance and a Monte Carlo procedure was used to determine 95% confidence intervals around mean daily displacement. Extent of movement for humpback chub was calculated as the linear distance between the most upstream relocation to the most downstream relocation. I used a one-way Kruskal-Wallis test to determine if there were differences in extent of movement between flow regimes and a Monte Carlo procedure to determine 95% confidence intervals around extent of movement. To assess the influence of changing discharge during the fluctuating flow regime on the spatial distribution of telemetered humpback chub a linear mixed-model was used to compare distance to shore to discharge level.

To determine the influence of turbidity on spatial distribution I used a linear mixed model to determine if distance from shore varied as a function of turbidity category and a Monte Carlo procedure to determine 95% confidence intervals around distance from shore. Three turbidity categories were considered. Low turbidity ranged from 0-30 NTU, medium turbidity levels ranged from 31-300 NTU and high turbidity levels ranged from 301-10,000 NTU. To evaluate if frequency of habitat use changed with increased turbidity a Pierson chi-square test was used.

Results

I recorded 1034 locations of 32 humpback chub implanted with ultrasonic transmitters during four two week sampling trips from July to October 2010. Tagged humpback chub were relocated 344 times during the fluctuating flow regime and 690 times during the experimental steady flow regime, respectively. The mean number of relocations for tagged humpback chub was 25 (SD=12.7) and the mean number of days a telemetered fish was observed was 46 (SD=16.2). The mean size of telemetered chub was 199 mm (SD=19.2) and ranged between 180 mm to 245 mm (Table 3-1). During the study two telemetered humpback chub likely suffered mortality or tag loss indicated by a lack of movement within and between sampling trips. Data from these fish was censored from analysis. The following data represents fish known to have stayed within the sampling area as we were not permitted to search for fish outside of our defined sampling reach. Only fish with a minimum of 15 relocations were included in subsequent analysis.

Selection Ratios

Habitat selection was assessed for 14 humpback chub during the fluctuating flow regime and for 25 humpback chub during the steady flow experiment. During both flow regimes locations used by humpback chub differed significantly (P-value <0.05) from availability for all habitat characteristics except for substrate category during the fluctuating flow regime (Table 3-2). Hydraulic type, habitat type and depth class exhibited the strongest patterns of selection (Figure 3-4). Humpback chub strongly selected eddy hydraulic types and were used in proportions greater than three times their availability. Runs were selected against in both flow regimes. Habitat types including cliff and debris fan shorelines were positively selected for during both flow regimes. Backwater habitat selection was highly uncertain during the fluctuating flow regime but strongly selected for during the steady flow experiment. Talus slopes were neutrally selected for during the fluctuating flow regime while being positively selected for during the steady flow regime. Offshore and sandbar habitats were selected against during both flow regimes. Telemetered humpback selected intermediate depths of 4-6 m while generally avoiding shallow (<2 m) and deep areas (> 10 m) during both flow regimes. Tagged fish neutrally selected substrate class during both flows with the exception of positive selection of the medium sized substrate class during the steady flow regime.

Resource Selection Function

The top resource selection function, ranked by AIC, indicated that a combination of hydraulic type, depth, substrate category and an interaction between hydraulic type and substrate category best explained the probability of habitat selection by humpback chub (Table 3-3). Hydraulic type was the strongest predicator of habitat selection causing the largest improvement in model fit (Table 3-3). Similar to the selection ratio analysis, eddy hydraulic types were used in much greater proportion to their availability and runs were selected against (Table 3-4). Telemetered chub used depths shallower than would be expected given the distribution of depths and selected substrate categories larger than would be expected given substrate category availability. There was a significant interaction effect between substrate category and hydraulic type. This interaction indicated that chub used a wide variety of substrate categories in eddies while being negatively associated with small substrates and positively associated with larger substrates in runs. Models that included a coefficient representing the flow experiment did not improve model significantly suggesting that habitat selection patterns did not change between the fluctuating and steady flow regime (Table 3-3). The top model effectively distinguished between used and available habitats (Fig 3-5).

Movement

Mean daily displacement observed for telemetered humpback chub was not significantly different between the fluctuating and experimental steady flow regime (χ^2=0.16, P=0.6867). During the fluctuating flow regime, tagged humpback chub moved a mean distance of 92 m per day (95% confidence interval, 67-123 m; Figure 3-6) while in the steady flow regime telemetered chub moved a mean distance of 106 m per day (95% confidence interval , 91-123 m; Figure 3-6). In both flow regimes, long distance daily movements (> 500 m) were rare. Significant differences in extent of movement were not observed between the fluctuating and steady flow regime for telemetered humpback chub (χ^2=0.14, P=0.7015). The mean extent of tagged fish during fluctuating flow was 414 m (95% confidence interval, 258-595 m; Figure 3-4) and during the steady flow experiment mean extent of movement was 515m (95% confidence interval, 333-743 m; Figure 3-4). No relationship was found between humpback chub distance from shore and discharge level (χ^2=1.56, P=0.20) suggesting that humpback chub do not alter spatial distribution in response to changing discharge under the discharge levels observed.

A significant relationship (χ^2=77.869, P<0.01) was found between distance from shore and turbidity level. During low turbidity conditions humpback chub were located further offshore than during high turbidity conditions (Figure 3-7). Similarly, during this study the frequency of nearshore habitat use for all nearshore habitat types increased with increased turbidity levels (χ^2=63.693, df=10, P<0.01). This pattern was strongest in backwater, cliff and debris fan habitat types (Table 3-4).

Discussion

Telemetered humpback chub exhibited strong selection of eddy hydraulic types in both the fluctuating and experimental steady flow regime. Nearshore habitats including debris fan and cliff faces located within eddies were also positively selected during both flow regimes. Prior research has demonstrated that humpback chub use eddy complexes extensively and that the distribution of humpback chub in Grand Canyon maybe related in part to the presence of large eddy complexes (Valdez and Ryal 1995). Kaeding et al. (1990) further postulated that humpback chub rely on large channel obstructions such as debris fans to create velocity refuges via eddy complexes. 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). I hypothesize that the mechanism causing strong selection of eddies by humpback chub is a result of food availability and reduced energetic expenditure. Residing in depositional environments adjacent to turbulent main channel flow may allow 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 occurring in small stream systems in the southeastern and southwestern United States (Rinne 1991, Freeman and Grossman 1993).

Humpback chub during this study made small daily movements and exhibited a restricted distribution. Most movements of tagged humpback chub were made within large eddy complexes. However, movement between eddy complexes and from runs to eddies were observed. Previous studies over both short and long temporal scales agree with my findings suggesting that humpback chub exhibit strong patterns of spatial fidelity (Valdez & Ryal 1995, Paukert et al. 2006). Seasonal movements of humpback chub are characterized by potadromous migrations between the mainstem Colorado River and the Little Colorado River between March and May (Gorman and Stone 1999, Coggins et al. 2006). This migration was not able to be documented because it occurred outside of my research trips. 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 low instances of immigration in this study it appears that long distance dispersal maybe relatively rare. Further research assessing movement in a meta-population framework should be conducted to determine rates of movement, frequency of long distance movements and the recruitment contribution of humpback chub occupying aggregations outside of the LCR confluence.

Strong selection of habitat and restricted movement patterns suggest that the presence of eddy hydraulic types may be a habitat requirement of humpback chub in the Colorado River in Grand Canyon. Humpback chub that occupy the mainstem Colorado River in close proximity to the LCR may be able to meet their requirements for foraging and resting within this limited spatial extent. Future research should focus on empirically measuring food availability in different habitat types and consider bioenergetic models which quantify the energy expenditure of occupying various habitats for humpback chub. Existing long-term catch data which includes the entire canyon corridor should be evaluated to determine if humpback chub strongly select eddies in downstream areas. If this pattern is exhibited canyon wide, restoration efforts which seek to increase mainstem humpback chub abundances should potentially consider canyon stretches with high eddy availability.

Humpback chub exhibited similar patterns of habitat selection and movement between the fluctuating flow and experimental steady flow regime. Fluctuations in discharge can influence the quantity and quality of available habitat for riverine fish which may influence patterns of habitat use and movement (Kraft 1972, Moog 1993, Dare et al. 2002). The majority of studies examining the effects of flow on fish have been conducted on stream and river populations of salmonids (Quinn and Kwak 2000, Dare et al. 2002, Scruton et. al 2006, Korman and Campana 2009) and suggest that during periods of high discharge fish occupy deeper areas and are associated with velocity refugia. Humpback chub monitored in this study exhibited habitat selection and movement patterns that appeared robust to discharge fluctuations. This study was conducted in a location comprised primarily of large eddy complexes adjacent to complex shoreline habitat. These habitats are relatively invariant to minor discharge fluctuations allowing telemetered humpback chub habitat selection patterns to be robust to changes in flow regime (Korman et al. 2004). Similar to Gerig (2012), I hypothesize that the magnitude of change in discharge between the fluctuating and experimental steady flow regime was not great enough to illict a detectable shift in habitat selection and movement patterns of humpback chub.

Overriding turbidity conditions appeared to have a stronger influence on the spatial distribution of humpback chub than the experimental steady flow regime. The proportion of relocations in nearshore habitats increased concomitantly with turbidity levels and the spatial distribution of humpback chub shifted closer to shore. In particular, backwater habitats were never used when turbidity conditions were less than 30. However, as turbidity increased, backwater habitats were used over 50 times. These patterns suggest that NTU levels may shift habitat use patterns of humpback chub which ultimately influence habitat selection. The shift in humpback chub spatial distribution maybe related to foraging behavior. Under low turbidity conditions humpback chub forage offshore on material entrained in eddy currents. As turbidity increases humpback chub use nearshore habitats and may become actively or opportunistically piscivorous (Valdez and Ryal 1995; Stone and Gorman 2006). Backwater seine surveys and short term tethering experiments which occurred concurrently to the telemetry study found that the frequency of large fish, including humpback chub captured in backwaters increased with increased turbidity and that under turbid conditions predation risk was observed to be highest (Dodrill 2012). Additionally, on two occasions during tethering experiments, humpback chub were observed to be foraging on tethered fish (M. Dodrill, Personnel Communication). Prior research suggests that the abundance of small bodied fish increased with turbidity as a result of dispersal from tributaries during floods (Yard et al. 2011). Correspondingly, these results suggest that humpback chub shift their habitat use patterns during turbidity fluxes to potentially forage on fish in nearshore habitats such as backwaters. Future research is needed to quantify diet plasticity in humpback chub and determine the extent to which they are piscivorous in the mainstem Colorado River.

Table 3-1. Biological attributes collected from humpback chub implanted with acoustic telemetry transmitters.

Trip	Length (mm)	Weight (g)	ID	Date Tagged	Last Contact	Tracking Duration (d)
1	185	52.73	711050	7/12/2010	9/15/2010	64
1	198	65.26	731070	7/12/2010	9/15/2010	61
1	188	55.46	751090	7/12/2010	8/12/2010	30
1	245	127.39	71990	7/15/2010	8/12/2010	59
1	187	54.54	73950	7/16/2010	8/18/2010	27
1	208	76.18	751030	7/16/2010	8/12/2010	26
1	180	48.38	71930	7/17/2010	9/15/2010	54
1	180	48.38	71910	7/20/2010	9/15/2010	57
1	256	146.22	75970	7/20/2010	9/15/2010	55
1	189	56.39	73930	7/21/2010	8/18/2010	52
1	187	54.54	75950	7/21/2010	9/15/2010	55
2	226	98.87	721060	8/7/2010	9/14/2010	36
2	201	68.42	70980	8/8/2010	9/15/2010	38
2	183	50.96	701040	8/8/2010	9/14/2010	36
2	184	51.84	721000	8/8/2010	10/21/2010	37
2	196	63.22	741020	8/9/2010	10/19/2010	70
2	220	90.86	741080	8/9/2010	9/15/2010	36
2	182	50.09	761040	8/9/2010	10/22/2010	73
2	201	68.42	761100	8/9/2010	9/15/2010	36
2	185	52.73	771050	8/9/2010	10/24/2010	75
2	217	87.02	771110	8/9/2010	9/15/2010	64
3	210	78.51	70900	9/4/2010	10/27/2010	59
3	205	72.79	70920	9/4/2010	9/15/2010	38
3	187	54.54	74940	9/4/2010	10/27/2010	52
3	215	84.53	74960	9/4/2010	10/27/2010	52
3	185	52.73	76960	9/4/2010	10/27/2010	52
3	185	52.73	76980	9/4/2010	8/12/2010	26
3	211	79.69	77970	9/4/2010	10/27/2010	52
3	210	78.51	72920	9/5/2010	9/15/2010	11
3	205	72.79	72940	9/5/2010	10/27/2010	51
3	183	50.96	77990	9/5/2010	10/27/2010	51
3	187	54.54	701060	9/5/2010	10/27/2010	51

Table 3-2. Chi-square statistics testing (1) the distribution and (2) selection of habitat characteristics of humpback chub during contrasting flow regimes.

		Distribution			Selection		
Habitat Characteristic	Flow Regime	χ^2	df	P	χ^2	df	P
Habitat Type	Fluctuating	83.87	60	0.02	402.85	65	<0.001
	Steady	164.07	105	<0.001	573.18	110	<0.001
Hydraulic Type	Fluctuating	30.32	12	<0.001	539.05	13	<0.001
	Steady	32.4	21	0.05	833.27	22	<0.001
Depth Class	Fluctuating	190.81	60	<0.001	242.56	65	<0.001
	Steady	220.08	105	<0.001	595.58	110	<0.001
Substrate Class	Fluctuating	26.2	24	0.32	29.34	26	0.26
	Steady	64.27	42	0.015	121.59	44	<0.001

Table 3-3. AIC ranking of mixed model logistic regression models used to determine habitat selection of telemetered humpback chub.

Model	LL[a]	AIC	ΔAIC	K[b]
Depth+Substrate+Hydraulic+(Substrate*Hydraulic Type)	-1073	2157	0	5
Depth+Substrate+Hydraulic Type+Flow Regime+(Substrate*Hydro)	-1072	2159	2	5
Depth+Substrate+Hydraulic Type+(Depth*Hydraulic Type)	-1076	2163	6	5
Depth+Substrate+Hydraulic Type+Flow Regime+(Depth*Hydraulic Type)	-1074	2165	8	6
Depth+Depth^2+Substrate+Hydraulic Type	-1080	2171	14	5
Depth+Substrate+Hydraulic Type	-1081	2172	15	4
Hydraulic Type	-1111	2228	71	2
Habitat Type	-1296	2607	450	6
Depth+Substrate	-1364	2736	579	3

[a] = Log Likelihood; [b] = # of parameters

Table 3-4. Coefficient estimates from best AIC ranked mixed model logistic regression for telemetered humpback chub during contrasting flow regimes

Parameter	Estimate	SE	z value	P
Intercept	-2.05	0.19	-10.67	<0.01
Depth	-0.07	0.015	-4.68	<0.01
Substrate	0.37	0.05	6.93	<0.01
Hydraulic Type	3.2	0.23	13.62	<0.01
Substrate * Hydraulic Type	-0.27	0.07	-4.1	<0.01

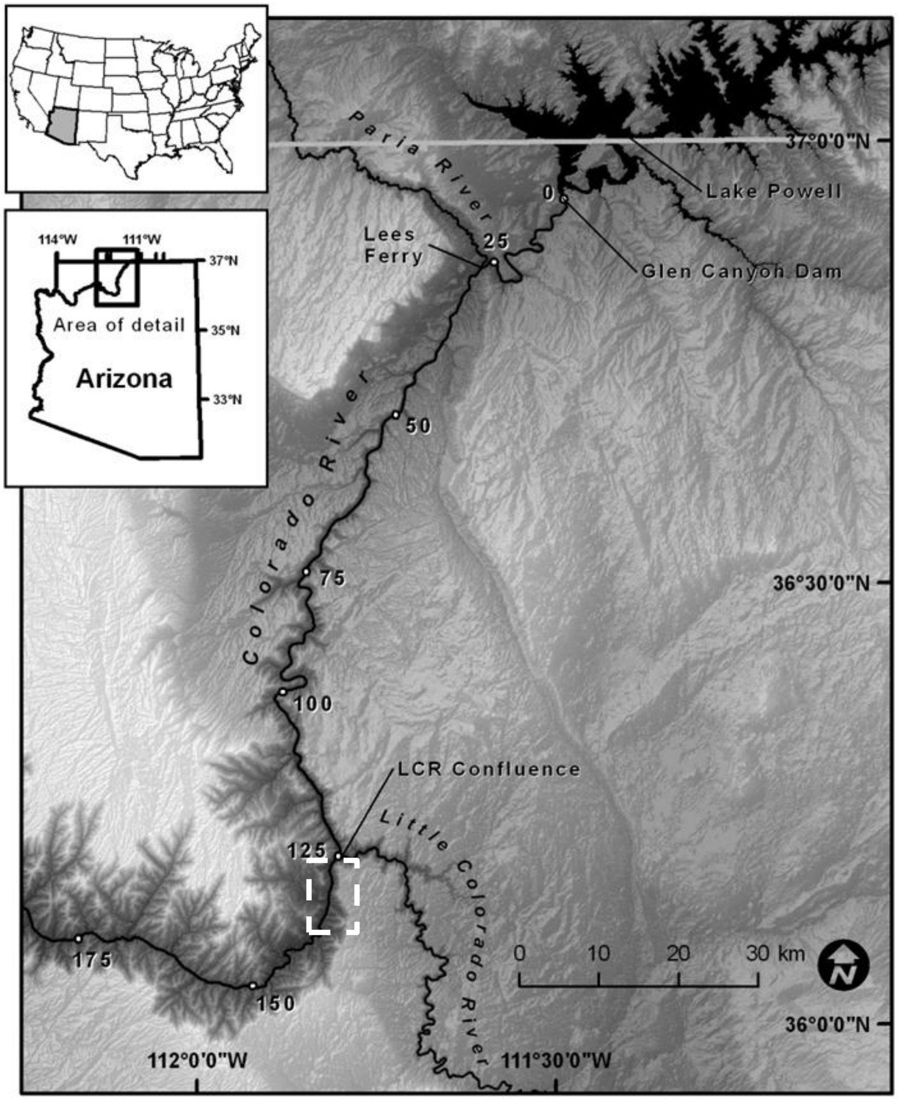

Figure 3-1. Map of the study site in the Colorado River in Grand Canyon, AZ. Study site was between Heart Island to Lava Chuar Rapid. White dashed box represents sampling area.

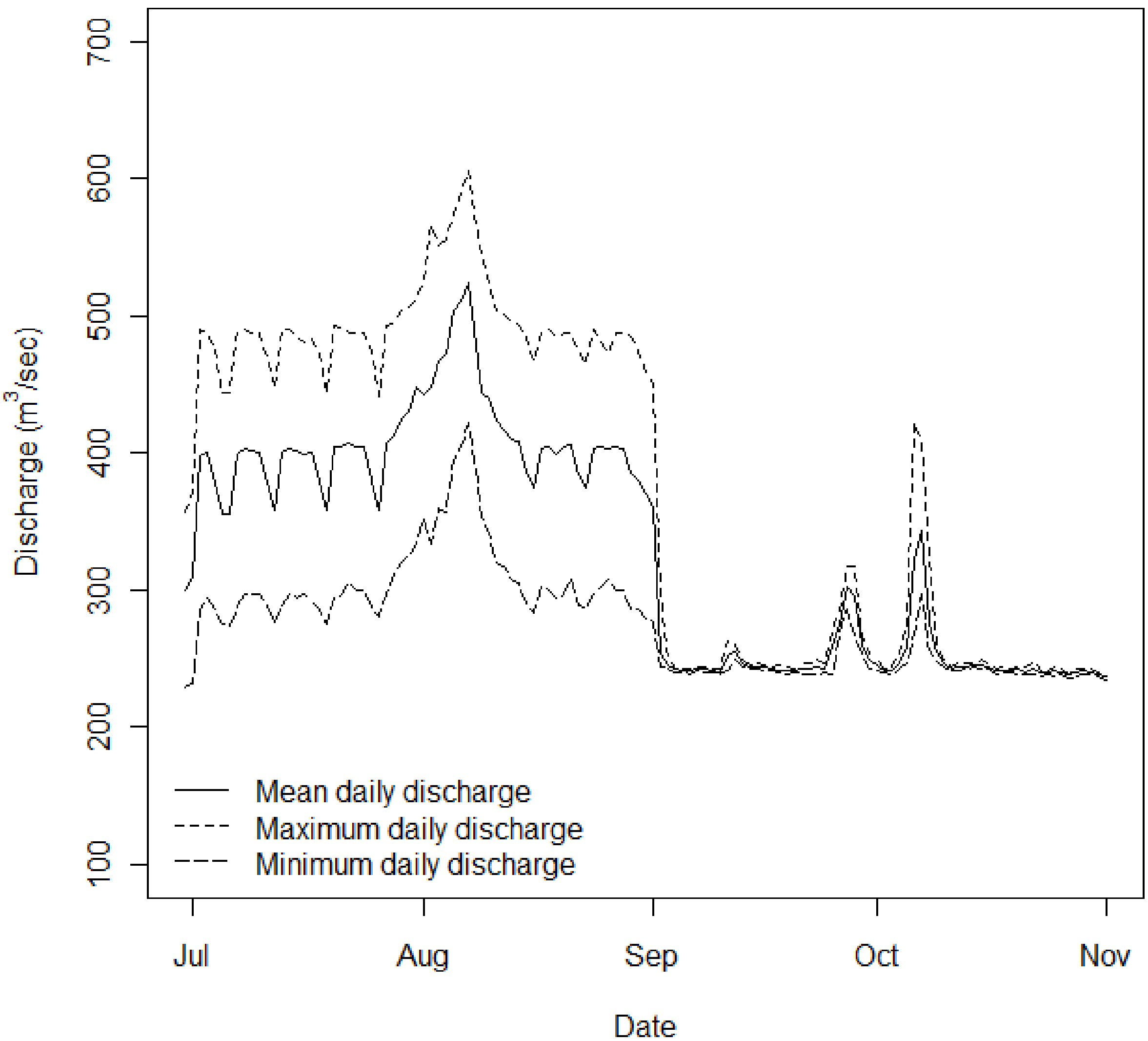

Figure 3-2. Mean, maximum and minimum daily discharge during the fluctuating flow regime and the experimental steady flow regime.

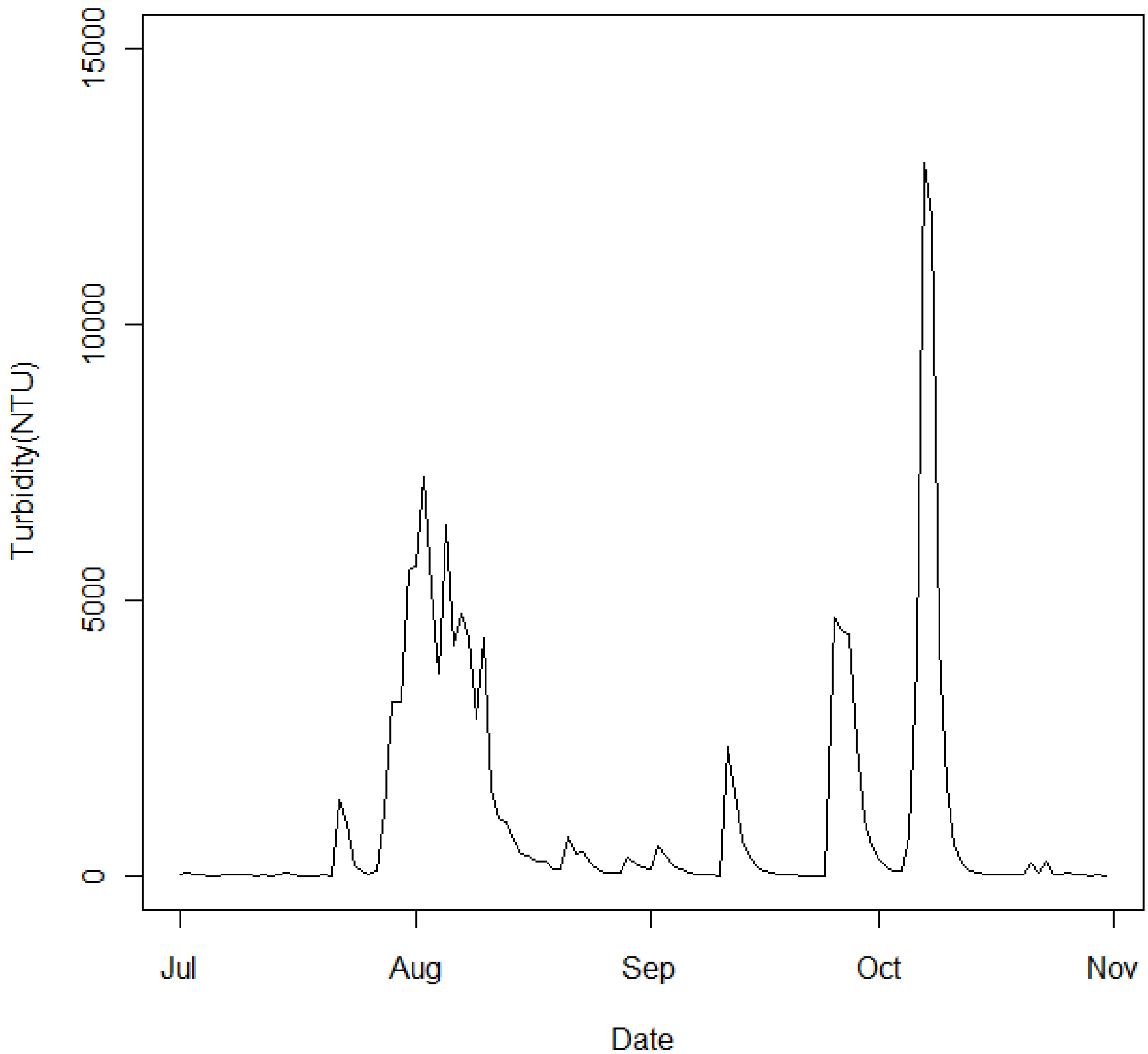

Figure 3-3. Mean daily turbidity measurements from July to October 2010 in the Colorado River in Grand Canyon.

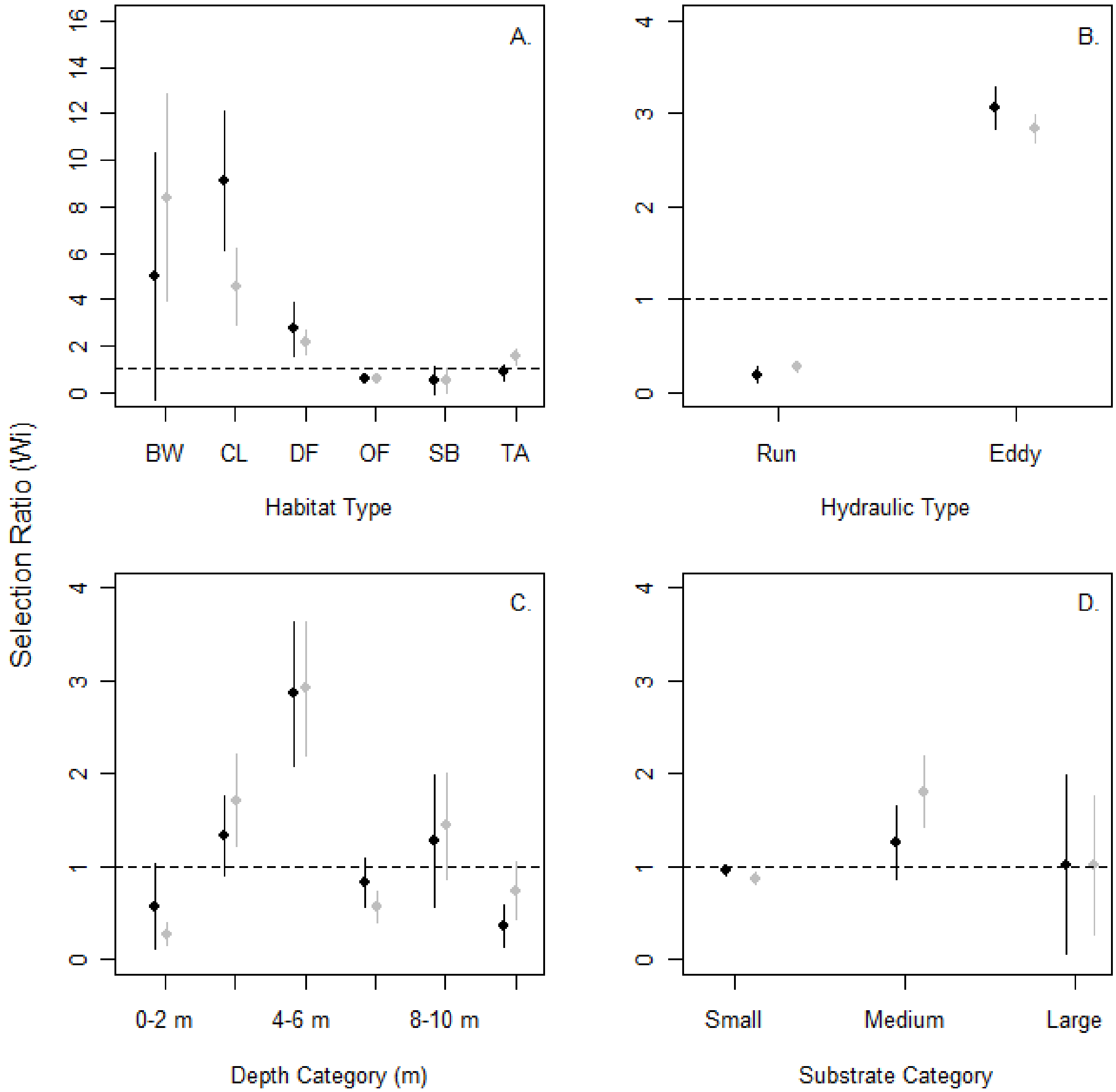

Figure 3-4. Selection Ratios with 95% Bonferroni confidence intervals of (A.) habitat type, (B.) hydraulic type,(C.) depth category (m) and (D.) substrate category.

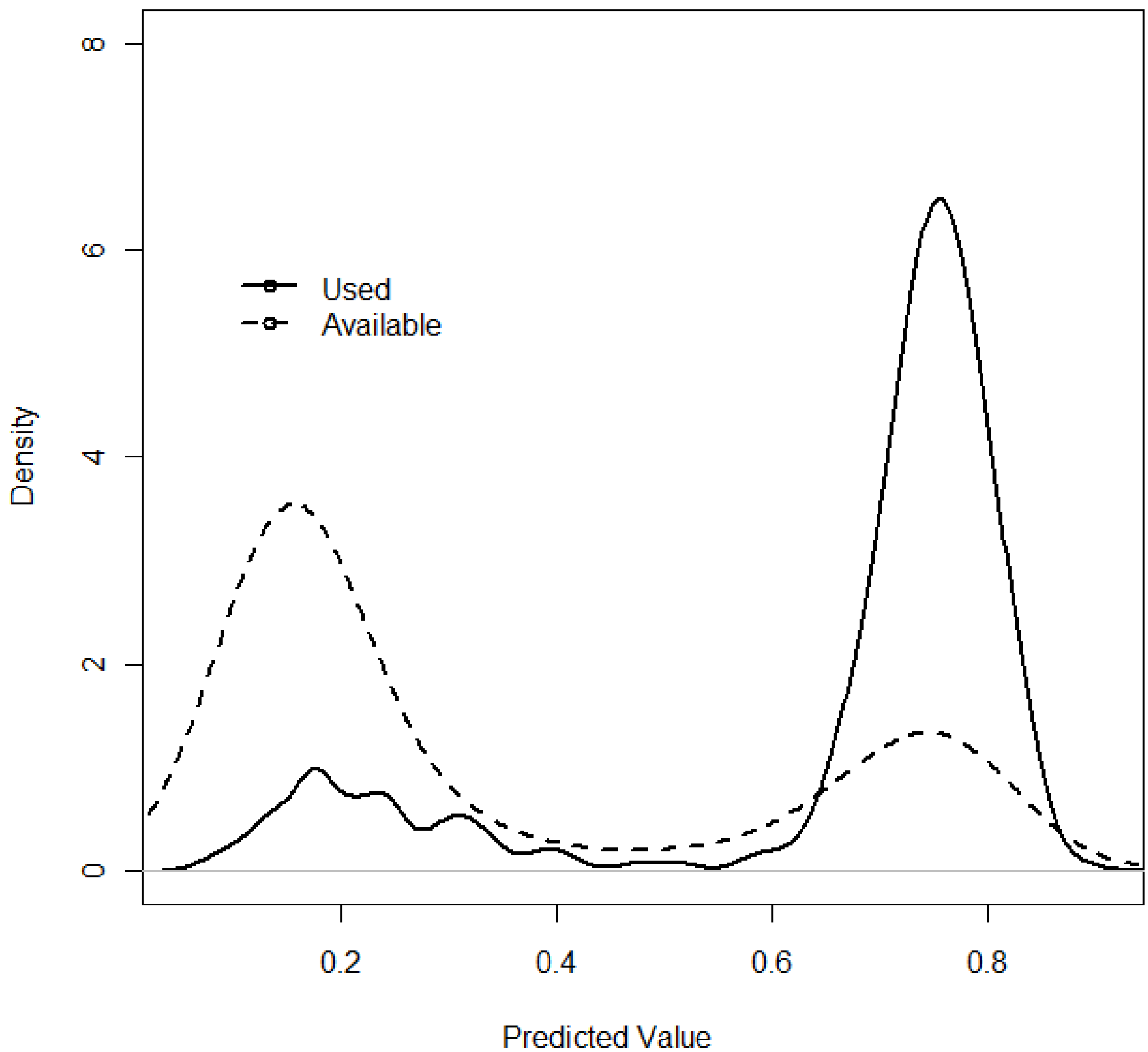

Figure 3-5. Kernel density plot of fitted values comparing used versus available locations for the top resource selection function.

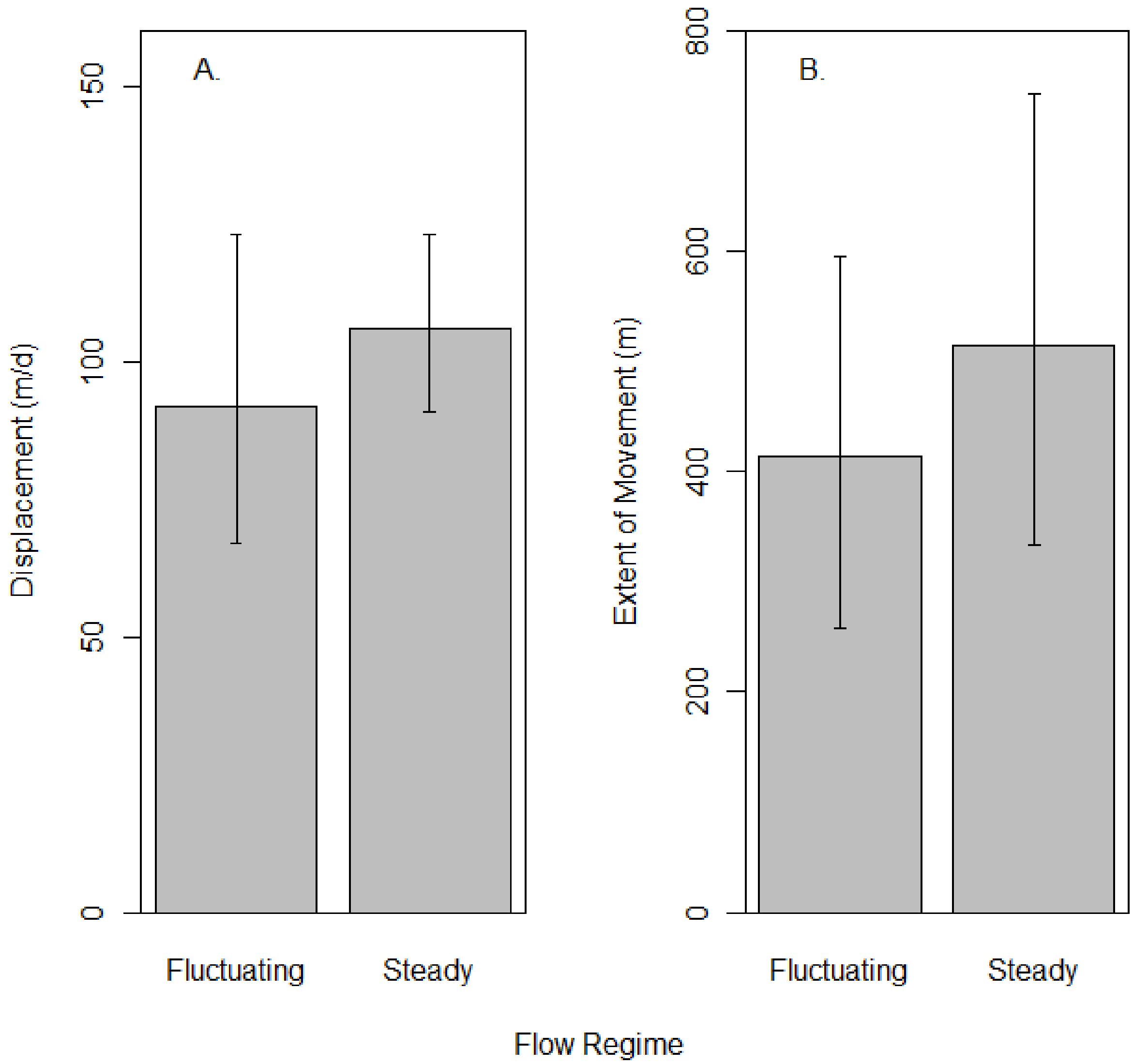

Figure 3-6. Movement of humpback chub during contrasting flow regimes. (A.) Daily displacement and (B.) spatial extent of telemetered humpback chub during the fluctuating and experimental steady flow regime.

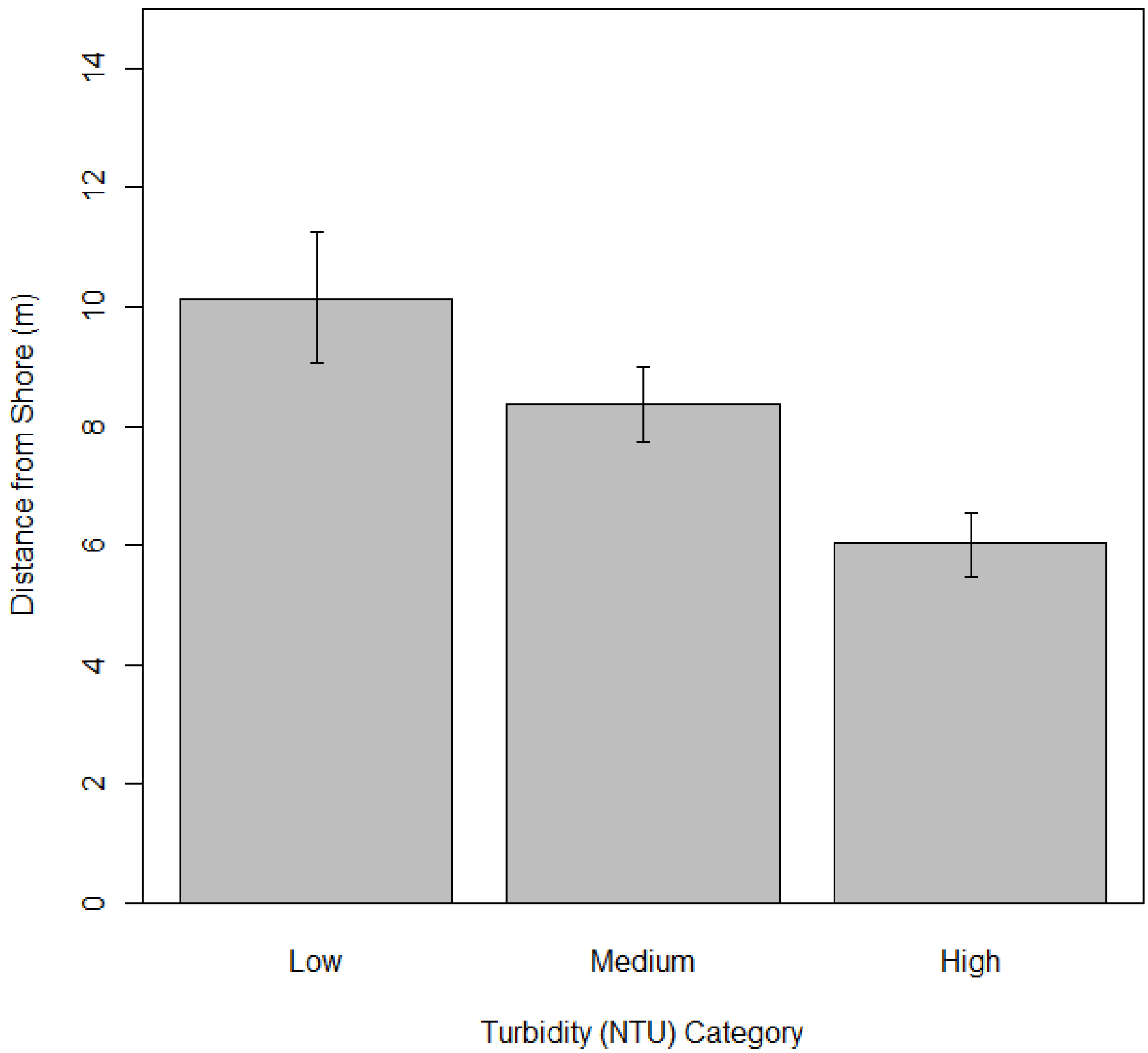

Figure 3-7. Observed distance from shore measurements of telemetered humpback chub during low, medium and high turbidity levels.

CHAPTER 4
SYNTHESIS AND CONCLUSIONS

This research study documented that the steady flow experiment from Glen Canyon Dam did not have the anticipated result. Occupancy probabilities were observed to be consistently high and there was no marked change in occupancy state between the fluctuating flow regime and the steady flow regimes. Similarly, analysis of humpback chub habitat selection and movement suggests that the steady flow regimes did not significantly influence their spatial distribution and movement rates. The lack of significant response to the flow experiment is important. Previous researchers have noted that it is difficult to derive predictable relationships between hydrologic change and fish response and that fish responses to management actions are often counterintuitive (Pine et al. 2009, Poff and Zimmerman 2010, Branford et al. 2011).

The use of the natural flow paradigm to structure how management proceeds in regulated river systems is appealing and this paradigm suggests that as flow regime is incrementally restored incremental changes in ecosystem function will be observed (Poff et al. 1997). However, my observations suggest small changes in flow regime independent of other physical conditions such as temperature did not alter how humpback chub use and select habitat. This observation doesn't suggest that flow is not an important variable in the structuring of lotic environments but points to the need integrate flow dependent variables that are strongly influenced by flow regulation such as turbidity and temperature. In regulated systems where physical processes such as turbidity and thermal regime have been decoupled from the flow regime, small changes to flow regime likely won't have appreciable results for biota because flow, turbidity and temperature do not operate independently. When considering optimal flow policies for fish in regulated rivers it is also important to consider the dynamic suite of factors including temperature, turbidity, food availability, competition and predation that interact with flow to shape patterns observed in field.

Using Glen Canyon Dam as a management tool has proved a powerful tool in assessing ecosystem functioning of aquatic resources in Grand Canyon. To maximize learning, careful planning should take place when flow experiments are designed. Specifically, it is paramount to consider the seasonal timing and magnitude of the flows when anticipating potential outcomes to the experiment. If this research had been conducted under flows with greater contrast and the steady flow experiments would have taken place in summer results may have been significantly different. To help evaluate policy actions which assess the relationship between humpback chub and Glen Canyon Dam operations research monitoring should continue to utilize an active adaptive management approach.

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BIOGRAPHICAL SKETCH

Brandon Gerig was born to Mark and Michelle Gerig in April of 1987. During childhood, Brandon grew up in South Bend, IN. Family trips spent in Michigan and Northern Ontario left a strong appreciation and perked his interest in ecology and fisheries. He graduated from Lake Superior State University in 2009 with a Bachelor of Science in fisheries and wildlife management. While at Lake State Brandon gained experience conducting research and running rivers of the Upper Great Lakes and Alaska. After completing his B.S., Brandon began graduate studies at the University of Florida where he studied the influence of experimental flow regimes on native fish populations in the Colorado River in Grand Canyon. He graduated in May 2012 with a Master of Science. Brandon hopes to continue graduate studies as a PhD student or work as a fisheries biologist.