

ACTIVE ADAPTIVE MANAGEMENT FOR NATIVE FISH CONSERVATION IN
THE GRAND CANYON: IMPLEMENTATION AND EVALUATION

By

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For Dad

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By

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My first objective was to evaluate the efficacy of a large scale non-native fish removal effort to benefit endemic fishes of the Colorado River within Grand Canyon. During 2003-2006, over 23,000 non-native fish, primarily rainbow trout *Oncorhynchus mykiss*, were removed from a 9.4 mile reach of the Colorado River. These removals resulted in a rapid shift in fish community composition from one dominated by cold water salmonids (>90%), to one dominated by native fishes and the non-native fathead minnow *Pimephales promelas* (>90%). Concurrent with the mechanical removal, data collected within a control reach of the river suggested a systemic decline in rainbow trout unrelated to the fish removal effort. Thus, the efficacy of the mechanical removal was aided by an external systemic decline, particularly in 2005-2006.

My second objective was to improve current knowledge of humpback chub *Gila cypha* growth to aid in length-based age determination, and to provide a tool to evaluate temperature-dependent changes in growth rate. I estimated a temperature-dependent growth function for humpback chub by predicting more than 14,000 growth increments from a mark-recapture database. Results suggest that humpback chub growth is strongly dependent on temperature and that previous growth curves based on paired age-length data tend to over-estimate the age of small fish and under-estimate the age of large fish.

My third objective was to update humpback chub stock assessment procedures following guidance from an external review panel. These recommendations were primarily to develop model selection procedures and to evaluate the effect of error in length-based age determination. I used both Pearson residual analysis and Akaike Information Criterion to evaluate candidate models – leading to the conclusion that the most general assessment model was required to adequately model patterns in capture probability. I used the temperature-dependent growth relationship to estimate probabilistic relationships between age and length. These age-length relationships were then used in Monte Carlo simulations to capture the effect of ageing error on subsequent estimates of recruitment and adult abundance. The results indicate that the adult humpback chub population has likely increased between 20-25% since 2001.

My fourth objective was to evaluate whether there was any evidence of effect from past adaptive management actions or uncontrollable factors on Grand Canyon fish populations, and to make recommendations for further adaptive management program development. These results are largely inconclusive except that the combined policy of mechanical removal and increased water temperatures is temporally correlated with increased native fish abundance in the mainstem Colorado River near the confluence of the Little Colorado River, a reach deemed critical habitat for humpback chub. I recommend that the adaptive management program invest additional effort in developing more explicit and measurable resource goals, particularly for focal Colorado River resources. I further recommend that additional investment in monitoring of juvenile native fish survival and growth in the mainstem is needed to adequately evaluate future adaptive management experiments. Finally, additional predictive capability is needed to both formalize *a priori* hypotheses about juvenile native fish survival and recruitment, and to screen future policy options.

CHAPTER 1 GENERAL INTRODUCTION

Modifications to river ecosystems to serve human interests are a ubiquitous feature of human occupied landscapes. Postel et al. (1996) estimated that 54% of global annual runoff was appropriated for human use in 1996, and forecast that this figure might approach 70% by the year 2025. A recent review by Nilsson et al. (2005) documented that 50% of the Earth's large river systems are fragmented by dams. Thus, anthropogenic modifications are a major, and frequently detrimental, influence on riverine ecosystems on a global basis.

Alterations to riverine ecosystems in the U.S. have led to an increase in river restoration projects and an active dialogue between scientists and policy makers (Poff et al. 2003). This has led to increased research in both river restoration science and the appropriate measures of river restoration success (Palmer et al. 2005). However, scientists frequently are unable to predict with great certainty the outcome of management actions designed to achieve restoration, and this uncertainty can lead to skepticism and mistrust on the part of policy makers. Given this uncertainty, adaptive management (Holling 1978, Walters 1986) has been widely advocated as a strategy to guide restoration programs (Poff et al. 2003). Adaptive management recognizes that predictions of system response to management actions are uncertain, and seeks to use thoughtful application of management actions to learn about system behavior and hence, how to achieve resource management goals.

The 1,470 mile course of the Colorado River begins at high altitude in the Rocky Mountains and terminates at the northern extent of the Gulf of California. The Colorado River drainage area encompasses seven U.S. states (AZ, CA, CO, NM, NV, UT, WY) and a small portion of northwestern Mexico (Benke and Cushing 2005). Described as the "Life-blood" of the southwestern U.S. (Reisner 1993) and one of the most highly regulated rivers in the world

(Nilsson et al. 2005), this river has enormous social, economic, recreational, and political importance. Additionally, the Grand Canyon of the Colorado River is widely recognized as one of the 7 natural wonders of the world and a national treasure of the United States. Following recognition of degraded conditions in the Grand Canyon reach of the Colorado River downstream of Glen Canyon Dam (NRC 1987), the Glen Canyon Dam Adaptive Management Program has attempted to use adaptive management for river restoration since its formation in 1996.

A focal resource of the Glen Canyon Dam Adaptive Management program is the native fishes endemic to this basin, particularly the federally listed endangered humpback chub *Gila cypha*. This dissertation is focused on evaluating the efficacy of the implementation of a specific adaptive management experiment and developing improved monitoring capability for humpback chub. In Chapter 2, I describe and evaluate an adaptive management experiment to remove non-native fish from a large section of the Colorado River heavily used and deemed critical for humpback chub and other native fishes. In Chapter 3, I used mark-recapture information to develop a temperature-dependent humpback chub growth model in support of improved monitoring and stock assessment. In Chapter 4, I used the growth model along with all available monitoring data through 2006 to provide an updated evaluation of recent humpback chub population dynamics. In Chapter 5, I provide a synthesis of available fish monitoring data to evaluate the effect of past adaptive management experiments, as well as to make recommendations for future adaptive management experimentation, monitoring, and research priorities.

CHAPTER 2

NON-NATIVE FISH CONTROL IN THE COLORADO RIVER IN GRAND CANYON, ARIZONA: AN EFFECTIVE PROGRAM OR SERENDIPITOUS TIMING?

Harvest, species introductions, and large-scale habitat alterations have resulted in dramatic changes in the structure and function of ecosystems on a global basis (Vitousek et al. 1997). Humans have modified all types of ecosystems through various interventions, yet despite more than a century of focused ecological research, there remains much uncertainty as to how ecosystems will respond to anthropogenic interventions (Holling 1973; Walters and Holling 1990). Partly as a result of this uncertainty, efforts to manage human activities using prescriptive science-based policies to achieve basic goals as they relate to ecosystems (e.g., sustainability or species conservation) have been widely unsuccessful (Christensen et al. 1996; Mangel et al. 1996). In response to these failures, adaptive environmental assessment and management or adaptive management (AM) has been proposed as a strategy to link scientific inquiry and natural resource management (Holling 1978; Walters 1986; Walters and Holling 1990).

Adaptive management assumes that successful management of natural resources can occur only if objectives are clearly defined and future management policy choices are informed and directed by past policy performance. Holling and Walters (1990) describe three classes of AM implementation: (1) “trial and error”, (2) passive adaptive, and (3) active adaptive. “Trial and error” is a structure where initial policy choices are completely uninformed, and later policy choices are selected from the set of best performing initial choices. A passive adaptive structure chooses policies based on historic data informing a single predictive model. A passive adaptive structure differs from trial and error by the use of a predictive model to screen policy choices. This model can be either conceptual or quantitative and is presumed to be accurate until proven otherwise. Finally, active adaptive management recognizes that there are usually multiple predictive models that can explain the historic data equally well, and seeks to implement specific

policies that can both optimize short-term system performance and provide insight into which model provides the best predictions. The predictive models then become hypotheses of system behavior under different management policies. If it is possible to quantify the likelihood of each hypothesis *a priori*, then policy choices are further selected considering tradeoffs in the future value of increased understanding of system behavior. Most basically, the concept of AM embraces three related ideas:

- (1) Predictive models of complex systems can never be fully trusted in their ability to structure management policies that unambiguously attain specific system objectives,
- (2) Detailed research into the processes that define system complexity (e.g., resilience, feedbacks, thresholds, or alternative stable states) can never fully resolve prediction ambiguity, and
- (3) Predictive models contain key uncertainties that may only be resolved (if ever) by observing the response of the system to particular interventions.

Though AM has been widely adopted as a conceptual strategy for the management of natural resources (Williams et al. 2007) including: waterfowl (e.g., Nichols et al. 1995), forests (e.g., Sit and Taylor 1998), wildlife (e.g., Pascual and Hilborn 1995), fisheries (e.g., Sainsbury 1991), large river systems (e.g., NRC 1999), wetlands (e.g., Walters et al. 1992), and others, critics argue that many management programs that supposedly operate within an adaptive framework have embraced this term as a “buzz word”, but fail to apply the strategy as originally proposed (Gunderson 1999; Lee 1999). A frequent failure in AM programs has been that following the rigorous knowledge assessment and modeling that characterizes the initial steps of the process, the subsequent implementation and monitoring of candidate policies is not completed (Walters 1997; Gunderson 1999; Ladson and Argent 2002; Schreiber et al. 2004). I have extensively reviewed the primary literature and found few true empirical tests of AM as a strategy for management of ecosystems (e.g., Allan and Curtis 2005). This study documents the

implementation of an ecosystem-scale adaptive management experiment in the Colorado River within Grand Canyon, Arizona.

Adaptive Management in Grand Canyon

Following the Final Record of Decision from the Environmental Impact Statement on the operation of Glen Canyon Dam (USDOJ 1995), the Glen Canyon Dam Adaptive Management Program was formed and charged with managing the Colorado River ecosystem (CRE) within Grand Canyon, Arizona. This program consists of a multi-stakeholder federal advisory committee that defines objectives for the CRE and makes recommendations to the U.S. Secretary of Interior regarding the operation of Glen Canyon Dam (GCD) and other management actions. This high-profile program is arguably the most successful example of an adaptive management program in a large U.S. river (Ladson and Argent 2002). However, this recognition is primarily the result of short-term experimentation with GCD operations designed to test policies for sediment conservation (Collier et al. 1997).

Native fish conservation is also a key goal of the Glen Canyon Dam Adaptive Management Program primarily because many of the species endemic to the Colorado River Basin are protected under the US Endangered Species Act (ESA). This protected status necessitates regular review of GCD operations to ensure that dam operations are not deleterious to Grand Canyon native fish stocks. Current knowledge suggests that likely factors influencing the population dynamics and ultimate recovery (as defined by the ESA mandated recovery criteria) of native fish in Grand Canyon include: (1) non-native fish (Gorman et al. 2005; Olden and Poff 2005), (2) water temperature (Robinson and Childs 2001), (3) flow regulation (Osmundson et al. 2002), (4) juvenile rearing habitat (Stone and Gorman 2006), and (5) parasites and disease (Choudury et al. 2004). Of these, previous modeling and data analyses have shown that factors 1-3 are likely dominant drivers of native fish population dynamics in this system

(Walters et al. 2000), and suggests that improving rearing conditions for native fish in the mainstem Colorado River will likely provide the most significant benefit to native fish. Additionally, of the factors possibly influencing native fish population dynamics, controlled manipulation of factors 1-3 in an experimental framework is most tenable and, in recent years, has been the focus of efforts in adaptive management for native fish conservation.

Beginning in 2003, the first multi-year program of experimentation specifically designed to test policies associated with native fish conservation was implemented in Grand Canyon. In January 2003, an experiment was begun to experimentally manipulate GCD operations and the abundance of non-native fishes in a 9.4 mile stretch of the Colorado River containing known critical habitat for humpback chub *Gila cypha* and other native fish species. Although the experimental design also called for manipulation of water temperature discharged from GCD in subsequent years (Coggins et al. 2002), only the experimental fish manipulations were implemented. The last of four years of manipulating the abundance of non-native fishes was 2006.

Fish Community Background

Over much of the last several decades, the fish community in the Grand Canyon stretch of the Colorado River has been dominated by the non-native salmonids rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* (Gloss and Coggins 2005). Introductions of non-native salmonids have been shown to adversely impact invertebrate (Parker et al. 2001), amphibian (Knapp and Matthews 2000), and fish (McDowall 2003) communities. These two species of fish have also been identified as among the top 100 worst invasive species (Lowe et al. 2000) principally because of the global scope of introductions – rainbow trout have been successfully established on every continent with the exception of Antarctica (Crawford and Muir *In Press*). Although it is unclear how detrimental these fish are to native fish in the Colorado

River, interactions with various non-native fish have been widely implicated in the decline of southwestern native fishes (Minckley 1991; Tyus and Saunders 2000). Non-native salmonids, particularly brown trout, have been shown to be predators of native fishes (Valdez and Ryel 1995; Marsh and Douglas 1997) in Grand Canyon and rainbow trout predation on native fish has also been documented in other southwestern U.S. systems (Blinn et al. 1993). Besides direct mortality through predation, both rainbow trout and brown trout have demonstrated other negative interactions with native fish in western U.S. river systems including interference competition, habitat displacement, and agonistic behavior (Blinn et al. 1993; Taniguchi et al. 1998; Robinson et al. 2003; Olsen and Belk 2005). These lethal and sub-lethal effects of interactions with native fishes have also been widely documented in New Zealand, Australia, Patagonia, and South Africa (McDowall 2006).

Objective

While control of non-native species is widely considered as a management option, it is rarely implemented and evaluated (Lessard et al. 2005; Pine et al. 2007), particularly for fish in large river systems. Removal of non-native organisms to potentially benefit native species is more frequently conducted in small streams (e.g., Meyer et al. 2006), in lakes and reservoirs (e.g., Hoffman et al. 2004; Vrendenburg 2004; Lepak et al. 2006) and in terrestrial environments (e.g., Erskine-Ogden and Rejmanek 2005; Donlan et al. 2007). However, recently much effort has been expended to remove or reduce non-native fishes in the Colorado River (Tyus and Saunders 2000). Unfortunately, little documentation is available to evaluate the efficacy of these efforts (Mueller 2005). This study describes one such effort and evaluates the efficacy of a program to reduce non-native fishes within humpback chub critical habitat. Given the ecological and management interest in non-native species removals, this portion of the GCD adaptive management program also represents an important first phase of active adaptive management to

benefit a focal biological resource, humpback chub. Specifically, the objectives of this study were to: (1) evaluate the effectiveness of non-native control efforts in the mainstem Colorado River, (2) investigate factors contributing to the effectiveness of control efforts, and (3) characterize changes in the non-native and native fish communities.

Methods

Mechanical Removal Reach: Study Areas and Field Protocols

The Little Colorado River (LCR) inflow reach of the Colorado River extends from 56.3 river mile (RM) to 65.7 RM, as measured downstream from 0 RM at Lees Ferry, and is recognized as having the highest abundance of adult and juvenile humpback chub in the Colorado River (Valdez and Ryel 1995; Figure 2-1). This reach also has a relatively high abundance of flannelmouth sucker *Catostomus latipinus*, bluehead sucker *Catostomus discobolus*, and speckled dace *Rhinichthys osculus* owing to the availability of spawning and rearing habitat in the LCR. Given the importance of this reach to native fishes, the LCR inflow reach was selected as the area to test non-native mechanical removal efforts and was divided into six river sections labeled A-F (Figure 2-1). Sections A and B are the right and left shore from RM 56.3 to RM 61.8. Sections C and D are the right and left shore between RM 61.8 to RM 62.1 and include the LCR confluence and the mixing zone below the LCR. Sections E and F are the right and left shore downstream of the LCR confluence from RM 62.1 to RM 65.7. I stratified the study area into these 6 sections to control for the effect of the LCR discharge into the mainstem Colorado River. Sections A and B are unaffected by the tributary and sections E and F are believed to be of sufficient distance downstream of the mixing zone to be affected uniformly throughout. Sections C and D include the LCR confluence and will be differentially affected by LCR discharge throughout their lengths. Within river sections A-B and E-F, the

shoreline was divided into 500 m sites. The number of sites within each river section was: A=19, B=19, E=13, and F=14. Sections C and D constitute single sites.

From January 2003 through August 2006, a total of 23 field trips were conducted to remove non-native fish with serial depletion passes using boat-mounted electrofishing within the mechanical removal reach. The majority of these trips removed fish during either 4 or 5 depletion passes; exceptions were in August 2003 (2 passes), September 2003 (3 passes), and July 2004 (6 passes). All sites within sections A-B, C, and E-F were sampled during each pass. Section D, encompassing the LCR confluence, was not sampled during any of the trips due to concerns about equipment damage associated with high water conductivity issuing from the LCR and possibly high native fish abundance near the confluence. All electrofishing occurred following the onset of darkness and each depletion pass required 2 nights to complete. Electrofishing crews consisted of a boat operator and a single netter. Two boat types (15-foot rubber-hulled sport boat and 15-foot aluminum-hulled sport boat) and two types of electrofishing control units (Coeffelt mark XXII and Smith-Root mark XXII) were used in this study. In an attempt to standardize among boat and control unit type, current output was adjusted to produce 5000W of power during all electrofishing operations. Non-native fish were euthanized, speciated, and total length (TL), and weight (g) recorded. Native fish were measured (TL) and native fish larger than 150 mm TL were implanted with a passive integrated transponder (PIT) tag.

To examine the effects of boat type, control unit type, location (either above or below the LCR confluence), and boat operator on capture probability, I varied the deployment of boat and control unit type to each river section in a systematic fashion during the first two years of the study. The overall strategy was to ensure that a rubber- and an aluminum-hulled boat were

always deployed on opposite shorelines (e.g., sections A and B) and their positions reversed on the subsequent trip. The two types of electrofishing control units were deployed on opposite shorelines and reversed after each set of three trips. Four boat operators were randomly assigned to a particular section and depletion pass within each trip. The same boat operators participated in each trip with the exception of boat operator 2 (absent during July 2003 and September 2004) and boat operator 3 (absent during January 2004). Experienced substitute boat operators (boat operators 5 and 6) were employed in these instances. During the final 11 trips in the second two years of the study, both electrofishing control unit type and boat operators were assigned to each reach haphazardly.

Control Reach: Study Areas and Field Protocols

To determine if changes in the fish community in the mechanical removal reach were related to environmental influences and not the mechanical removal, a control reach was established upstream of the removal reach in an area of high rainbow trout density (44 RM-52.1 RM; Figure 2-2). This reach was stratified into 60, 500 m sites (30 on each shoreline). During most trips, 24 sites were randomly chosen and sampled using identical capture methods as outlined above in the mechanical removal reach. Exceptions occurred in January 2003 and August 2003 when 25 and 11 sites were sampled. All captured non-native fish were speciated, measured (TL), and fish ≥ 200 mm TL were implanted with a uniquely numbered external tag and their left pelvic fin removed prior to release – all non-native fish were released alive.

Mechanical Removal Reach: Data Analysis

Following Dorazio et al. (2005), I used a hierarchical Bayesian modeling (HBM) framework to estimate abundance and capture probability from data collected among the serial removal passes. This framework assumes that the overall population is a collection of subpopulations (defined below), each with different abundance and experiencing different

capture probability during removal efforts. Subpopulation abundance and capture probability are sampled from common population level distributions conditional on unknown hyperparameters (i.e., parameters that govern the population level distributions). This hierarchical structure allows a model-based aggregation of data among subpopulations and can be thought of as an intermediary between analyses that operate on data pooled over all subpopulations, and those that operate on each subpopulation independently. The structure allows sharing of information among subpopulations, particularly for subpopulations for which the data are relatively uninformative or imply extreme parameter values. In these cases, the subpopulation parameter values are more heavily influenced by the population distribution and are thus pulled, or shrunk (Gelman et al. 2004), towards the population distribution means. The amount of shrinkage is a function of both the difference between subpopulation and population distribution means and the population distribution variance.

I defined closed subpopulations to correspond to fish within each mechanical removal site. I assumed that the observed numbers of removals from site i ($1, \dots, I$) among removal pass j ($1, \dots, J$) were drawn from a multinomial distribution with number of trials equal to the site abundance (N_i) and cell probability vector $\bar{\pi}_i = [\pi_{i,1}, \pi_{i,2}, \dots, \pi_{i,J}]$. If I first assume that capture probability is constant among removal passes within each site i , then the cell probability in site i in the j th depletion pass is given by

$$\pi_{ij} = \theta_i (1 - \theta_i)^{j-1}, \quad (2-1)$$

where θ_i is a constant capture probability in site i . The likelihood for the overall model is given as

$$L(N_i, \bar{\pi}_i | \bar{x}_i) = \frac{N_i!}{c_i(N_i - x_i)!} (1 - \theta_i)^{J(N_i - x_i)} \prod_{j=1}^J (\pi_{i,j})^{x_{ij}}, \quad (2-2)$$

where x_{ij} is the number of fish captured in site i and depletion pass j , $x_i = \sum_{j=1}^{J_i} x_{ij}$ is the total number of fish captured in site i , and $c_i = \prod_{j=1}^{J_i} x_{ij}!$.

Equation (2-2) is the familiar Zippin (1956) estimator and as above assumes that capture probability θ_i is constant within a site. To cast this model in a HBM framework, I assumed that capture probability within a set of sites is sampled from a common distribution. The set of sites could either be all sites within the removal reach, or a subset of sites belonging to a common stratum. Because there is good reason to believe that electrofishing capture probability is influenced by abiotic factors such as turbidity (Reynolds 1996) and because there is frequently higher turbidity below the LCR confluence (Yard 2003), I chose to stratify the overall removal reach into sites upstream (sections A and B) and downstream (sections C, E, and F) of the LCR confluence and fit separate distributions to each strata. Similarly, fish abundance typically differs upstream versus downstream (Gloss and Coggins 2005) of the LCR so separate distributions of abundance were also used.

Following Dorazio et al. (2005), I assumed that the site specific capture probabilities were sampled from beta distributions in each of the strata as $\theta_{i,k} \sim \text{Beta}(\alpha_k, \beta_k)$, where k is either 1 (upstream stratum) or 2 (downstream stratum) and α_k and β_k are the hyperparameters. The mean (μ_k) of the distribution is $\alpha_k / (\alpha_k + \beta_k)$ and the variance is $\mu_k (1 - \mu_k) / (\tau_k + 1)$, where the similarity parameter (τ_k) is $\alpha_k + \beta_k$. I assumed that the site specific abundances were sampled from Poisson distributions with mean and variance λ_k . For convenience, I estimated μ , τ , and ψ ($\psi = \ln \lambda$) for each stratum. I chose diffuse prior distributions for each hyperparameter as: $\mu_k \sim \text{Uniform}(0,1)$, $\tau_k \sim \text{Uniform}(0,100)$, $E(\psi_k) \sim \text{Normal}(0,0.01)$, and $\text{SE}(\psi_k) \sim \text{Uniform}(0,10)$.

To examine the effect of the covariates mentioned above on capture probability, I also re-analyzed a subset of the data collected during 2003-2004 using a model that allowed capture probability to vary among sites and passes as a function of covariate values. To accomplish this, I assumed that capture probability was a logit function:

$$\theta_{i,j} = \frac{1}{1 + \exp(-(\beta_0 + \beta_1 x_{1(i,j)} + \beta_2 x_{2(i,j)} + \beta_3 x_{3(i,j)} + \beta_4 x_{4(i,j)} + \beta_5 x_{5(i,j)} + \beta_6 x_{6(i,j)} + \beta_7 x_{7(i,j)} + \beta_8 x_{8(i,j)}))}, \quad (2-3)$$

where β_1 is the location coefficient ($x_1=1$ for upstream sections A and B, $x_1=0$ for downstream sections C, E, and F), β_2 is the boat hull type coefficient ($x_2=1$ for rubber hull and $x_2=0$ for aluminum hull), β_3 is the electrofishing control unit coefficient ($x_3=1$ for the Smith Root Mark XXII and $x_3=0$ for the Coeffelt Mark XXII), β_4 is the boat operator 2 coefficient ($x_4=1$ for operator 2 and $x_4=0$ for not operator 2), β_5 is the boat operator 3 coefficient ($x_5=1$ for operator 3 and $x_5=0$ for not operator 3), β_6 is the boat operator 4 coefficient ($x_6=1$ for operator 4 and $x_6=0$ for not operator 4), β_7 is the boat operator 5 coefficient ($x_7=1$ for operator 5 and $x_7=0$ for not operator 5), and β_8 is the boat operator 6 coefficient ($x_8=1$ for operator 6 and $x_8=0$ for not operator 6). Lastly, this coding scheme implies that β_0 is the untransformed capture probability for boat operator 1 in downstream sites in an aluminum-hulled boat outfitted with the Coeffelt Mark XXII electrofishing control unit. I assumed that the site and removal pass specific values of each of the coefficients (β_z) were sampled from normal distributions with hyperparameter mean ($\mu_{\beta(z)}$) and standard deviation ($\sigma_{\beta(z)}$), where $Z=0, 1, \dots, 8$. I specified diffuse priors for each hyperparameters as: $\mu_{\beta(z)} \sim \text{Normal}(0,0.01)$, and $\sigma_{\beta(z)} \sim \text{Uniform}(0,10)$.

I implemented these analyses in programs R (R Development Core Team 2007) and Winbugs (Lunn et al. 2000). For each trip analyzed, I characterized the distribution of each

parameter among 20,000 Markov Chain Monte Carlo samples with a thinning frequency of 10 and discarding the first 10,000 burn in samples. I examined convergence using Gelman and Rubin's potential scale reduction factor (R Development Core Team 2007).

Control Reach: Data Analysis

I assessed the abundance of rainbow trout within the control reach using electrofishing catch rate and mark-recapture-based open population abundance estimates. Because all rainbow trout marked with external tags were also given a secondary fin clip, I attempted to incorporate the rate of tag loss into the mark-recapture-based estimates of survival, capture probability, and abundance. I estimated tag loss rate by comparing the observed and predicted proportion of recaptured fish that retained tags each trip. This proportion is not influenced by survival or capture probability under the assumption that survival and capture probability are independent of tag retention.

To derive this estimator, I first assumed that tag loss rate during the first month after initial tagging could be different from the rate experienced in subsequent months. This allows for the possibility that tags may be lost at a higher rate initially (e.g., as a result of improper placement), but that the rate of tag loss declines after this initial loss. I predict the number of tagged fish in month t as

$$\hat{T}_t = S(\hat{T}_{t-1}(1-l_2) + F_{t-1}(1-l_1) + R_{t-1}(1-l_1)), \quad (2-4)$$

where S is the monthly survival rate, \hat{T}_t is the number of tagged fish available for capture just prior to sampling in month t , l_2 is the monthly secondary tag loss rate, F_{t-1} is the number of newly tagged fish in month $t-1$, l_1 is the monthly initial tag loss rate (suffered in the month following tagging), R_{t-1} is the number of fish that had lost their tag prior to month $t-1$ and were

retagged in month $t-1$. Conversely, I predict the number of fish that have lost their tag in month t as

$$\hat{L}_t = S(\hat{L}_{t-1} - R_{t-1} + \hat{T}_{t-1}(l_2) + F_{t-1}(l_1) + R_{t-1}(l_1)), \quad (2-5)$$

where \hat{L}_t is the number of fish that have lost their tag and are available for capture just prior to sampling in month t . The predicted tag retention rate ($\hat{\eta}_t$) of recaptured fish in the population in month t is then

$$\hat{\eta}_t = \frac{\hat{T}_t}{\hat{T}_t + \hat{L}_t}. \quad (2-6)$$

Note that equations (2-4) and (2-5) are linked by the R term such that when recaptured fish without a tag are observed, they are fitted with a new tag and thus decremented from L and added to T . To estimate l_1 and l_2 , I minimized the sum of squares between observed and predicted retention rate among the 22 sampling occasions following the first one. It is worth noting that because the monthly survival rate (S) appeared in each term of equation (2-6), there was no need to estimate it in order to estimate tag loss rates.

I estimated monthly survival rate (\hat{S}_t) and capture probability (\hat{p}_t) conditional on tag loss rates generally following a single age recoveries only model (Brownie et al. 1985). However, for computational simplicity, I assumed that observed recaptures followed a Poisson rather than a multinomial distribution. Under this structure, the complete capture history is not used and the predicted numbers of fish released in month e and recaptured with tags in a subsequent month t is

$$\hat{r}_{e,t} = (F_e + R_e)(1 - l_1)(1 - l_2)^{(t-e-1)} \left[\prod_{i=e}^{t-1} \hat{S}_i \right] \hat{p}_t. \quad (2-7)$$

To reduce the number of parameters to be estimated, I set the monthly survival rate among months not sampled equal to the survival rate of the next sampled month. Assuming that the observed numbers of fish released in month e and recaptured with tags in a subsequent month t ($r_{e,t}$) represent independent samples from Poisson distributions with means given by equation (2-7), the log-likelihood function ignoring terms involving only the data is

$$\ln L(r|\bar{p}, \bar{S}) = \sum_{e=1}^{22} \sum_{t>e}^{23} [-\hat{r}_{e,t} + r_{e,t} \ln(\hat{r}_{e,t})], \quad (2-8)$$

where \bar{p} and \bar{S} are the unknown capture probability and monthly survival rate vectors to be estimated. The model was implemented in a Microsoft Excel spreadsheet using Solver (Ladson and Allan 2002) as the non-linear search procedure. As a measure of uncertainty, I computed 95% likelihood profile confidence intervals on \bar{p} and \bar{S} using Poptools (Hood 2000). I estimated the abundance of rainbow trout ≥ 200 mm TL by dividing the numbers of fish captured by the capture probability. Approximate 95% confidence intervals on these abundance estimates were calculated using the confidence bounds on the capture probability estimates.

Results

Mechanical Removal Reach

Over 36,500 fish from 15 species were captured in the mechanical removal reach during 2003-2006 (Table 2-1). The majority of these fishes (23,266; 64%) were non-natives and were comprised primarily by rainbow trout (19,020; 82%), fathead minnow *Pimephales promelas* (2,569; 11%), common carp *Cyprinus carpio* (802; 2%), and brown trout (479; 1%). Catches of native fish amounted to 13,268 (36%) and were comprised of flannelmouth sucker (7,347; 55%), humpback chub (2,606; 20%), bluehead sucker (2,243; 17%), and speckled dace (1,072; 8%). The contribution of rainbow trout to the overall species catch composition fell steadily through the course of the study from a high of approximately 90% in January 2003 to less than 10% in

August 2006 (Figure 2-3). Overall, non-native fish comprised more than 95% of the catch in 2003, but following July 2005 generally contributed less than 50%. Owing to particularly large catches of flannelmouth sucker and humpback chub in September 2005, the non-native contribution to the catch in that month was less than 20%. While the catch of non-native fish generally fell through the course of the study, catches of non-native cyprinids (dominated by fathead minnows) increased in 2006.

Using the HBM, the estimated abundance of rainbow trout in the entire removal reach ranged from a high of 6,446 (95% credible interval (CI) 5,819-7,392) in January 2003 to a low of 617 (95% CI 371-1,034) in February 2006; a 90% reduction over this time period (Table 2-2). Between February 2006 and the final removal effort in August 2006, the estimated abundance increased by approximately 700 fish to 1,297 (95% CI 481-2,825). Though this increase was more than double the February 2006 estimate, the August 2006 estimate was much less precise. The estimated abundance in the downstream stratum of the mechanical removal reach was typically approximately 30% of that in the upper stratum (Figure 2-4) and the density was also typically lower (Table 2-2). The estimated capture probability in the upper stratum ranged from 4% to 34% (Figure 2-4). The estimated capture probability was generally lower in the lower stratum and ranged between 2% and 19%.

Net immigration rate estimates indicate that fish were moving into both strata within the removal reach at a higher rate during 2003-2004 than during 2005-2006 (Figure 2-5). Additionally, it appears that net immigration may be lowest in the late fall through early winter, and highest between January and March. During 2005-2006, there were only two time intervals that suggest net immigration rate was different than zero in the downstream stratum and one in the upstream stratum. However, since these estimates are the difference between two

distributions, each with their own error, the net immigration estimates were imprecise for many of the time periods (Figure 2-5).

The results of the covariate analysis indicated that most of the factors had little influence on capture probability (Figure 2-6). In fact, there was little indication that any factor had a strong directional effect in either raising or lowering capture probability. The exceptions were that on four of the trips, the boat operator 2 effects were significantly less than zero indicating that this operator had a negative effect on capture probability compared to operator 1. Additionally, operator 3 tended to have a slightly positive effect on capture probability. Operators 5 and 6 participated in only 1 and 2 trips, respectively, but did not seem to affect capture probability relative to operator 1. Neither boat type nor type of electrofishing control unit had a strong directional effect on capture probability. The factor that had the largest effect on capture probability was location in the overall reach. Though there was no indication that capture probability was uniformly higher or lower in the upstream stratum versus the downstream stratum, several of the trips indicated that capture probability was significantly different among strata. This result supports the use of separate distributions to describe capture probabilities in the overall HBM to estimate abundance, capture probability, and net immigration rate.

Control Reach

A total of 11,221 fish representing 7 species were captured during control reach sampling (Table 2-3). The majority of fish captured were rainbow trout (95%), followed by flannelmouth sucker (3%), and brown trout (1%). A general pattern of decreasing rainbow trout abundance was observed throughout the study, particularly following spring of 2005 (Figure 2-7). Initial (l_1) and secondary (l_2) monthly tag loss rate estimates were 11% and <1%, respectively,

suggesting that most tag loss occurred shortly after tagging. Rainbow trout abundance within the control reach was estimated at between 5,000 and 10,000 fish during 2003-2004 and between 2,000 and 5,000 during 2004-2005 (Table 2-4 and Figure 2-7). This analysis coupled with the catch rate assessment (Figure 2-7) suggests that rainbow trout abundance likely declined by one half or more between the first and last two years of the study. Capture probability ranged between 3% and 13% with no strong temporal pattern (Figure 2-7). Estimated monthly survival rate ranged from a low of approximately 0.72 to a high approaching 1 (Figure 2-8). The lowest survival rates were observed during 2005.

Comparison of Mechanical Removal and Control Reaches

The abundance of rainbow trout declined through the study both in the mechanical removal reach and in the control reach; however, the pattern of decline was dissimilar among reaches (Figure 2-9). In the mechanical removal reach, the largest decline (62%) occurred between January 2003 and September 2004. Rainbow trout abundance in this reach declined much less rapidly from January 2005 to August 2006. In contrast, rainbow trout abundance in the control reach was constant to slightly declining from March 2003 through September 2004, but displayed a strong negative trend subsequently. These patterns suggest that removal efforts likely affected abundance in the mechanical removal reach predominantly during 2003 and 2004.

Another difference between the mechanical removal and control reaches was the seasonal patterns in rainbow trout abundance. In the removal reach, a pattern of declining abundance during each three-month bout of removal efforts (e.g., January-March) was followed by an increase in abundance at the beginning of the next series of removal efforts (e.g., July-September), particularly during 2003-2004 (Figure 2-4). This pattern would be expected if the removal rate was greater than the immigration rate only during each removal series. This pattern was not evident in the control reach considering either the catch rate or abundance estimates

(Figure 2-7) suggesting that mechanical removal was influencing the abundance of rainbow trout in the removal reach.

These seasonal patterns in rainbow trout abundance are mirrored by trends in the average length (Figure 2-10). Average length among the two reaches tended to converge in July of each year followed by a period of divergence. One possible explanation of this pattern is selective removal of larger individuals followed by reinvasion, particularly following the winter/spring removal efforts, of larger individuals from upstream sources. This pattern was not observed in July 2005 and was preceded by a significant decline in average length in the control reach. Taken together, these observations suggest a disruption in the net immigration pattern, possibly from upstream sources, into the removal reach during 2005.

Discussion

Mechanical Removal: Effective Program?

Results suggest that the mechanical removal program was successful in reducing the abundance of non-native fishes, primarily rainbow trout, in a large segment of the Colorado River in Grand Canyon. However, maintenance of low rainbow trout abundance in the removal reach was also facilitated by reduced immigration rates during 2005-2006 and a systemic decline in abundance. Common features of this study and other successful non-native mechanical removal efforts are significant and sustained removal effort. Bigelow (2003) demonstrated that population level changes were not evident in removal efforts aimed at non-native lake trout *Salvelinus namaycush* in Yellowstone Lake until the latter years of a four year study when additional support for the project (e.g., funding and equipment) allowed increases in total removal effort and efficiency. Similarly, removal objectives for non-native brook trout *Salvelinus fontinalis*, golden trout *Oncorhynchus mykiss aguabonita*, and rainbow trout from small high altitude lakes in the Sierra Nevada were achieved with year-round gillnet fishing

(Knapp et al. 2007). In combination with increased predation from stocked predators, Hein et al. (2006; 2007) demonstrated effective control of non-native crayfish *Orconectes rusticus* using mechanical removal, but only with sustained and significant removal effort. The necessity for sustained “maintenance” control of non-natives is not uncommon (Pine et al. 2007) as many non-native species demonstrate high resilience, and are well adapted to their introduced environment as evidenced by their invasion success and warranted need for management action.

In contrast, Meyer et al. (2006) document a recent unsuccessful effort to remove brook trout from a 7.8 km reach of a second-order stream in Idaho using electrofishing. Crews removed fish over 3 days in August during each year for four years. While the capture technique was likely appropriate, the overall effort was apparently insufficient to significantly reduce the population. In the present study and considering the net immigration rates of rainbow trout into the mechanical removal reach during 2003-2004, much smaller and possibly undetectable reductions in overall abundance would have been realized had removal efforts been applied only once per year.

Serendipitous Timing: What Led to the Decline of Rainbow Trout in the Control Reach?

The decline of rainbow trout abundance observed in the control reach was likely precipitated by at least two factors. First, rainbow trout abundance in the Lees Ferry reach (-15 RM at GCD to RM 0) of the Colorado River increased during approximately 1992-2001 and abundance in this reach steadily fell during 2002-2006 (Makinster et al. 2007). With the exception of limited spawning activity in select tributaries of the Colorado River in Grand Canyon, rainbow trout reproductive activity appears to be limited mainly to the Lees Ferry reach (Korman et al. 2005). Examination of length frequency distributions of rainbow trout captured using electrofishing from Glen Canyon Dam to RM 56 during 1991 through 2004 also supports the idea that Lees Ferry is the primary spawning site, as the juvenile size class of rainbow trout is

largely absent from collections downstream of RM 10 (Figure 2-11). Thus, it is reasonable to conclude that at least for the last 10-15 years, the natal source of most rainbow trout in this system is the Lees Ferry reach. This is significant because it suggests that abundance of rainbow trout in Grand Canyon is partially influenced by trends in rainbow trout abundance and reproduction in the Lees Ferry reach.

Second, it has been widely demonstrated that the density of rainbow trout is not uniform in the Colorado River below GCD and distribution patterns are likely influenced by food resources and foraging efficiency (Gloss and Coggins 2005). Rainbow trout density generally declines with downstream distance from GCD but exhibits punctuated declines below the confluences of the Paria River and the LCR. The density of algae and invertebrates in the Colorado River also decline along this gradient (Kennedy and Gloss 2005) suggesting a possible linkage between distance from the dam and primary production. A major factor likely influencing these distributional patterns is sediment delivery from tributaries and the subsequent effects of elevated turbidity in the Colorado River in downstream sections. Yard (2003) demonstrated that these tributary inputs of sediment contribute to high turbidity and limit aquatic primary production. Trout are predominantly sight feeders – thus, high turbidity is likely to adversely affect foraging efficiency by decreasing encounter rate and reactive distance to prey items (Barrett et al. 1992).

From September 2004 through January 2005, the discharge and sediment load from the Paria increased to the point that a threshold outlined in the Glen Canyon Dam Adaptive Management Program related to rebuilding depleted Colorado River sandbars was reached triggering an experimental high flow from GCD in November 2004. It is possible that the high flow event and the associated period of elevated turbidity may have influenced rainbow trout density downstream of the Paria River confluence, possibly through elevated mortality rates.

Estimated survival rates in the control reach generally support the notion that rainbow trout may have experienced diminished survival rates during late 2004 and early 2005 (Figure 2-8).

Other Species

Beginning in September 2005, large increases in the catch of non-native fathead minnow and black bullhead *Ameiurus melas* were observed compared to the previous 17 trips, suggesting either increased immigration and/or survival of these fishes in the mechanical removal reach. Since these fish are not captured with any regularity in the control reach nor in other sampling upstream of RM 44 (USGS, unpublished data), it is reasonable to conclude that their source is not upstream. Stone et al. (2007) documented the presence of these species and other warm water non-natives in the LCR \approx 132 km upstream from the confluence and suggested this tributary as the likely source of fathead minnow, black bullhead, and 6 other non-native fish frequently encountered in the lower LCR and the mechanical removal reach. Thus, one possibility for the elevated catch of fathead minnow and black bullhead in the mechanical removal reach during this latter timeframe is an elevated emigration rate of these fishes from the LCR. Alternatively, increasing water temperature, particularly in 2005 (Figure 2-12), and the concurrent reductions in rainbow trout biomass, may have influenced the survival and activity of these fishes causing them to be both more abundant and more susceptible to capture.

Bias in Capture Probability and Abundance Estimates

Capture probability estimates from the upper stratum of the mechanical removal reach and the control reach are surprisingly different. Neither of these reaches is differentially influenced by large tributary inputs and they share similar overall channel morphology – yet capture probability estimates are generally nearly twice as high in the removal reach as in the control reach. Several authors have demonstrated that capture probability is typically over-estimated using electrofishing depletion-based methods (Peterson et al. 2004; Rosenberger and Dunham

2005). The typical mechanism for this finding is heterogeneity in capture probability among individuals in the population. As a result, the fish remaining after each successive pass have overall lower capture probability than those in preceding passes. This bias in capture probability then leads to negative bias in abundance. Because of this bias, it is likely that the depletion-based capture probabilities estimated in this study are higher than were actually realized.

In principle, the additional information available from mark-recapture should provide less biased estimates of capture probability in the control reach. However, this may not be true due to possible inadequate mixing of fish between each mark-recapture sampling event. Because only 40% of the available sites were sampled during each mark-recapture event, if fish did not mix completely between passes it is possible that capture probability may have been underestimated since not all fish had an equal probability of capture within each event. Theoretically this assumption is met by the random selection of sampled sites each trip. In practice, however, only 40% of fish (assuming uniform distribution) actually had an opportunity to be captured. Additionally, it is possible that there was sampling induced heterogeneity in capture probability. This is a common feature of mark-recapture experiments for small mammals (Otis et al. 1978) and a recent paper by Askey et al. (2006) suggests that fish may develop anti-capture behavior as well. Therefore, the realized capture probabilities were likely between those estimated in the control reach and those estimated in the removal reach. If true, abundance and density estimates are likely over-estimated in the control reach and under-estimated in the removal reach.

Recommendations for Future Mechanical Removal Operations

I recommend that further effort be spent better documenting the preferred habitat of target non-native species. This information could then be used to more effectively distribute removal effort among habitat types that contain the highest density of non-native species. Bigelow et al. (2003) describe the use of hydroacoustic surveys to better target areas of high lake trout

abundance, increasing the efficiency of the control program. A possible technique to better determine these high density areas in the mechanical removal reach would be to employ a finer scale shoreline habitat-based delineation of removal sites, rather than the coarse 500 m sites used in the present study. Serial depletion data could then be analyzed with the HBM to include a habitat covariate for density. This approach has been successfully used to describe patterns in the density of organisms as a function of habitat characteristics (Royle and Dorazio 2006).

Results from the present covariate analysis indicate that most variability in capture probability is related to site location rather than methodological issues. In the context of designing future removal efforts and the larger monitoring program for non-native salmonids in Grand Canyon, this is a fortunate result as it suggests that current levels of standardization among equipment will have a reasonably high likelihood of producing index data useful for determining trends in salmonid abundance and distribution. However, the observed variability among boat operators implies that additional training to reinforce consistent methodologies may be useful to further minimize that source of variability. A more significant finding is the heterogeneity in capture probability among upstream and downstream strata. If these differences are primarily related to uncontrollable factors such as turbidity or shoreline and substrate type as suggested by Speas et al. (2004), additional research should be conducted to better describe these relationships. Unfortunately, I was not able to obtain robust measurements of turbidity with sufficient regularity to investigate the effect of turbidity on capture probability. However, assuming serial depletion methods are likely to be used in future fish control programs, these efforts may provide the ideal setting to explore these associations.

Adaptive Management in Grand Canyon: The Future

As stated at the beginning of this chapter, this study documents the implementation of an ecosystem-scale adaptive management action aimed at testing the efficacy of a particular

management policy (i.e., non-native control) in order to improve the status of native fish resources in Grand Canyon. Though this study focuses on the efficacy of implementing the policy, the more interesting, important, and difficult questions are related to evaluating whether the policy will have the intended effect. I predict that if non-native salmonids are a significant and uncompensated mortality source for native fish attempting to rear in the mainstem Colorado River, then the survival rate and abundance of juvenile native fish in the mainstem should increase during 2003-2006. I would further predict that humpback chub recruitment associated with the 2003-2006 brood years should increase.

There are some indications that the abundance of native fish has increased in the removal reach during 2003-2006 (Figure 2-3; Chapter 5) suggesting either increased survival rate, increased production of juvenile fish, or both. However, these initial signals are not adequate to infer the success of the policy for two important reasons. First, the unplanned increases in release water temperature are nearly perfectly temporally correlated with the magnitude of the non-native fish reduction (Figures 2-4 and 2-12). As water temperature is also a controlling factor affecting quality of rearing habitat in the mainstem river (Gloss and Coggins 2005), this confounding makes separation of these two effects impossible at this time. Second, since there is not a monitoring program for estimating temporal trends in survival rate, likely the most reliable available measure of a native fish response is humpback chub recruitment. Because the age-structured mark-recapture model (Chapter 4) is not able to provide estimates of year class strength until fish reach age-4, the best data to infer change in survival are not yet available.

One strategy to separate out the effects of non-native fish versus increased water temperature would be to implement a future experiment with one of these factors changed from the 2003-2006 condition. However, since temperature control is not available at this time and

since rainbow trout abundance appears diminished system-wide, there may be limited near-term opportunities to manipulate the system further. Determining what future experiments to conduct will be determined by the Glen Canyon Dam Adaptive Management Program using input from studies such as this – but it should be noted that the implementation and ultimate success of even the best designed experiments will be dependent on unmanageable factors such as climate (Seager et al. 2007) and unexpected biotic interactions.

Table 2-1. Electrofishing catch by species in the mechanical removal reach for each month, 2003-2006.

Trip Date	# Removal Passes	Species ^a															
		BBH	BHS	BNT	CCF	CRP	FHM	FMS	GSF	HBC	PKF	RBT	RSH	SMB	SPD	STB	SUC
Jan-03	5		8	87		80	17	188		26	1	3,605			7		2
Feb-03	5		18	24		33	21	165		26		1,913	1		2		
Mar-03	5	3	11	21	1	22	8	89		13	1	1,195	1		8		
Jul-03	5	4	12	63		29	4	267		124		2,278	1		6		3
Aug-03	2	2	4	12		14		79		17		779					5
Sep-03	3	1	19	11		31	4	119		37	2	818	1		18		4
Jan-04	4	3	32	88		23	18	169		51		1,330			53		3
Feb-04	4	9	37	29	1	9	13	110		52		622			34		
Mar-04	5	5	24	22		18	44	218		61	6	867			92		3
Jul-04	6	9	84	29	1	26	32	296		142	9	1,464	3		47		
Aug-04	4	6	33	7		16	6	190		27	3	480	2		7		
Sep-04	4	11	72	17		29	13	258		43		687	5		19		
Jan-05	4	8	54	14		27	72	244		61	1	623	9		52		
Feb-05	4	3	38	4	1	14	39	191		49	2	283	2		39		
Mar-05	4	8	51	4		14	73	176		82	3	318	4		51		
Jul-05	4	17	159	9	2	45	9	480	1	220		432	2		38	2	1
Aug-05	4	9	124	4		36	17	419		86	1	295	4		24		24
Sep-05	4	14	576	7		47	190	1,140		600		230	15		187		4
Jan-06	4	23	197	9		38	685	545		249		357	13		115		1
Feb-06	4	15	98	5		10	300	529		171	1	103			70		
Mar-06	4	12	96	2		8	322	365	1	196	1	66	2		84		
Jul-06	4	15	331	8		64	192	554		145	2	159	2		56		
Aug-06	4	13	165	3	1	169	490	556		128	34	116	1	1	63		9
Total		190	2,243	479	7	802	2,569	7,347	2	2,606	67	19,020	68	1	1,072	2	59

^a BBH=black bullhead (*Ameiurus melas*), BHS=bluehead sucker (*Catostomus discobolus*), BNT=brown trout (*Salmo trutta*), CCF=channel catfish (*Ictalurus punctatus*), CRP=common carp (*Cyprinus carpio*), FHM=fathead minnow (*Pimephales promelas*), FMS=flannelmouth sucker (*Catostomus latipinnis*), GSF=green sunfish (*Lepomis cyanellus*), HBC=humpback chub (*Gila cypha*), PKF=plains killifish (*Fundulus zebrinus*), RBT=rainbow trout (*Oncorhynchus mykiss*), RSH=red shiner (*Cyprinella lutrensis*), SMB=smallmouth bass (*Micropterus dolomieu*), SPD=speckled dace (*Rhinichthys osculus*), STB= striped bass (*Morone saxatilis*), SUC=unidentified sucker.

Table 2-2. Estimated abundance and density of rainbow trout in the mechanical removal reach at the beginning of each month, 2003-2006. Uncertainty estimates (95% CI) are 95% Bayesian credible intervals.

Trip Date	Total Reach Abundance		Upper Stratum Abundance		Lower Stratum Abundance		Density (Fish/Km)	
	N	95% CI	N	95% CI	N	95% CI	Upper Stratum	Lower Stratum
Jan-03	6,446	5,819-7,392	4,977	4,519-5,640	1,469	1,168-1,996	1,512	563
Feb-03	3,073	2,802-3,492	2,437	2,226-2,778	637	489-879	740	244
Mar-03	2,372	1,939-3,014	2,023	1,606-2,671	349	289-485	615	134
Jul-03	5,253	4,249-7,616	3,614	3,164-4,183	1,639	902-3,776	1,098	629
Aug-03	1,574	1,253-2,199	1,237	1,001-1,652	336	178-845	376	129
Sep-03	3,008	1,964-4,197	2,399	1,438-3,507	609	345-1,187	729	233
Jan-04	2,207	1,953-2,635	1,684	1,472-2,002	523	385-851	512	201
Feb-04	1,611	1,098-2,809	845	732-1,026	767	293-2,009	257	294
Mar-04	1,425	1,227-1,710	1,075	925-1,325	350	269-516	327	134
Jul-04	3,445	2,533-5,284	1,718	1,566-1,925	1,727	856-3,627	522	662
Aug-04	932	734-1,536	677	515-1,266	255	183-455	206	98
Sep-04	2,459	1,647-3,752	1,980	1,296-3,290	479	199-1,060	602	184
Jan-05	989	819-1,275	722	675-786	266	115-539	219	102
Feb-05	869	519-1,785	386	317-516	483	142-1,388	117	185
Mar-05	975	636-1,548	782	498-1,377	193	80-427	238	74
Jul-05	1,626	742-5,837	736	560-1,085	891	128-5,056	224	341
Aug-05	690	498-1,080	415	339-549	275	115-638	126	105
Sep-05	697	460-1,291	411	288-601	286	108-893	125	110
Jan-06	710	514-1,121	502	386-719	208	100-580	153	80
Feb-06	617	371-1,034	479	258-879	138	61-290	145	53
Mar-06	669	280-1,460	367	154-860	302	69-992	111	116
Jul-06	726	376-2,210	538	251-1,853	188	89-410	163	72
Aug-06	1,297	481-2,825	767	262-2,087	530	136-2,090	233	203

Table 2-3. Electrofishing catch by species in the control reach for each month, 2003-2006.

Trip Date	Control Sites	Species ^a								
		BBH	BHS	BNT	CRP	FMS	HBC	RBT	SPD	SUC
Jan-03	25			10	1	1		444		
Feb-03	24			8		1		548		
Mar-03	24			5		1		888		
Jul-03	24			8	1	2		416		
Aug-03	11			4	1			256		
Sep-03	24			7	2	7		1,036		1
Jan-04	24			5				702		
Feb-04	24			3	1	1		434		
Mar-04	24		2	14		3		851		
Jul-04	24			2		9	1	491		
Aug-04	24			9		6		346		
Sep-04	24			8	1	4		498		2
Jan-05	24			1		1		503		
Feb-05	24			9		4		476	1	
Mar-05	24		1	9		5		540		
Jul-05	24		1	11		34		277		
Aug-05	24			5		21		332		
Sep-05	24		1	2	1	72		284	1	
Jan-06	24		2	2	1	31		277	1	
Feb-06	24			4	2	53		243		
Mar-06	24			5		23		336		
Jul-06	24		5	2	5	47	1	176	12	
Aug-06	24	1	10	1	1	52	1	294		
Total		1	22	134	17	378	3	10,648	15	3

^a BBH=black bullhead (*Ameiurus melas*), BHS=bluehead sucker (*Catostomus discobolus*), BNT=brown trout (*Salmo trutta*), CRP=common carp (*Cyprinus carpio*), FMS=flannelmouth sucker (*Catostomus latipinnis*), HBC=humpback chub (*Gila cypha*), RBT=rainbow trout (*Oncorhynchus mykiss*), SPD=speckled dace (*Rhinichthys osculus*), SUC=unidentified sucker.

Table 2-4. Estimated abundance and density of rainbow trout in the control reach at the beginning of each month, 2003-2006. Uncertainty estimates (95% CI) are 95% profile likelihood confidence intervals.

Trip Date	Total Abundance		Density (Fish/Km)
	N	95% CI	
Feb-03	5,058	3,500-7,262	1,018
Mar-03	10,571	8,064-14,136	2,128
Jul-03	10,106	6,572-16,367	2,034
Aug-03	8,819	5,494-13,593	1,775
Sep-03	8,051	6,004-10,860	1,621
Jan-04	9,952	6,491-15,662	2,003
Feb-04	8,998	5,570-15,024	1,811
Mar-04	7,939	5,379-11,798	1,598
Jul-04	8,758	5,895-13,254	1,763
Aug-04	6,981	4,519-11,171	1,405
Sep-04	7,208	4,733-10,795	1,451
Jan-05	4,138	2,853-6,090	833
Feb-05	4,527	3,344-6,202	911
Mar-05	5,253	3,939-6,907	1057
Jul-05	3,163	1,967-5,245	637
Aug-05	3,247	2,126-4,900	654
Sep-05	2,955	1,877-4,604	595
Jan-06	4,032	2,502-6,694	812
Feb-06	2,992	1,957-4,804	602
Mar-06	2,518	1,594-3,443	507
Jul-06	2,131	1,113-4,062	429

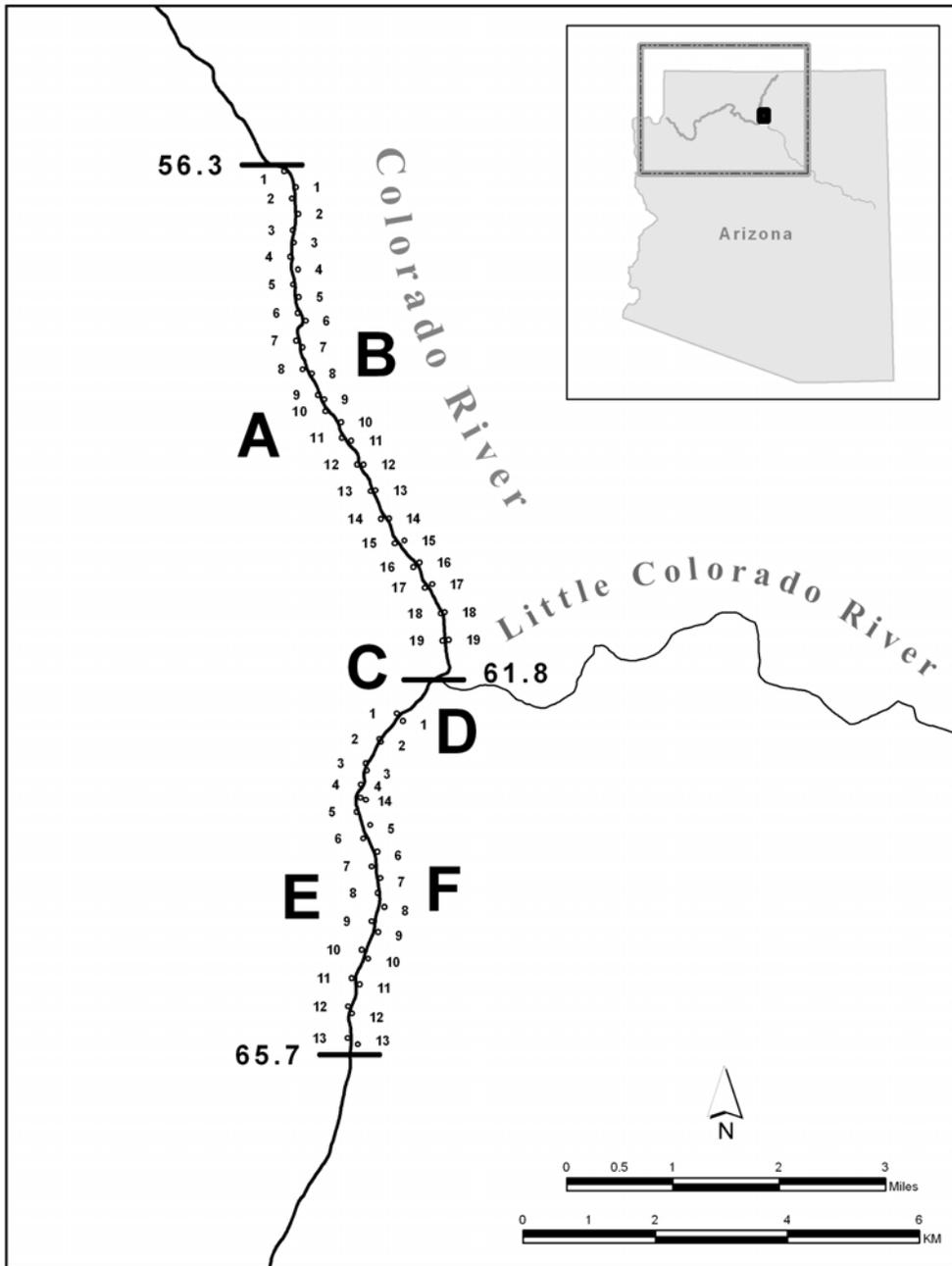


Figure 2-1. Map of the mechanical removal reach of the Colorado River within Grand Canyon, Arizona. Depicted on the map are the reach sections (A-F) and the sites within each reach (e.g., 1-19). The number of river miles downstream from Lees Ferry, Arizona is indicated at demarcation lines.

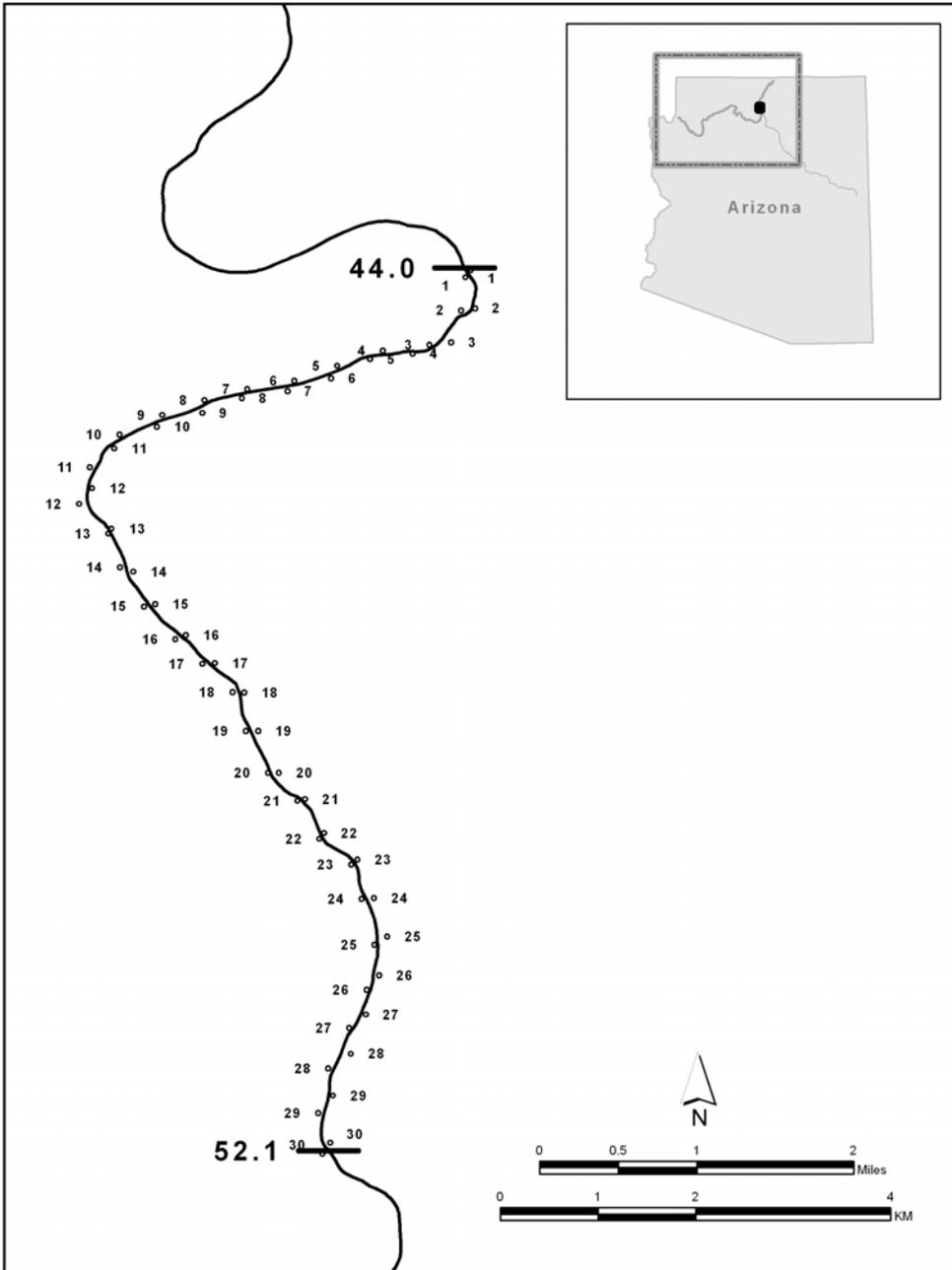


Figure 2-2. Map of the control reach of the Colorado River within Grand Canyon, Arizona. Depicted on the map are the sites within the reach. The number of river miles downstream from Lees Ferry, Arizona is indicated at demarcation lines.

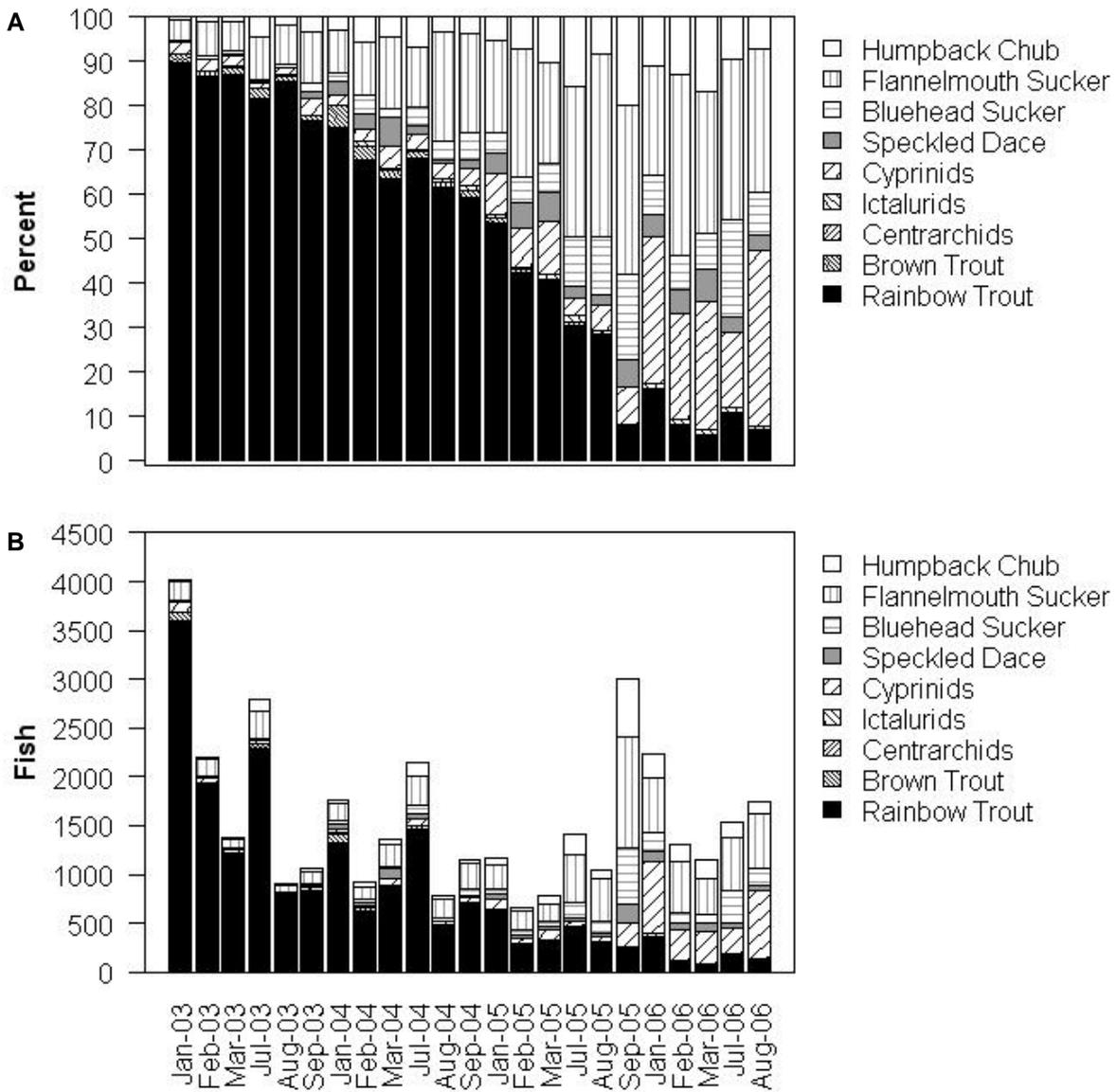


Figure 2-3. Percent composition (A) and number of fish (B) by species captured with electrofishing in the mechanical removal reach among months, 2003-2006.

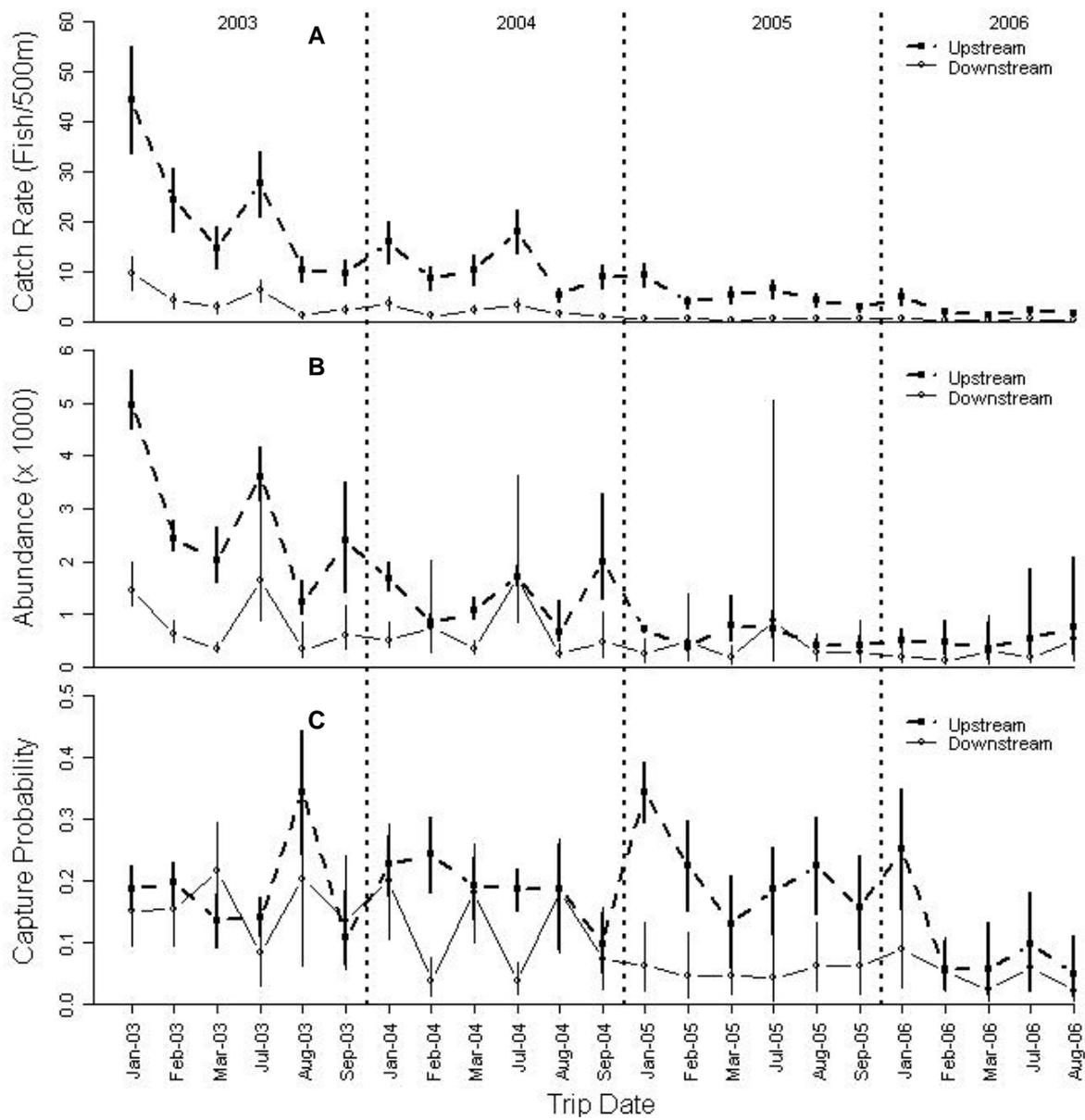


Figure 2-4. Estimated catch rate (A), abundance (B), and capture probability (C) for rainbow trout in both the upstream and downstream strata in the mechanical removal reach among months, 2003-2006. Error bars represent 95% Bayesian credible intervals.

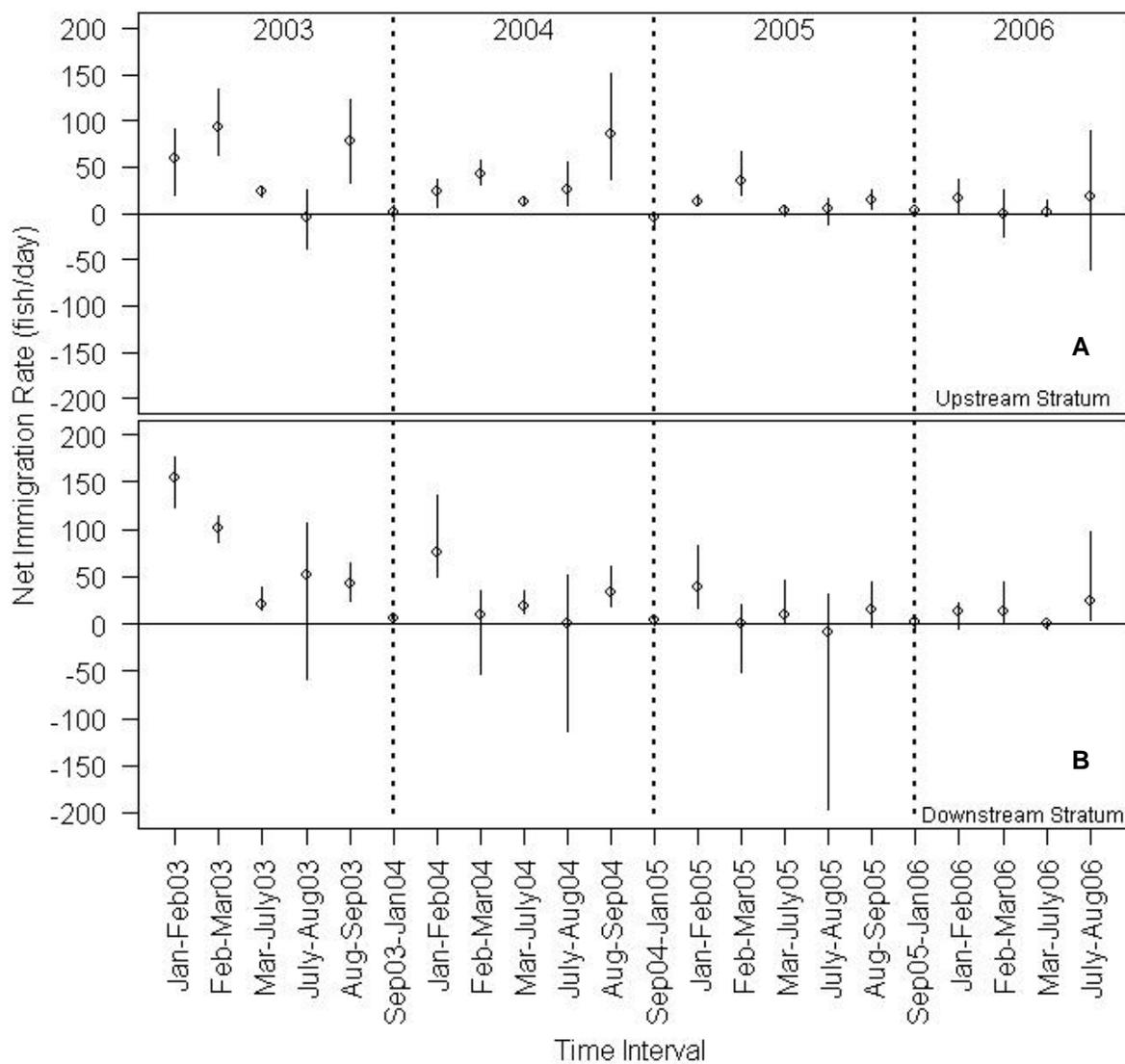


Figure 2-5. Net immigration rate into the upstream (A) and downstream (B) strata of the mechanical removal reach within time intervals between January 2003 and August 2006. Error bars represent 95% Bayesian credible intervals.

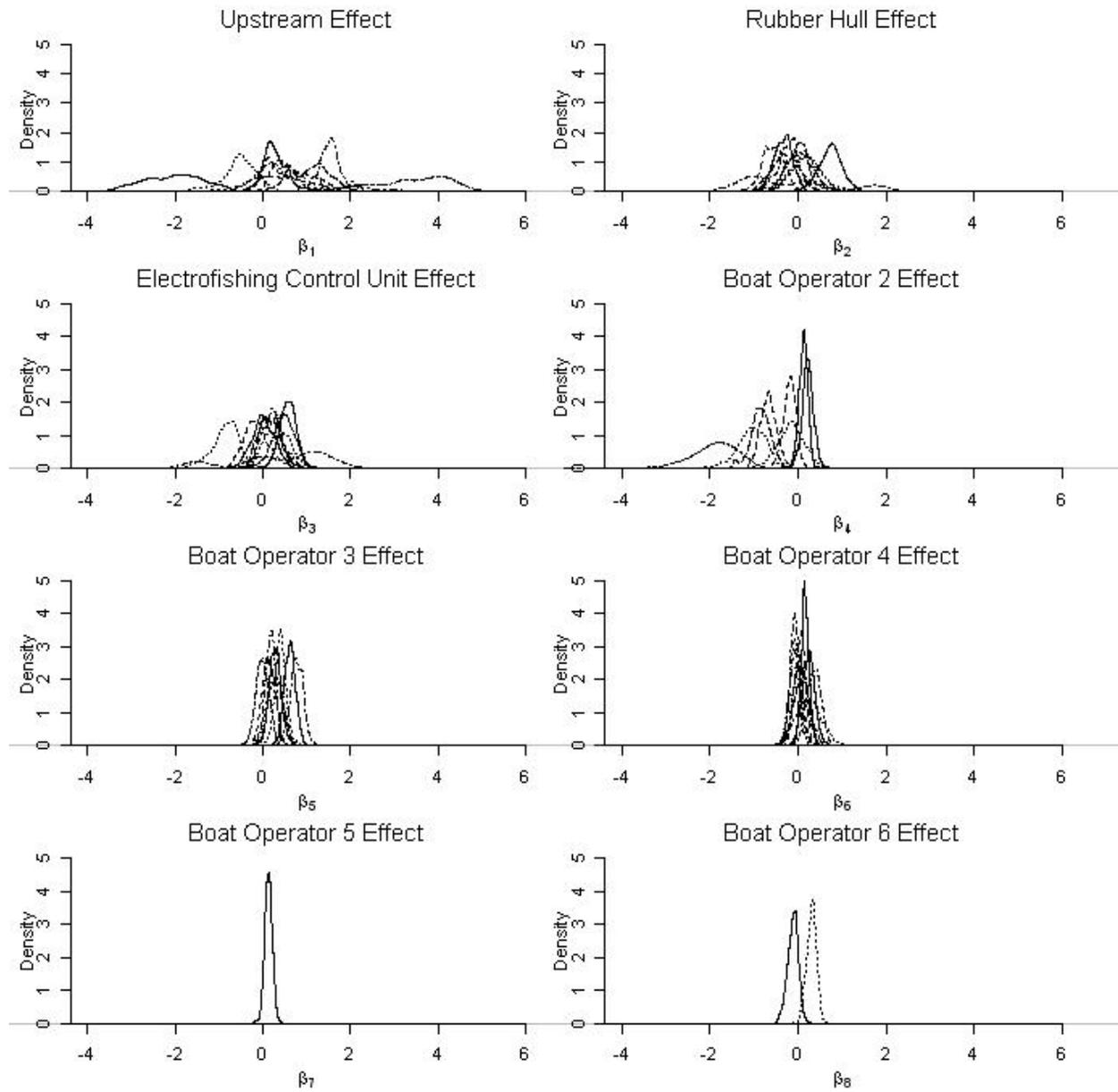


Figure 2-6. Probability plots for coefficient values influencing capture probability among 10 trips (January 2003-July 2003; January 2004-September 2004). Within each plot, each line is the estimated probability density for the coefficient in a trip.

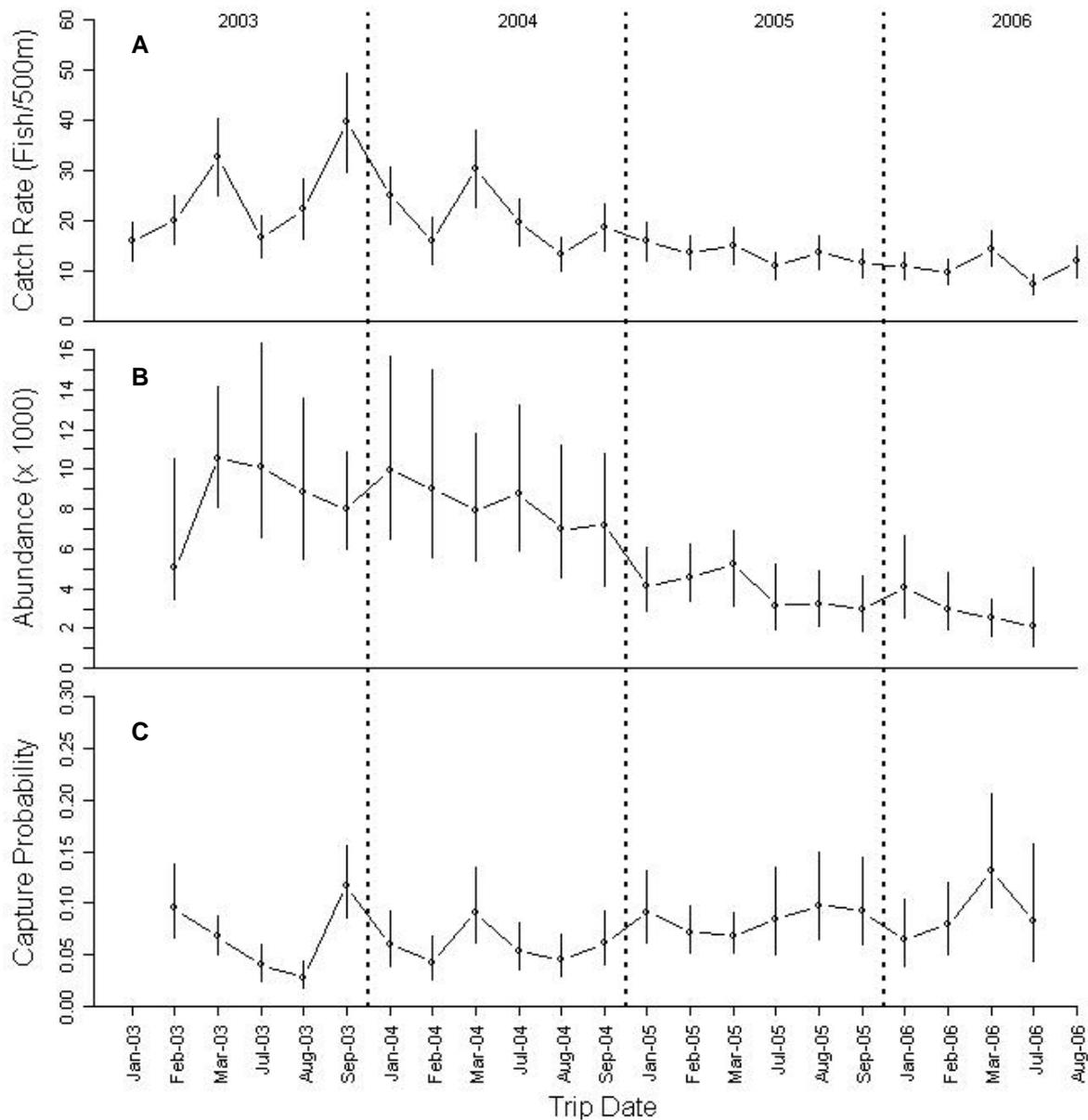


Figure 2-7. Estimated catch rate (A), abundance (B), and capture probability (C) for rainbow trout in the control reach among months, 2003-2006. Error bars represent 95% profile likelihood confidence intervals.

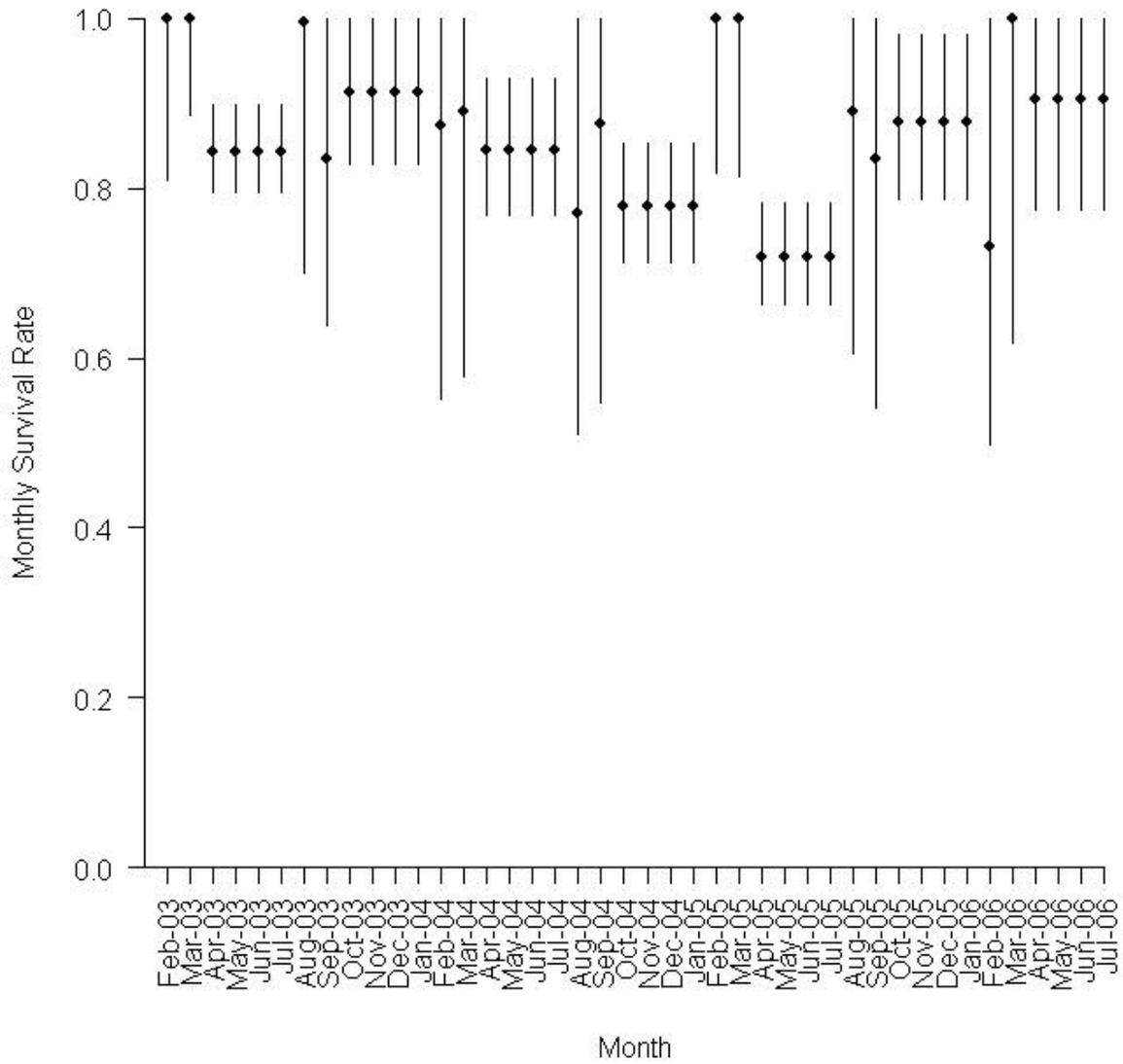


Figure 2-8. Estimated monthly survival rate of rainbow trout in the control reach during 2003-2006. Error bars represent 95% profile likelihood confidence intervals.

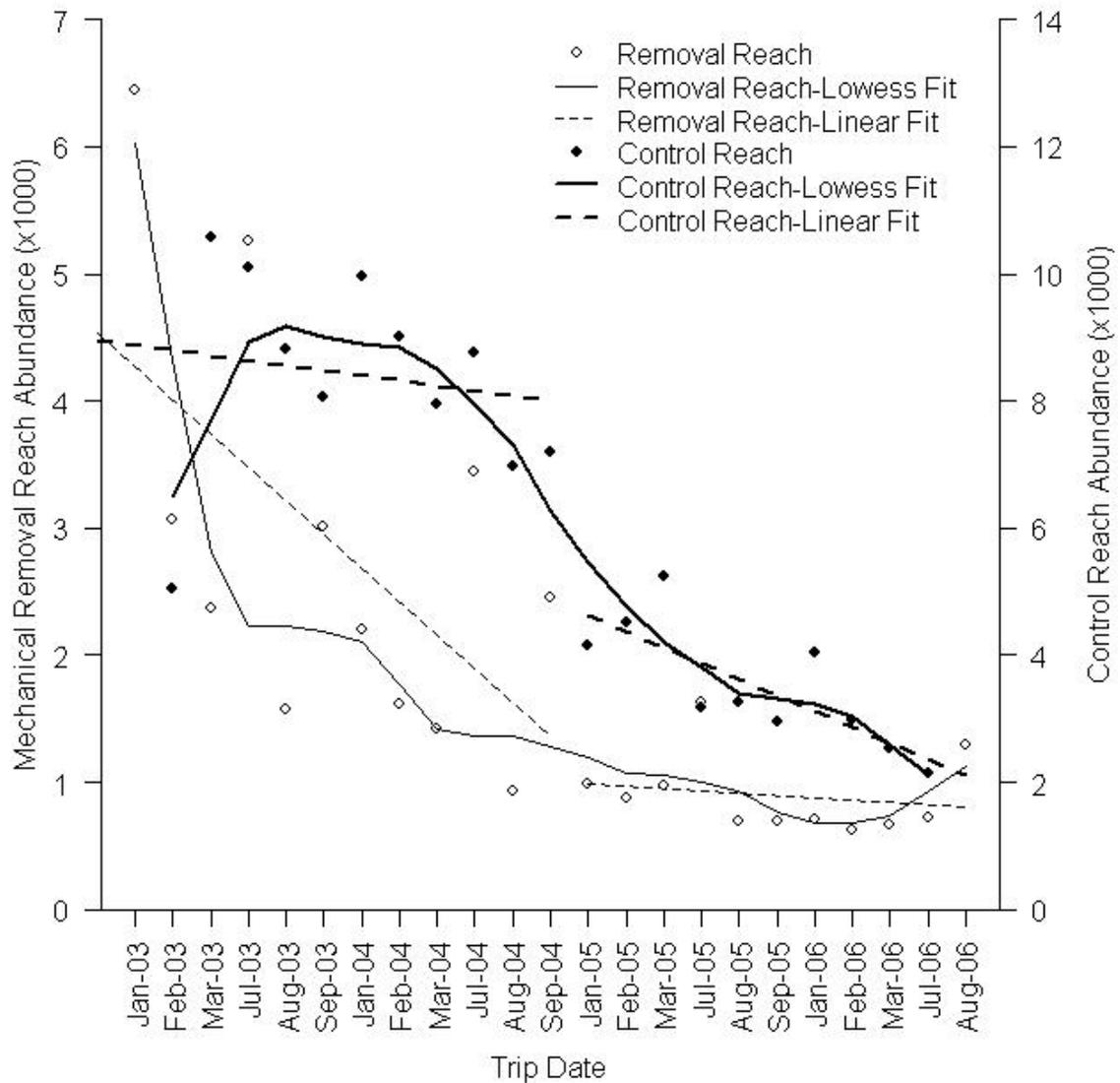


Figure 2-9. Estimated rainbow trout abundance in both the mechanical removal and control reaches at the beginning of each trip during 2003-2006. The solid lines represent the locally weighted polynomial regressions (Lowess) fit to each time series. The dashed lines represent linear regressions fit to either the 2003-2004 or 2005-2006 portions of the time series.

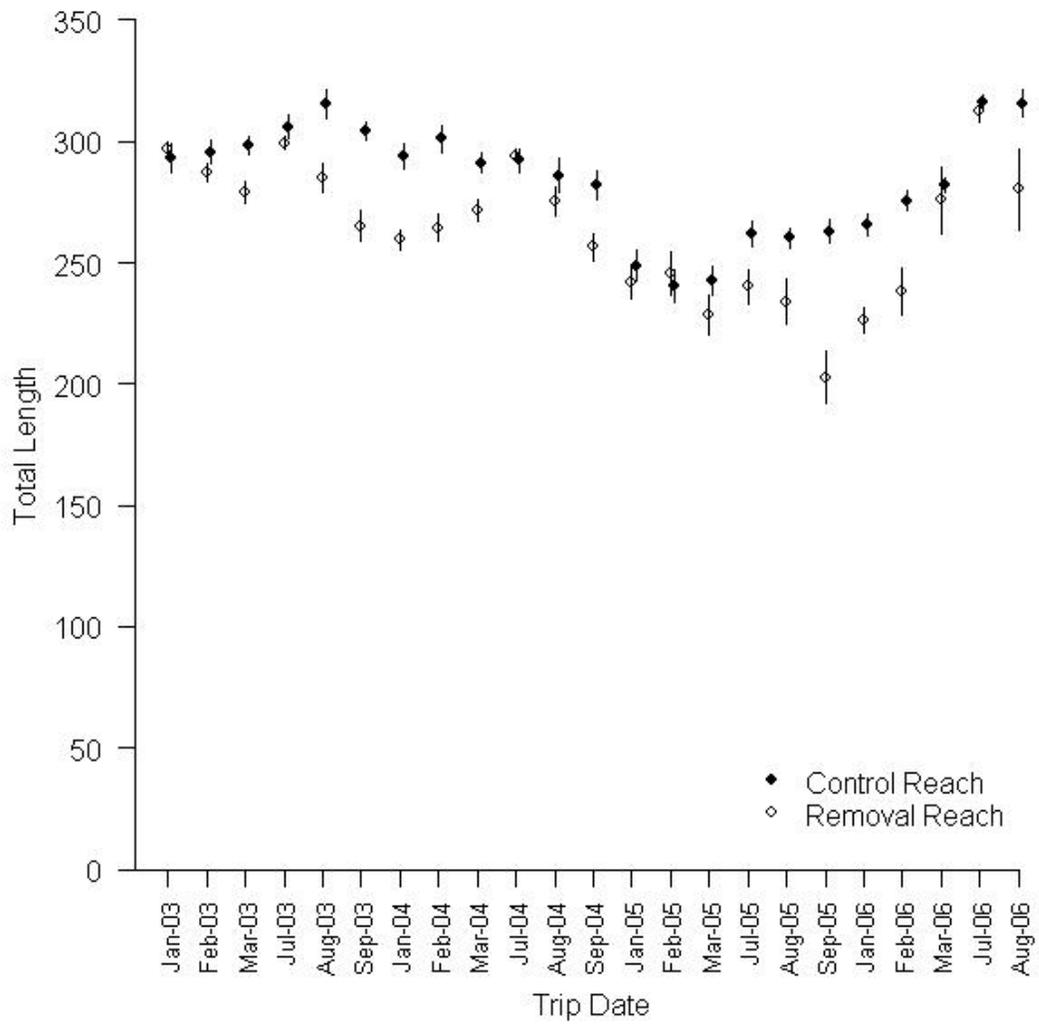


Figure 2-10. Estimated total length and 95% confidence intervals of rainbow trout captured in both the mechanical removal and control reaches during 2003-2006.

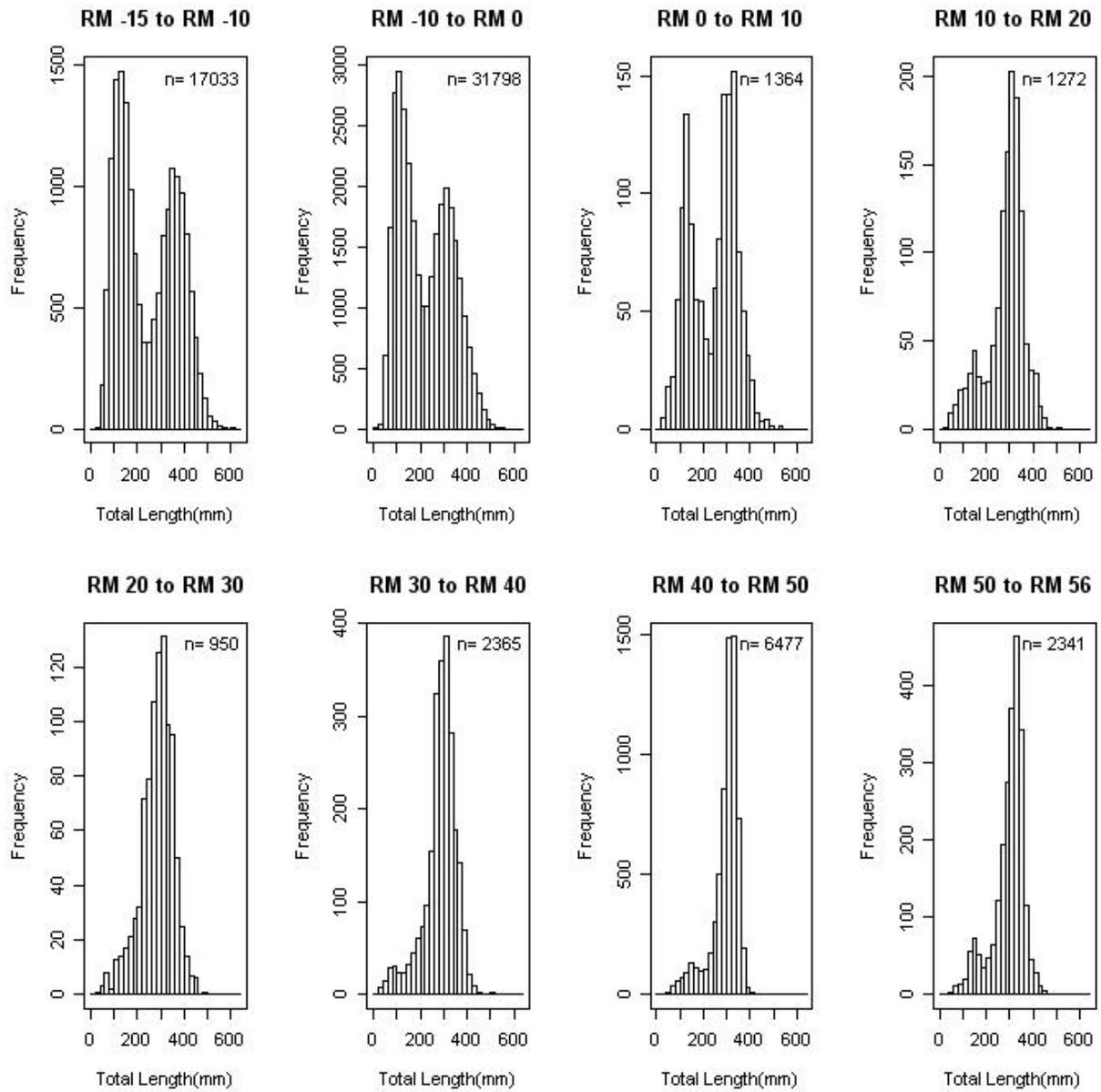


Figure 2-11. Length frequency distributions of rainbow trout captured using electrofishing in the Colorado River from river mile -15 to river mile 56. Each panel represents captures of fish within the identified river segment.

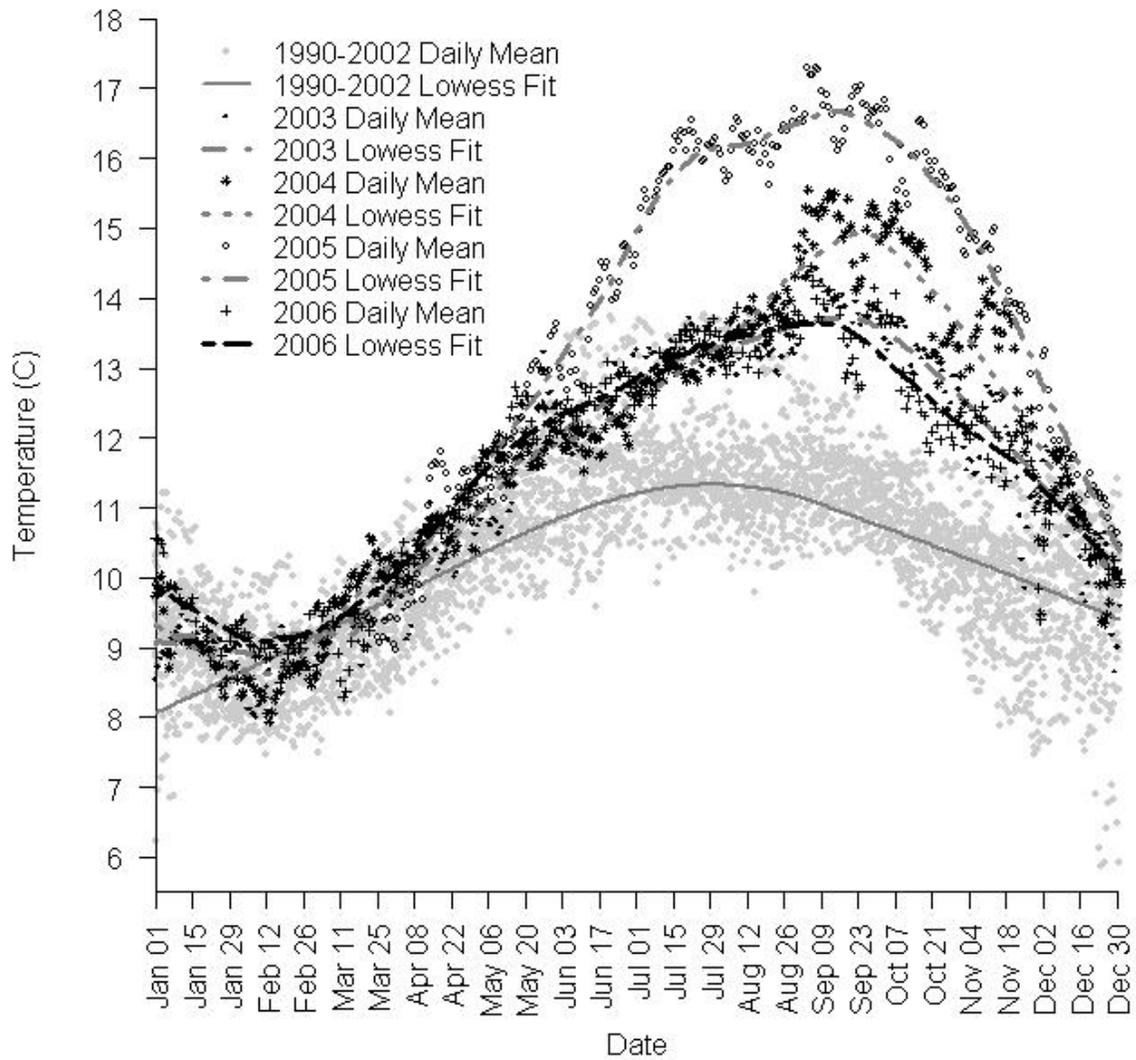


Figure 2-12. Daily mean water temperatures observed in the Colorado River at approximately river mile 61, 1990-2006. Lines indicate locally weighted polynomial regressions (Lowess) fits to the indicated data set.

CHAPTER 3

DEVELOPMENT OF A TEMPERATURE-DEPENDENT GROWTH MODEL FOR THE ENDANGERED HUMPBAC CHUB USING MARK-RECAPTURE DATA

A primary interest of fisheries biologists is to understand how fishes grow and the processes and factors that influence that growth. Such information is critical for research addressing questions about basic ecological relationships such as the tradeoff between growth and survival, and for management strategies associated with maximizing yield. In the latter case, growth information is frequently used to populate assessment models with vital rates (Pauly 1980; Beverton 1992; Jensen 1996) and age-specific length, weight, fecundity, and vulnerability to exploitation (Walters and Martell 2004). Additionally, information on growth may be used to estimate the age of fish based on size (e.g., Kimura and Chikuni 1987). Given the importance of understanding growth, much effort has been expended to understand factors that influence growth, to develop models to describe observed growth patterns, and to estimate the parameters of those models (Ricker 1975; DeVries and Frie 1996).

Though many models of fish growth have been proposed (Ricker 1975; Schnute 1981), perhaps the most widely used is the von Bertalanffy model (Bertalanffy 1938). The parameters of this model are typically estimated by comparing predicted with observed size-at-age or growth increment data (Fabens 1965; Quinn and Deriso 1999). Obtaining growth increment data is usually accomplished via mark-recapture studies where the sizes of individual fish are measured before and after known times at liberty. A significant advantage of using growth increment data to estimate growth model parameters is that ages of individual fish are not required – growth is simply measured over the times that individual fish have been at liberty. Since determination of age frequently involves inspection of various calcareous structures (e.g., otoliths) that often involves sacrificing the animal, use of increment data is preferable when working with endangered or rare species.

The federally endangered cyprinid humpback chub *Gila cypha* is endemic to the Colorado River drainage in the southwestern United States and is generally found in swift, canyon bound river reaches (Minckley 1973). The Little Colorado River (LCR) population of humpback chub within Grand Canyon is a focal resource of the Glen Canyon Dam Adaptive Management Program (Gloss and Coggins 2005). Periodic stock assessments of this population serve as the core monitoring tool and status metric for this resource. These assessments require accurate age assignments of fish captured in a long-term sampling program (Coggins et al. 2006a) in order to employ open population mark-recapture assessment methods that include age-dependent effects. Due to endangered listing status, longevity, and difficulty determining the age of individual humpback chub, little information is available on the relationship between size and age for this species. At present, individual age assignments are based on size and rely on a growth curve estimated from a limited set (≈ 60) age-length observations (USFWS 2002). This lack of growth information promotes uncertainty and possibly bias in length-based age assignment, and this potential bias has been identified as an area of concern by past external reviews of the humpback chub assessment program used by the Glen Canyon Dam Adaptive Management Program (Kitchell et al. 2003).

I used growth increment data to estimate the parameters of a generalized growth model for the LCR population of humpback chub. This effort is undertaken to supplement the available information on humpback chub growth and to inform length-based age assignments for stock assessments. Because the older fish in this population exhibit a potadromous migration between the seasonally warm LCR and the constant cold mainstem Colorado River within Grand Canyon (Gorman and Stone 1999), I evaluated ontogenetic temperature-dependent effects in the growth model. The results of this work should be useful to researchers studying humpback chub or

wishing to estimate temperature-dependent growth models using growth increment data for other species that make major ontogenetic shifts in thermal habitat use.

Methods

An extensive monitoring program for the LCR population of humpback chub has been ongoing since the late 1980s (Coggins et al. 2006a). As a result of routinely capturing and implanting humpback chub with passive integrated transponder (PIT) tags, I was able to compile over 19,000 growth increments with which to evaluate growth rate (or measurement error in the case of recaptures made shortly after tagging). The basic technique for estimating growth model parameters from growth increment data is to predict the amount of growth in the elapsed time between capture and recapture. Assuming standard von Bertalanffy growth curve predictions of length at time t and at time $t+\Delta t$, Fabens (1965) developed the most basic model where the predicted growth increment is given as

$$\Delta L = L(t + \Delta t) - L(t) = (L_{\infty} - L(t))(1 - e^{-k\Delta t}), \quad (3-1)$$

where t is time at initial capture, Δt is the elapsed time between initial capture and recapture, and L_{∞} and k are the asymptotic length and the rate at which length approaches L_{∞} , respectively (Quinn and Deriso 1999). Parameter estimates are found by minimizing the difference between predicted and observed growth increments.

Though this technique has been widely applied, numerous authors have pointed out resulting parameter estimates will be biased if individual fish exhibit growth variability (e.g., Sainsbury 1980; Kirkwood and Somers 1984; Francis 1988). Using this technique, k will typically be negatively biased and L_{∞} will be positively biased. Recognition of these problems has led to the development of alternative models which attempt to minimize these biases (e.g., James 1991; Wang et al. 1995; Laslett et al. 2002). I attempted to estimate standard von

Bertalanffy growth parameters for humpback chub using two of these methods (Wang et al. 1995; Laslett et al. 2002) and generally obtained poor results, characterized by an inability of the models to predict growth increments exhibited by small fish and large fish simultaneously. Examination of growth rate as a function of size reveals that the basic problem with fitting a standard von Bertalanffy model to these data is the lack of a simple linear relationship between growth rate and length (Figure 3-1) as is implied by this model. It is apparent that the fish less than approximately 250 mm TL have a larger von Bertalanffy k parameter value (i.e., more negative slope of the growth rate vs. length plot) than do fish larger than 250 mm TL. These results suggest a “kink” in the growth curve as would be found if fish grew along one curve when small and then switched to another when larger.

Because water temperature is a major determinant of basal metabolic rate and hence the von Bertalanffy k parameter among poikilotherms (Paloheimo and Dickie 1966; Essington et al. 2001), the “kink” hypothesis is consistent with fish that are demonstrating an ontogenetic shift among habitats that have different water temperatures. For humpback chub, this would be a transition from the warm LCR spawning and rearing habitat to the cooler mainstem Colorado River adult habitat (Valdez and Ryel 1995; Gorman and Stone 1999). To account for this apparent pattern of changing growth rate, I fit growth increment data to a general growth model (Paloheimo and Dickie 1965) describing the rate of change in weight as

$$\frac{dW}{dt} = HW^d - mW^n . \quad (3-2)$$

Here, the first term describes anabolism (i.e., mass acquisition) and is governed by a term representing the mass normalized rate at which the animal acquires mass (H), the mass of the animal (W), and a parameter (d) describing the scaling of anabolism with mass. The second term represents catabolism (i.e., mass loss through basal metabolism or activity) where m is the mass

normalized rate at which the animal loses mass and n is the scaling factor of catabolism with mass. Assuming a constant relationship between length and weight over time as

$$W = aL^b, \quad (3-3)$$

where L is length and a and b are constant, it is possible to derive an analogous relationship for the rate of change in length as

$$\frac{dL}{dt} = \alpha L^\delta - \kappa L^\eta. \quad (3-4)$$

Constants in this relationship are related to those in (3-2) and (3-3) as

$$\alpha = \frac{a^{d-1}H}{b}, \quad (3-5)$$

$$\kappa = \frac{a^{n-1}m}{b}, \quad (3-6)$$

$$\delta = bd - b + 1, \text{ and} \quad (3-7)$$

$$\eta = bn - b + 1. \quad (3-8)$$

Essington et al. (2001) review these relationships and describe the derivation of the standard von Bertalanffy growth function as the integral of equation (3-4) when $n=1$, $b=3$, and $d=2/3$. This is the situation where catabolism (plus mass loss to reproductive products) scales linearly with mass, the length-weight relationship is isometric, and anabolism scales as the 2/3 power of mass resulting in the standard von Bertalanffy growth model:

$$L(t) = L_\infty(1 - e^{-k(t-t_0)}), \quad (3-9)$$

where t_0 is the theoretical age where body length is equal to zero.

To estimate growth model parameters, I first assumed that measurement errors in the length of fish are normal with variance σ_m^2 , and that all fish follow a standard von Bertalanffy

growth curve (equation 3-9) with shared k and individual L_∞ . The predicted length of fish at time of recapture can be found by rearranging the Fabens (equation 3-1) as

$$L(t + \Delta t) = L(t) + (L_\infty - L(t))(1 - e^{-k\Delta t}). \quad (3-10)$$

Assuming that individual L_∞ is normally distributed with variance σ_L^2 , the variance of each $L(t + \Delta t)$ is

$$\sigma_{L(t+\Delta t)_i}^2 = \sigma_m^2(1 + e^{-2k\Delta t_i}) + \sigma_L^2(1 - e^{-k\Delta t_i})^2. \quad (3-11)$$

Deviations between observed and predicted growth increment for individual fish i are given as

$$D_i = L(t + \Delta t)_i - L(t)_i - (L_\infty - L(t)_i)(1 - e^{-k\Delta t_i}). \quad (3-12)$$

It is then possible to estimate the parameter vector $\theta = \{L_\infty, k, \sigma_L^2, \sigma_m^2\}$ by maximizing the log-likelihood function:

$$\ln L(\theta | L(t), L(t + \Delta t)) = -\frac{s}{2} \sum_i \frac{D_i^2}{\sigma_{L(t+\Delta t)_i}^2} - \frac{1}{2} \sum_i \sigma_{L(t+\Delta t)_i}^2, \quad (3-13)$$

where s is the number of growth increments. This is essentially an inverse variance weighting strategy where growth intervals that have high recapture length variance are down-weighted in the fitting procedure.

Though this procedure is applicable assuming fish growth is described by equation (3-9), if fish growth is described by equation (3-4) then there is no analytical solution for $\sigma_{L(t+\Delta t)}^2$ as in equation (3-11). However, by estimating θ , and in particular k , using equations (3-11 through 3-13) and assuming that the individual variances computed using equation (3-11) are an adequate approximation, deviations from the general model (equation 3-4) can be used in the log-likelihood. These deviations are computed as

$$D_i = L(t + \Delta t)_i - \int_{t=t_i}^{t=t_i+\Delta t_i} (\alpha L^\delta - \kappa L^\eta) dt. \quad (3-14)$$

After specifying the parameters a and b for equation (3-3), estimation proceeds as above with the parameter vector $\theta = \{H, d, m, n, \sigma_L^2, \sigma_m^2\}$.

I implemented this procedure in both Microsoft Excel using Solver (Ladson and Allan 2002) and AD Model Builder (Fournier 2000) to obtain estimates of θ . I reduced the parameter set by specifying $\sigma_m^2 = 31.8 \text{ mm}^2$ based on an analysis of the observed error between consecutive measurements of identical fish within 10 days. I also specified the a and b parameters for equation (3-3) as 0.01 and 3, respectively. To calculate the conditional variance of each $L(t + \Delta t)$, I specified $k = 0.145$ based on previous analyses. Additionally, I included penalty terms in the log-likelihood equation (3-13) to constrain d and n so that they did not deviate too far from the theoretical values assuming standard von Bertalanffy growth of 2/3 and 1, respectively. I evaluated alternative weight values on these penalty terms to find an appropriate tradeoff between minimum weights and decreased log-likelihood.

Because all the information contained in the mark-recapture data are for fish larger than 150 mm TL, extrapolating results to the growth rate of smaller fish could be problematic. Fortunately, Robinson and Childs (2001) conducted monthly sampling of juvenile humpback chub in the LCR during 1991-1994. They used these data to estimate (by modal progression analysis) average monthly length from age-0 months to age-32 months. I utilized these data in an additional log-likelihood term to constrain the predicted lengths from the general model to be similar to those reported by Robinson and Childs (2001). Using these auxiliary data and assuming normal deviations allowed me to incorporate information on the growth rate of fish

before they are large enough to be implanted with PIT tags. With these constraints in place, the full log-likelihood is

$$\ln L(\theta|L(t)_i, L(t + \Delta t)_i) = -\frac{s}{2} \sum_i \frac{D_i}{\sigma_{L(t+\Delta t)_i}^2} - \frac{1}{2} \sum_i \sigma_{L(t+\Delta t)_i}^2 - \frac{1}{2\lambda} \left(d - \frac{2}{3} \right)^2 - \frac{1}{2\lambda} (n-1)^2 - \frac{mos}{2} \sum_{i=1}^{mos} \ln \left(\frac{L(i) - \ell(i)}{\sigma_\ell} \right)^2, \quad (3-15)$$

where λ is the weighting value for the penalty terms, $L(i)$ is the predicted length in month i from the general model, and $\ell(i)$ is the predicted length over $mos=32$ months as reported by Robinson and Childs (2001). I specified that the variance of the observed lengths σ_ℓ^2 was unity. The weighting term can be interpreted as the prior variance on the standard von Bertalanffy parameters ($d = 2/3$, and $n=1$).

An important logical extension of the general model is to assume temperature dependence in growth rate. Accounting for changes in growth rate as a function of temperature is likely to be important for the analysis of this dataset for two reasons. The first is to account for the differences in growth rate with occupancy in either the LCR or the mainstem Colorado River. The second is to account for seasonal changes in water temperature within the LCR. The importance of the second consideration is further magnified by the temporal distribution of sampling within the LCR. Sampling in the LCR typically occurs in the spring and fall. Therefore, much of the observed growth increment data corresponds to either summer growth (i.e., observations of fish captured in spring and again in fall) or winter growth (i.e., observations of fish captured in fall and the following spring). Because growth rate varies with temperature (Paloheimo and Dickie 1966), I expect growth increments to be smaller during winter than during summer. This general prediction is also consistent with both field (Robinson and Childs 2001) and laboratory (Clarkson and Childs 2000) observations of humpback chub.

To allow temperature dependence in equation (3-4), I defined temperature-dependent multipliers of α and κ as

$$f_c(T) = Q_c \frac{(T-10)^{10}}{10^{10}}, \quad (3-16)$$

$$f_m(T) = Q_m \frac{(T-10)^{10}}{10^{10}}, \quad (3-17)$$

where $f_c(T)$ is the temperature-dependent multiplier of α and $f_m(T)$ is the temperature-dependent multiplier of κ . The consumption and metabolism coefficients (Q_c and Q_m) of a Q10 relationship allow these multipliers to increase or decrease with temperature (T). One can think of these constants as the amount that anabolism or catabolism will change with an increase in temperature from 10° C to 20° C. Inclusion of these temperature-dependent multipliers into equation (3-4) yields

$$\frac{dL}{dt} = \alpha L^\delta f_c(T) - \kappa L^n f_m(T). \quad (3-18)$$

Equation (3-18) accounts for growth rate differences as a function of temperature, but does not account for movement between the two thermal habitats. I used a logistic function to model occupancy in either the LCR or the mainstem Colorado River. I assumed that the probability of LCR occupancy is given as

$$PLCR = 1 - \frac{0.8}{1 + e^{\frac{(L-L_t)}{20}}}, \quad (3-19)$$

where L is fish total length and L_t is the fish total length where the probability of residing in the LCR year round is 0.6. The behavior of this model is such that the probability of year-round LCR residency approaches unity at lengths much less than L_t and decreases to 0.2 at lengths much larger than L_t . The number 20 in the denominator of the exponent governs the rate at

which the probability changes from near unity to near 0.2. Small denominator values cause a more abrupt transition (i.e., complete the transition over a small length range) while larger values imply a smoother transition. The asymptote at 0.2 requires at least some LCR residency for even the largest fish and is consistent with the observation that adult humpback chub use the LCR for spawning (Gorman and Stone 1999). This function can be considered analogous to the proportion of the year that fish of given size occupy the LCR.

I then defined a weighted temperature function experienced by fish of a particular length as

$$T(t) = (PLCR)T_{LCR}(t) + (1 - PLCR)T_{MS}(t), \quad (3-20)$$

where $T_{LCR}(t)$ is the time-dependent water temperature in the LCR and $T_{MS}(t)$ is the time-dependent water temperature in the mainstem Colorado River. This overall temperature experienced by a fish of a given length is then used in equation (3-18) to predict growth rate considering time-dependent changes in water temperature and size-dependent changes in LCR versus mainstem Colorado River occupancy.

To model the time-dependent water temperature in the LCR, I utilized data reported by Voichick and Wright (2007) to predict average monthly water temperature considering data 1988-2005. I fit these data with a sine curve as

$$T_{LCR}(t) = T_{ave} + (T_{max} - T_{ave})\sin(2\pi(t + t_{peak})), \quad (3-21)$$

where t is time in fraction of a year starting April 1, t_{peak} is a phase shift allowing predicted peak temperature to align temporally with the observed peak temperature, T_{ave} is the $\frac{1}{2}$ amplitude temperature and roughly corresponds to the average annual temperature, and T_{max} is the maximum annual temperature. I estimated t_{peak} , T_{ave} , and T_{max} by minimizing the squared difference between observed and predicted monthly temperature.

Annual water temperature variation in the mainstem Colorado River near the confluence of the LCR is much less variable (range 8-12°C) than within the LCR (Voichick and Wright 2007). Thus, I assumed constant water temperature in the mainstem Colorado River of 10° C. This value corresponds roughly to the average water temperature within the LCR inflow reach of the Colorado River during much of the time when the growth increments were observed (1989-2006).

I estimated the parameter vector $\theta = \{H, d, m, n, Q_c, L_t\}$ by maximizing the log-likelihood equation (3-15). With this more complex model, predicted recapture lengths were found by integrating the temperature-dependent growth model (equation 3-18) with respect to time. These predictions were then used in the second term of equation (3-14) to compute the deviations between observed and predicted growth. Following guidance from a meta-analysis by Clark and Johnson (1999), I specified Q_m as 2 to reduce the parameter set. I specified the weighting term for the log-likelihood penalties equal to that used in the previous analysis. To further reduce the parameter set, I specified $\sigma_L^2 = 2,000$ to correspond with a coefficient of variation of about 10% as is the minimum typically observed in fish populations (S. Martell and C. Walters, University of British Columbia, personal communication). I compared model fit for the temperature-independent growth model and the temperature-dependent growth model using AIC techniques (Burnham and Andersen 2002).

Results

I fit both the temperature-independent (TIGM) and temperature-dependent (TDGM) growth models to 14,971 observed growth increments extracted from the humpback chub mark-recapture database. All fish were larger than 150 mm TL and the time interval between capture and recapture exceeded 30 days. Although greater than 60% of the fish were at large for 1 year

or less, a small fraction of the observations were for much longer time intervals with the longest interval about 15 years (5,538 days). I estimated the measurement error contained in the dataset by computing the observed difference in measured lengths of fish captured and recaptured within 10 days. This resulted in a measurement error variance of 31.8 mm² across all sizes of fish, implying that most TL measurements were within 11 mm of the true TL. This amount of measurement error is not unexpected considering the difficulty in measuring live fish. Although this error rate is rarely reported, it is likely similar across a wide range of fish species and field conditions when handling live animals.

I fit the TIGM with prior variance weighting terms on the d and n parameters $\lambda = \{0.00001, 0.0001, 0.001, 0.01, 0.1, 0.5, 1, 10, 100, 1,000, \text{ and } 10,000\}$ to explore the effect of constraining these parameters to values near standard von Bertalanffy values. The log-likelihood was nearly identical for all values of $\lambda = 0.01$ and greater, but reducing λ below 0.01 caused large changes in the log-likelihood. Therefore, I specified $\lambda = 0.01$ as the weighting value for both the TIGM and TDGM.

To estimate the parameters of the TDGM, I first had to fit the time-dependent LCR water temperature model. Fortunately, the sine curve function with parameters $t_{peak} = -0.011$, $T_{ave} = 17.9$, and $T_{max} = 23.2$ fit the observed average monthly temperatures very well (Figure 3-2).

The estimated parameters, log-likelihood, and AIC statistics for the TIGM and TDGM are presented in Table 3-1. The parameter values for the TIGM suggest that anabolism scales as 0.5 mass and catabolism scales as 1.15 mass. These values are different than assumed by the standard von Bertalanffy model and also result in an average L_{∞} value that is smaller than would be predicted from simple inspection of the data. In contrast, the estimated scaling parameters ($d = 0.61$ and $n = 0.89$) for the TDGM are not much different than what would be expected under the

standard von Bertalanffy model where the anabolic scaling parameter (d) should be close to $2/3$ and the catabolic scaling parameter (n) should be close to unity. AIC results show strong support for the TDGM over the TIGM (Table 3-1). However, the parameter correlation matrices for each of these models show very high correlation, indicating that all of the parameters are not separately estimable (Table 3-2 and Table 3-3). In situations such as this where the model is not full rank, it has been shown that the AIC (Burnham and Andersen 2002) is undefined (Viallefont et al. 1998; Bozdogan 2000) suggesting that the AIC criteria may not be appropriate for this comparison.

An alternative way to arbitrate among these two models is to simply graphically examine the model fit to the data. The measured growth rate as a function TL at the start of the interval is extremely variable, particularly at smaller sizes (Figure 3-3). This variability is not surprising considering that the rate is measured as a difference between two imprecise length measurements and, for most measurements, expanded by dividing by a short time increment. It is also apparent that all three lines differed from a strict linear relationship that would be implied using a standard von Bertalanffy model, though the TDGM fits are reasonably linear through the portion of the predicted curves populated with data. The temperature-independent model is somewhat of a compromise between the temperature-dependent summer fit and the temperature-dependent winter fit. I also extracted two subsets of seasonal data that had only either summer growth or winter growth that suggest oscillating growth rate with temperature (Figure 3-4).

Each of the models was used to predict length as a function of age. In addition to the two models fit above, I also predicted length-at-age using the growth function reported in the USFWS recovery goals document (USFWS 2002) and length-at-age using the TDGM for a constant temperature of 10°C (Figure 3-5). This last curve is equivalent to a fish experiencing a

constant 10° C temperature and is a prediction of length-at-age for a fish spending its entire life in the mainstem Colorado River. Examination of these curves show that the USFWS growth curve predicted somewhat smaller sizes at young ages and larger sizes at older ages than is implied by the mark-recapture data. The TIGM and TDGM predict very similar length-at-age with the exception of ages 10-25. Two features are apparent TDGM predictions: (1) a temperature-dependent periodic change in growth rate at ages younger than about age-5, and (2) an apparent “bend” in relationship at approximately age-4. This age corresponds to the length at transition (L_t) where humpback chub are rapidly shifting from primarily LCR occupancy to primarily mainstem Colorado River occupancy. A L_t length of 236 mm TL was most strongly supported by the data and the TDGM (Table 3-1).

Finally, it is informative to utilize the TDGM to predict monthly growth increments as a function of TL. These predictions based solely on field data can be compared to laboratory observations of the same or similar species. I plotted growth rate predictions from both the LCR population and a population that is experiencing constant 10° C temperatures (Figure 3-6). This latter curve is presented as a prediction of monthly growth rates that would be observed in the mainstem Colorado River.

Discussion

Growth model parameter estimation is typically accomplished using paired observations of individual fish age and length (Quinn and Deriso 1999). Obtaining this information often requires sacrificing the animal so that calcareous structures may be examined to determine age. The TIGM and TDGM seek to obtain this information through non-lethal sampling using information that is frequently collected in routine mark-recapture studies. Particularly for endangered species such as the humpback chub, a non-lethal method to obtain information on growth is mandatory.

Estimating growth model parameters using increment data is not a recent development. Indeed, quite complicated frameworks have been developed that consider multiple growth model formulations and model error in length measurements at both capture and recapture occasions (Laslett et al. 2002). The model described herein takes a somewhat different approach by starting with a very general growth model allowing many different functional forms to describe the relationship between size and age. Additionally, the model parameterization allows intuitive inclusion of the effect of temperature on anabolism and catabolism that have direct interpretation in a bioenergetics framework (Essington et al. 2001).

Recent papers to estimate growth of marbled lungfish *Protopterus aethiopicus* (Dunbrack et al. 2006) and wels catfish *Silurus glanis* (Britton et al. 2007) propose methods similar to those described in this work. Interestingly, this methodology is clearly motivated by a similar problem – the inability to obtain information on the age of individual fish. However, the methods proposed in these studies do not explicitly allow growth to be influenced by temperature, even though this is clearly an issue, particularly in the wels catfish case (Britton et al. 2007).

This study addresses the effect of temperature on humpback chub growth and attempts to estimate the length at which fish transition from primarily LCR occupancy to primarily mainstem occupancy. The general implication from my findings is that growth rate will increase substantially with a temperature increase from 10° C to 20° C as indicated by the values of $Q_c=4.6$ and $Q_m=2.0$. These coefficients suggest that anabolism will more than double relative to catabolism across this temperature range. However, Petersen and Paukert (2005) constructed a bioenergetics model for juvenile humpback chub and found $Q_c \approx Q_m \approx 2.4$ suggesting much less potential for increased growth with increased temperature. Though some of the difference in estimated Q_c between my analysis and that of Petersen and Paukert (2005) may be related to the

highly correlated parameters in the TDGM (i.e., may be able to obtain nearly as good a fit with lower Q_c and higher H , d , and m ; see Table 3-3.), it is also likely that laboratory observations of growth rates may not accurately represent field conditions (Rice and Cochran 1984). In particular, the field estimate of Q_c represents not only physiological (laboratory) constraints on feeding, but also effects of any seasonal variations in food availability that are positively correlated with temperature (e.g., insect emergence during spring and summer).

Clarkson and Childs (2000) conducted laboratory experiments to evaluate the growth rate of juvenile humpback chub at 10° C, 14° C, and 20° C. They report monthly growth rates of 1 mm, 13 mm, and 17 mm per month for these temperatures, respectively. Considering the estimated monthly growth rates from the TDGM in Figure 3-6, the TDGM tends to over-estimate the growth rates reported by Clarkson and Childs (2000) at 10° C and under-estimate the growth rate at 20°. However, the TDGM results are in overall agreement with this laboratory study.

In their study of reproductive ecology of humpback chub in the LCR, Gorman and Stone (1999) conclude that adult fish demonstrate a potadromous migration between the mainstem Colorado River and the LCR to spawn. Based on catch rates of humpback chub within the LCR, they suggest that fish larger than 300 mm TL remained in the LCR only long enough to complete spawning activity. They also report that catch rate of fish between 200-300 mm TL declined by only half following the spawning period. The implication is that fish between 200-300 mm TL may occupy the LCR for longer periods of time than fish larger than 300 mm TL. The TDGM estimate of L_t (236 mm TL) is in agreement with these observations suggesting that fish greater than 236 mm TL should predominantly reside in the mainstem Colorado River.

This case history should be useful to those studying humpback chub throughout the Colorado River Basin, and to researchers seeking to estimate the relationship between fish age

and size using non-lethal techniques. This technique shows considerable promise to extract useful information on fish growth from field data, rather than laboratory studies where such information is typically obtained.

Table 3-1. General growth model results.

Model	H	d	m	n	L_{∞}	σ_L^2	Q_c	L_t	AIC	Parameters	Rank	Δ AIC
TIGM	163	0.52	0.0007	1.15	391	961	--	--	133,658	6	2	38,493
TDGM	21.0	0.61	0.46	0.89	434	2000	4.59	236	95,165	8	1	0

Table 3-2. Parameter correlation matrix for the temperature-independent growth model.

	H	d	m	n
H	1			
d	-0.99	1		
m	-0.66	0.73	1	
n	0.62	-0.72	-0.99	1
σ_L^2	0.14	-0.19	-0.38	0.38

Table 3-3. Parameter correlation matrix for the temperature-dependent growth model.

	H	d	m	n	Q_c
H	1				
d	0.74	1			
m	0.88	0.94	1		
n	-0.86	-0.93	-0.99	1	
Q_c	-0.98	-0.82	-0.89	0.88	1
L_t	0.55	0.16	0.35	-0.34	-0.46

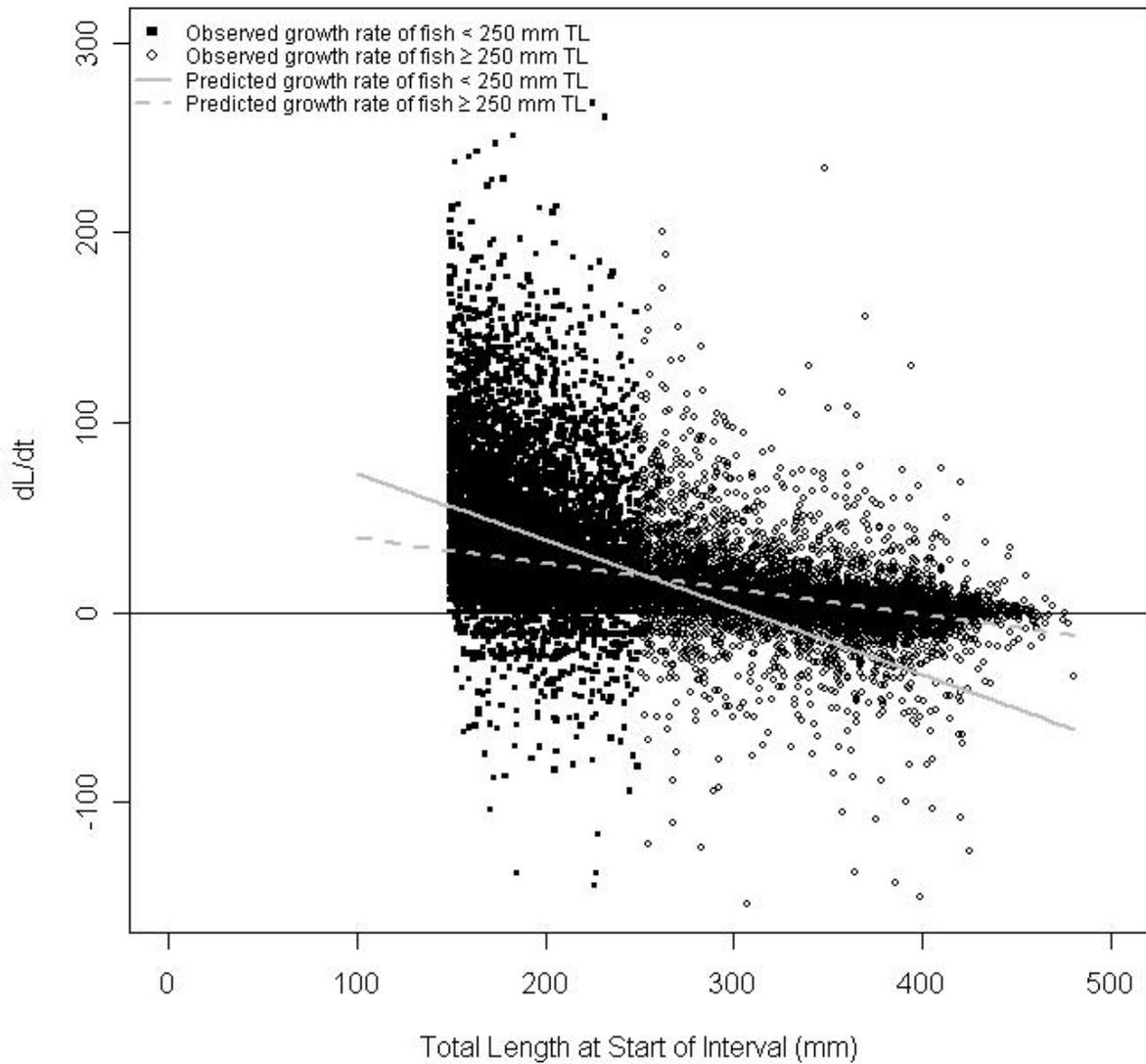


Figure 3-1. Predicted and observed growth rate (dL/dt) as a function of total length (TL) at the start of the time interval. Solid squares are observed growth rate of fish initially captured with $TL < 250$ mm and open circles are observed growth rate of fish initially captured with $TL \geq 250$ mm. Predicted growth rates are simple linear regressions on observed growth rate of fish initially captured with $TL < 250$ mm and of fish initially captured with $TL \geq 250$ mm.

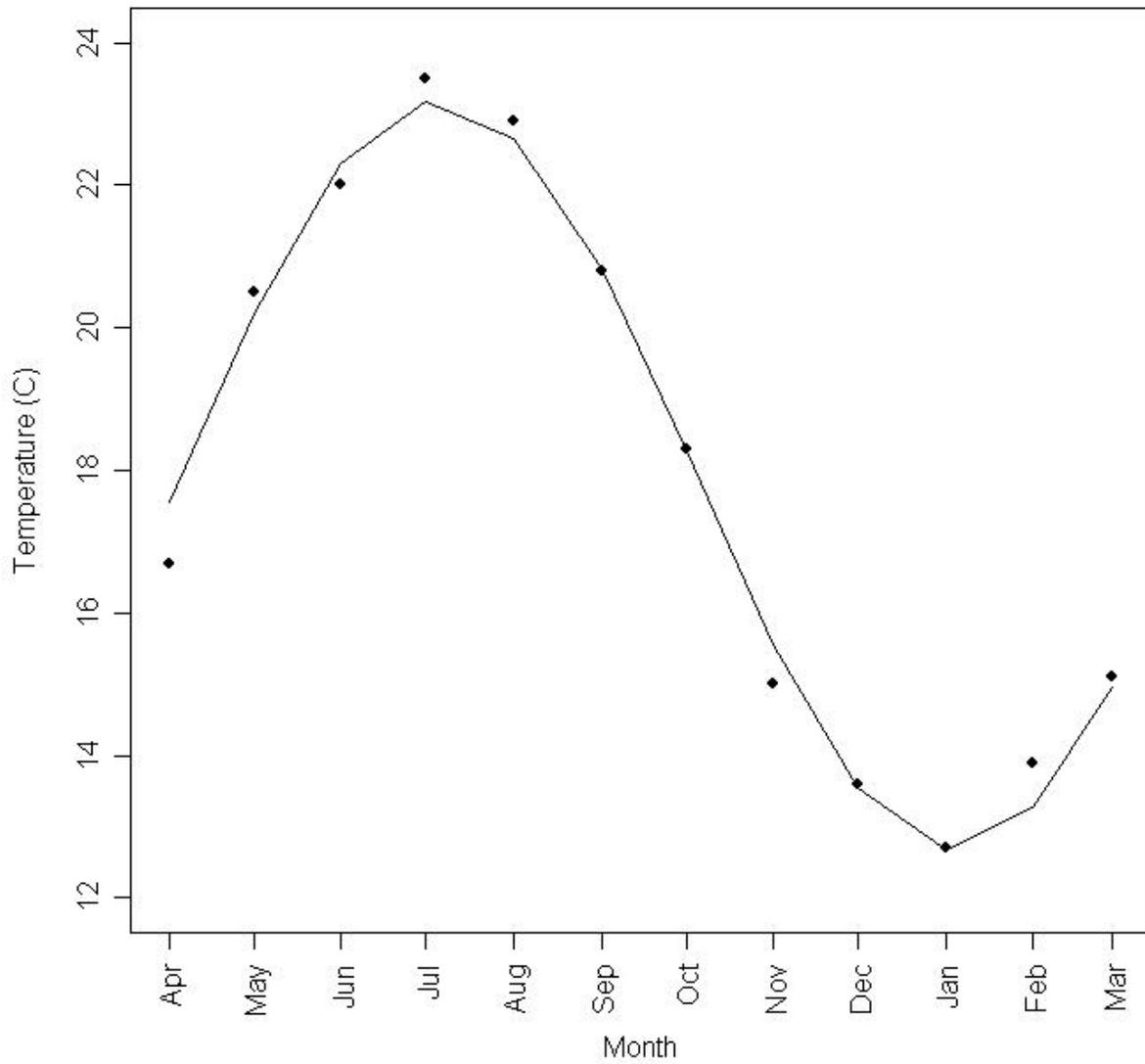


Figure 3-2. Observed and predicted monthly Little Colorado River water temperature. The points are the average observed monthly temperature and the line is the predicted monthly temperature.

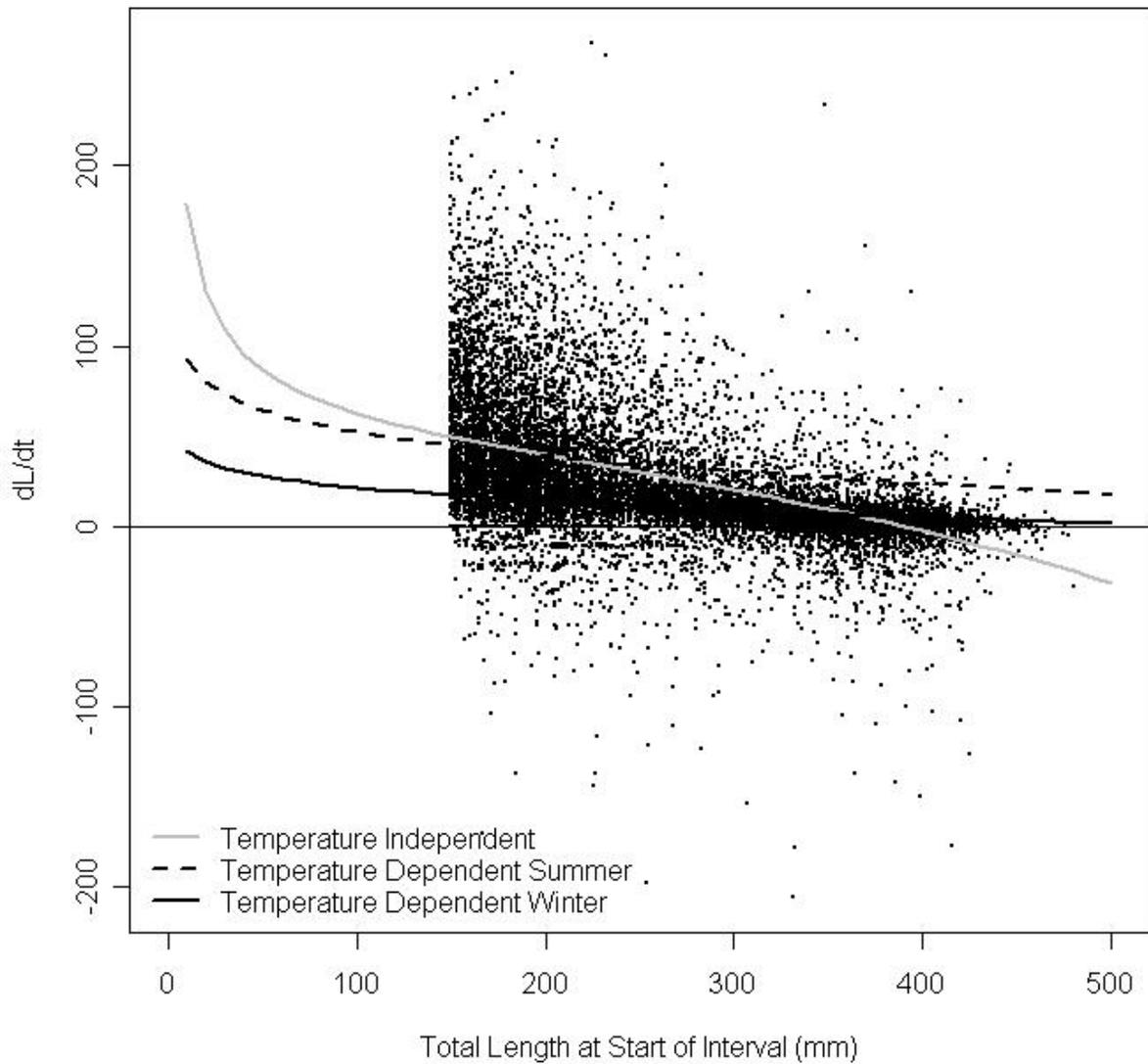


Figure 3-3. Observed and predicted humpback chub growth rate (dL/dt) from the temperature-independent growth model and the temperature-dependent growth model during summer and winter.

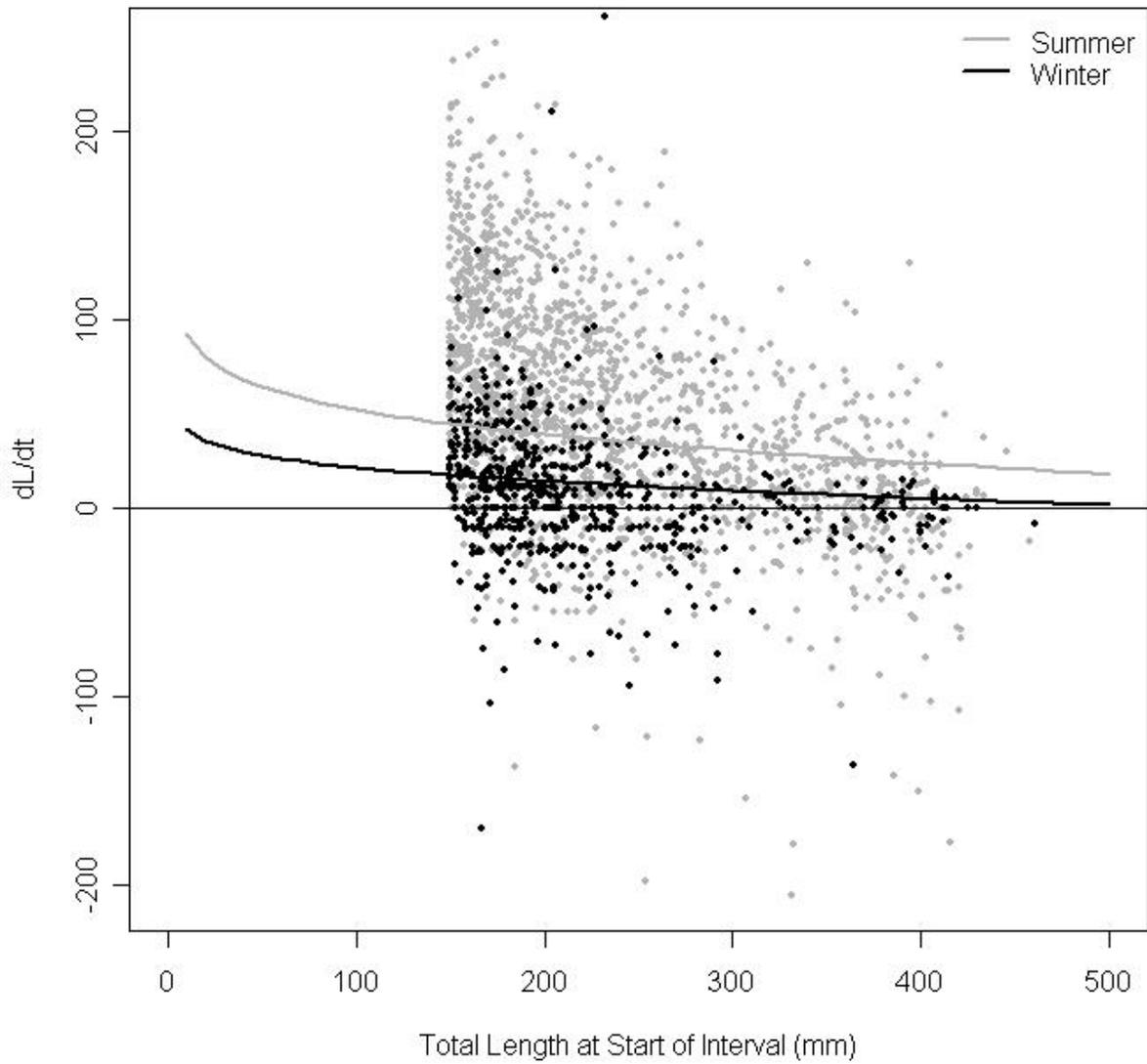


Figure 3-4. Observed and predicted humpback chub growth rate (dL/dt) from the temperature-dependent growth model during summer and winter.

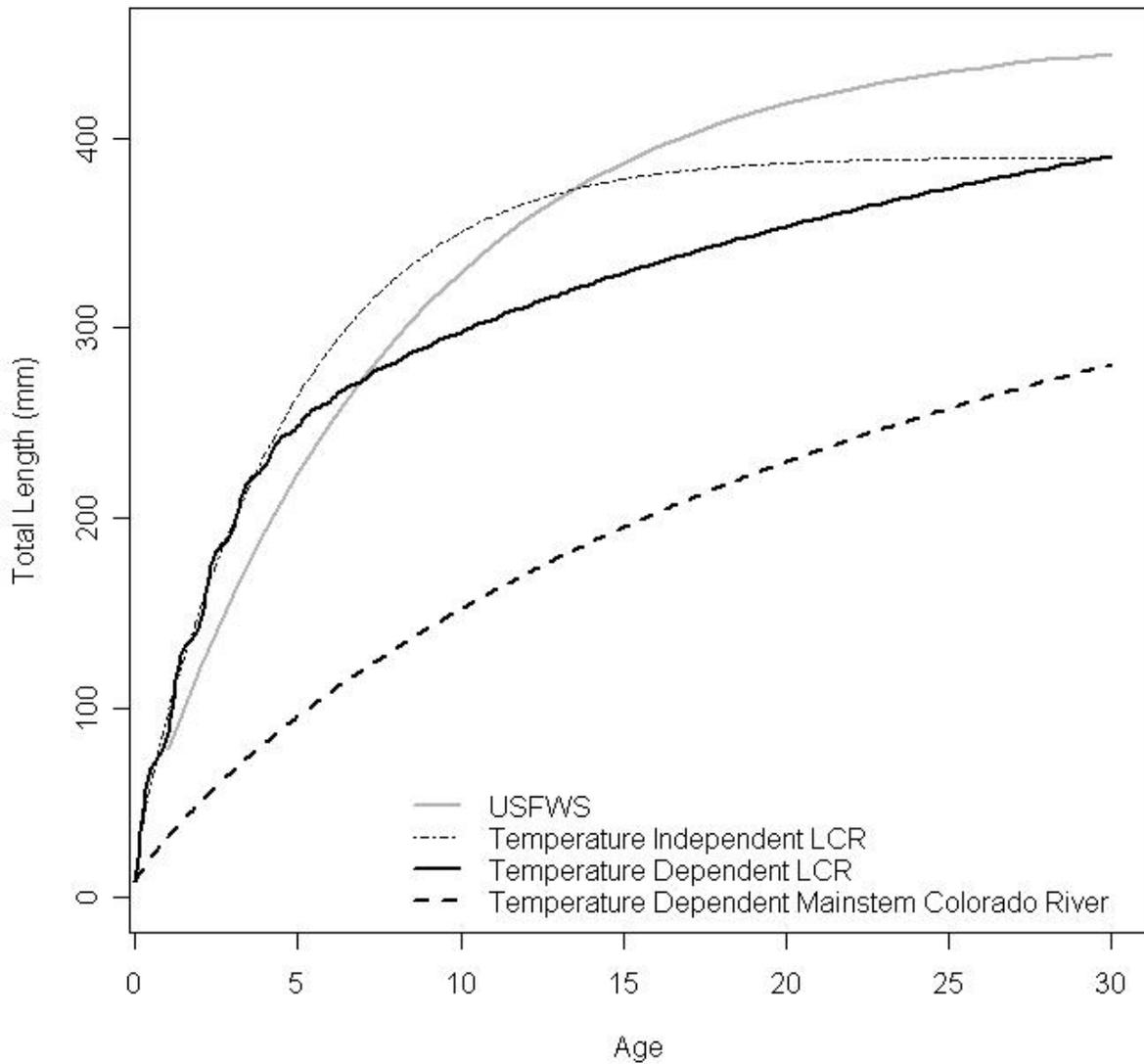


Figure 3-5. Predicted humpback chub length-at-age from the U.S. Fish and Wildlife Service (USFWS) growth curve, the temperature-independent growth model, the temperature-dependent growth model for the Little Colorado River (LCR) humpback chub population, and the temperature-dependent growth model for humpback chub living in the mainstem Colorado River under a constant temperature of 10°C.

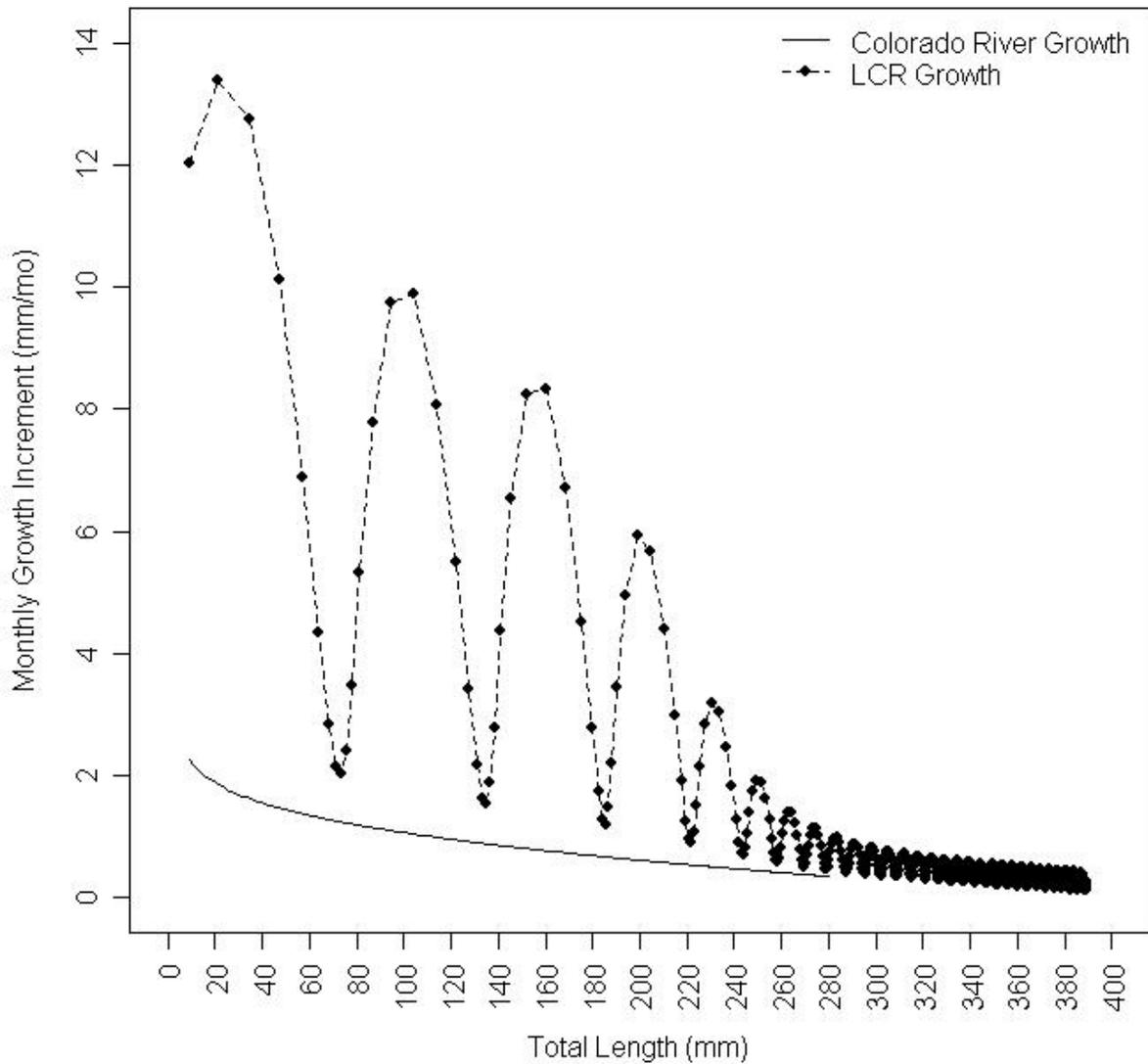


Figure 3-6. Predicted monthly growth rate from the temperature-dependent growth model for the Little Colorado River (LCR) population of humpback chub and for humpback chub living in the mainstem Colorado River under a constant temperature of 10°C.

CHAPTER 4
ABUNDANCE TRENDS AND STATUS OF THE LITTLE COLORADO RIVER
POPULATION OF HUMPBAC CHUB: AN UPDATE CONSIDERING DATA 1989-2006

Effective monitoring to evaluate endangered species status is a vital component of most endangered species recovery plans (Campbell et al. 2002). Monitoring results are typically used to evaluate species' status with regard to established goals towards changing its listing under the U.S. Endangered Species Act. Resource monitoring is also a critical component of adaptive management (Walters and Holling 1990). In the context of adaptive management, monitoring not only evaluates the status of the resource, but combined with probing management experiments it serves to inform managers about how the resource responds to various management actions. This paradigm of "learning by doing" places a premium on an accurate and reliable monitoring program (Parma et al. 1998).

Prompted by a National Research Council sponsored evaluation of the Glen Canyon Dam Adaptive Management Program (GCDAMP; NRC 1999), the Grand Canyon Monitoring and Research Center (GCMRC) has devoted significant resources to developing long-term monitoring programs over the last 8 years. As an example, much effort has been expended to synthesize existing data on fisheries resources in order to portray trends in these populations. Of particular importance is the humpback chub (*Gila cypha*), a federally listed endangered cyprinid endemic to the Colorado River Basin in the southwestern U.S. (Gloss and Coggins 2005). Because of this species' unique ecological role as one of the few remaining endemic aquatic species within Grand Canyon and their endangered listing status, the humpback chub is a focal resource of the GCDAMP (Gloss et al. 2005).

The objective of this chapter is to provide updated information on the status and trend of the Little Colorado River population of humpback chub in light of new information and refined assessment methodology. Such information constitutes the cornerstone of the humpback chub

monitoring program within the adaptive management program and is also relevant to U.S. Fish and Wildlife Service recovery goals for this species (USFWS 2002).

The unique life-history attributes of Little Colorado River population (LCR) of humpback chub and the large variety of sampling and monitoring programs ongoing since the 1980s (Coggins et al. 2006a) prompted the development of a new type of age-structured, open population, mark-recapture model called the age-structured mark-recapture model (ASMR; Coggins et al. 2006b). This model was subsequently used in combination with other mark-recapture and index-based assessments to provide a comprehensive assessment of the LCR humpback chub population (Coggins et al. 2006a). The ASMR approach has been subjected to a series of independent peer evaluations both as part of the GCDAMP (e.g., Kitchell et al. 2003) and through peer review as part of the publication process. Since publication of the last assessment, I have continued development of the ASMR model to address concerns presented in previous reviews (Kitchell et al. 2003). These improvements include incorporation of a formal model comparison approach and consideration of the uncertainty in assigning age to individual fish.

A central problem in conducting humpback chub stock assessment is the assignment of age to individual fish. Though this problem is ubiquitous in fish assessment programs (Coggins and Quinn 1998; Sampson and Yin 1998), it is particularly difficult when working with endangered fish and when sacrificing the animal is necessary to determine age. In this situation, individual fish ages must be assigned based on fish lengths and assuming some relationship between length and age. In past humpback chub assessments (Coggins et al. 2006a), I assumed that this relationship was adequately described from a growth curve based on a limited collection of paired age and length observations (USFWS 2002). However, this age-length relationship is

based on an extremely small sample size and is therefore suspect. Additionally, when assigning individual age based on this relationship, I assumed that fish could be aged without error. This is clearly not a valid assumption and presumes much more certainty in the assignment of age than is warranted. To alleviate these shortcomings, in Chapter 3, I presented a method to estimate the relationship between fish age and length using mark-recapture data. In this chapter, I use that relationship to translate uncertainty in the determination of age from length to uncertainty in abundance and recruitment estimates from ASMR. These analyses offer insight into the humpback chub assessment and other monitoring programs for aquatic and terrestrial species where mark-recapture methodologies serve as the core of the assessment approach, but where estimated trends in recruitment and mortality are influenced by uncertainty in age assignment.

The ongoing monitoring program for humpback chub in Grand Canyon has varied in intensity over the years, but the primary sample locations, techniques, and personnel have remained remarkably consistent (Coggins et al. 2006a). Conducting the annual stock assessment and continuously evaluating the performance of the assessment through retrospective analyses, independent peer evaluation, and testing of the model with simulated data all provide insight into the performance of the model-based on the available data. This comprehensive examination may prove useful to other adaptive management programs that seek to develop a robust monitoring component, and in particular to provide insight into: (1) limitations of monitoring alone to assign cause and effect associated with prescriptive management actions, (2) pathologies associated with large changes in monitoring protocols, and (3) a realistic assessment of the considerable uncertainty in results for a rare, elusive, long-lived animal even after many years of intensive monitoring.

Methods

Monitoring efforts for the LCR population of humpback chub began in 1987 when a standardized hoop net sampling program was implemented in the lower reaches of the LCR. During the subsequent 19 years, 4 sampling periods can be generally defined corresponding to different levels of sampling effort and protocol, particularly in the LCR (Coggins et al. 2006a). The first period of sampling lasted until 1991 and consisted mainly of limited hoop netting in the lower 1,200 m of the LCR. Sampling period 2 (1991-1995) involved an intensive sampling effort in both the LCR and the mainstem Colorado River as part of an environmental impact study on the operation of Glen Canyon Dam (USDOI 1995). The third sampling period began in 1996 with severely reduced intensities compared to period 2. Finally, beginning in fall 2000 a period of higher sampling intensity relative to period 3 (but less intensive than period 2) began and continued through 2006. During each of these sampling periods, humpback chub have been collected using multiple gear types (by many of the same personnel) including hoop nets and trammel nets in the LCR, and these same gears plus pulsed DC electrofishing in the mainstem Colorado River (Valdez and Ryel 1995; Douglas and Marsh 1996; Gorman and Stone 1999; Coggins et al. 2006a).

Index-Based Metrics

Although index-based metrics (e.g., catch rate) can be unreliable to track trends in population size with great precision (MacKenzie et al. 2006), these indices are frequently examined and are potentially useful for comparison to previous assessment efforts. With this caveat in mind and following Coggins et al. (2006a), I updated two long-term catch rate time series with data from 2003-2006: (1) hoop net catch rate of humpback chub in the lower 1,200 m of the LCR, and (2) trammel net catch rate of humpback chub in the LCR inflow reach of the Colorado River (defined as approximately 9 km upstream and 11 km downstream of the

confluence; Valdez and Ryel 1995). Details about these sampling programs are provided by Coggins et al. (2006a).

Tagging-Based Metrics

The heart of the tagging-based assessment is the large number of uniquely tagged sub-adult (150 mm-199 mm total length; TL) and adult (>200 mm TL) humpback chub that have been captured, measured, and implanted with passive integrated transponder (PIT) tags. Since 1989, over 19,000 humpback chub have been released with unique identifiers. These data are maintained in a central database housed at the GCMRC.

Capture-recapture-based methods to assess population abundance and vital rates have been widely used in fisheries and wildlife studies for well over 50 years, and numerous reviews have been conducted highlighting the general approaches (e.g., Seber 1982; Williams et al. 2002). Traditional methods (e.g., Jolly-Seber type methods) generally rely on recaptures of tagged or marked individuals to estimate abundance, recruitment, and survival. The approach is to create a known population of marked fish that are repeatedly sampled to obtain time series estimates of mark rate (i.e., proportion of the overall population that is marked) and the number of marked fish alive in the population. These estimates are subsequently used to estimate capture probability, abundance, recruitment, and survival.

Here, I briefly describe the overall ASMR method and refer readers to Coggins et al. (2006b) for full details. The ASMR model differs from the traditional approach because in general it contains more structural assumptions through the specification of a population accounting structure governing transition of both marked and unmarked animals through ages and time. A standard fisheries virtual population analysis framework (Quinn and Deriso 1999) is used to annually predict the numbers of marked and unmarked fish available for capture. The total number of marked fish depends on numbers of fish recently marked as well as previously

marked fish decremented by mortality rate. Numbers of unmarked fish depend on the time series of recruitment, the numbers of fish marked from those cohorts, and the mortality rate. These annual predictions of the abundance of marked and unmarked fish are further segregated by age such that age-specific survival and capture probability may be considered. Parameters are estimated by comparing predicted and observed age- and time-specific captures of marked and unmarked fish in a Poisson likelihood framework.

The ASMR model has three different parameterizations (ASMR 1-3) that vary in how the terminal abundance is estimated and how age- and time-specific capture probability is modeled. Both ASMR 1 and 2 assume that age- and time-specific capture probability can be modeled as the product of an annual overall capture probability multiplied by age-specific vulnerability. This is the common parameterization of fishing mortality in many assessment models under the “separability assumption” (Megrey 1989) and diminishes the size of the parameter set since it is not necessary to separately estimate each age- and time-specific capture probability. ASMR 1 and 2 further assume that vulnerability is asymptotic with age. As such, vulnerability is assumed to be unity for fish age-6 and older and estimated only for the younger fish. Finally, annual age-specific vulnerabilities are assumed to be equal among each sampling period as described above. Implicit in this assumption is that within a sampling period, annual age-specific capture probabilities differ only as a scalar value proportional to the annual overall capture probability.

The primary difference between ASMR 1 and ASMR 2 is how the terminal abundances are calculated. ASMR 1 estimates an overall terminal year capture probability and calculates age-specific terminal abundances (both marked and unmarked fish) as the ratio of age-specific catch (both marked and unmarked fish) and age-specific capture probability (i.e., product of the terminal year capture probability and sampling period 4 age-specific vulnerability). In contrast,

ASMR 2 treats age-specific terminal abundances up to age-13 as individual parameters.

Terminal abundances for subsequent ages are estimated by applying age-specific survivorship to the age-13 abundance. This difference in formulations decreases the parameter count for ASMR 1 relative to ASMR 2 at the expense of assuming that the vulnerability schedule in the terminal year is identical to the rest of period 4.

ASMR 3 is the most general model in that it makes no assumption as to the age- or time-specific pattern in capture probability. The conditional maximum likelihood estimates of age- and time-specific capture probability are used to predict the age- and time-specific catch of marked and unmarked fish. Full details of each of the models are provided by Coggins et al. (2006b).

In addition to the ASMR assessments, I also update the time series of the annual spring abundance estimates in the LCR. Abundance of humpback chub in the LCR ≥ 150 mm TL was estimated during the early 1990s and 2001-2006 using closed population models. These models included the program CAPTURE suite of models (Otis et al. 1978) and simple Chapman modified Lincoln-Petersen length-stratified models (Seber 1982). The recent estimators use data collected annually during two sampling occasions in the spring. Full details of the sampling and estimation methods are provided by Douglas and Marsh (1996) and Coggins et al. (2006a).

Coggins et al. (2006b) recommended exploring the use of individual capture histories within the ASMR framework to reduce confounding between capture probability and mortality. Though the updated ASMR models presented in this chapter do not yet incorporate individual capture histories, they do model recaptured fish by annual tagging cohort with the intent of reducing parameter confounding by increasing the number of observations available for parameter estimation. In the non-tag cohort or pooled version of ASMR described by Coggins et

al. (2006b) and above, age- and time-specific predictions of recaptured fish are not separated by year of tagging. As an example, assume that ASMR 3 predicts that 50 marked age-6 humpback chub should be captured in 2002. These 50 fish could be comprised of fish tagged as: age-5 in 2001, age-4 in 2000, age-3 in 1999, or age-2 in 1998. However, as the model is currently formulated, all age-6 fish recaptured in 2002 are pooled for a single observation. Assuming that the age- and time-specific captures of marked and unmarked fish are Poisson distributed, the log-likelihood ignoring terms involving only the data is computed as

$$\ln L(\theta|m, r) = \sum_{a=1}^A \sum_{t=1}^T [-\hat{m}_{a,t} + m_{a,t} \ln(\hat{m}_{a,t})] + \sum_{a=1}^A \sum_{t=2}^T [-\hat{r}_{a,t} + r_{a,t} \ln(\hat{r}_{a,t})], \quad (4-1)$$

where $m_{a,t}$ is the observed number of age a unmarked fish captured in year t , $\hat{m}_{a,t}$ is the predicted number of unmarked fish captured, $r_{a,t}$ is the observed number of marked fish captured (i.e., recaptures), $\hat{r}_{a,t}$ is the predicted number of marked fish captured, and θ is the parameter vector to be estimated. Notice in the second term that the individual log-likelihood terms are summed over age and time. However, it may be more informative to stratify the recapture data by tagging cohort. The proposed log-likelihood is then

$$\ln L(\theta|m, r) = \sum_{a=1}^A \sum_{t=1}^T [-\hat{m}_{a,t} + m_{a,t} \ln(\hat{m}_{a,t})] + \sum_{a=1}^A \sum_{t=2}^T \sum_{c=1}^{T-1} [-\hat{r}_{a,t,c} + r_{a,t,c} \ln(\hat{r}_{a,t,c})], \quad (4-2)$$

where c is the tag cohort (i.e., all fish marked in year t). In principle, this stratified log-likelihood should provide additional information on time-specific capture probability and may improve parameter estimation.

Evaluating Model Fit

Following Baillargeon and Rivest (2007), I used standardized Pearson residuals of observed and predicted age composition for both unmarked and marked fish to evaluate model fit

among the three different ASMR models. The standardized Pearson residual is the difference between the observed and predicted values scaled by an estimate of the standard deviation as

$$r_{a,t} = \frac{o_{a,t} - p_{a,t}}{\sqrt{\frac{p_{a,t}(1-p_{a,t})}{n_t}}}, \quad (4-3)$$

where n_t is the number of observations (e.g., the number of marked fish recaptured each year) and $o_{a,t}$ and $p_{a,t}$ are the proportions of fish in each year and age class observed and predicted, respectively. I plotted the individual Pearson residuals for each combination of age and time to look for consistent bias for individual brood year cohorts. Additionally, I used Quantile-Quantile (Q-Q) plots to compare the distribution of the Pearson residuals to a theoretical normal distribution. The slope of the theoretical curve is approximately the standard deviation of the distribution of Pearson residuals where a small value of the slope indicates a narrow distribution of the residuals. Deviations from the theoretical curve indicate a non-normal distribution of the Pearson residuals and imply that the model error is not well distributed (e.g., tending to more often either over- or under-predict age proportions) and possibly inducing bias in parameter estimates.

In addition to examination of model fit using Pearson residuals, I chose to also rely on information theory to aid in model evaluation. This approach is increasingly common in ecological studies to arbitrate among competing models and is primarily concerned with estimating the Kullback-Leibler (K-L) distance between the model and the “truth” as a measure of model support (Burnham and Andersen 2002). The Akaike Information Criterion (AIC; Akaike 1973) is the standard estimator for the relative K-L distance and is computed as a function of model likelihood and number of model parameters. Following external review of the ASMR method, Kitchell et al. (2003) pointed out that although ASMR uses a quasi-likelihood

structure of estimating equations and true likelihood, estimates of relative K-L distance using AIC, though not strictly appropriate, would be valuable to consider for model selection. Therefore, in addition to the evaluation based on Pearson residuals, I also conducted an AIC evaluation.

Incorporation of Ageing Error in ASMR Assessments

As mentioned above, Coggins et al. (2006a) assigned age to individual fish strictly as an inverse von Bertalanffy function. This procedure ignores variability in the age of fish of a particular length and tacitly assumes that age assignments can be made much more precisely than is true. To account for uncertainty in the assignment of age using length, I estimated the probability of age for fish having length within a particular length interval $P(a|l)$. Following methods reported by Taylor et al. (2005), I define this procedure by first specifying that the probability of an age a fish having length within length bin l is

$$P(l|a) = \frac{1}{\sigma_a \sqrt{2\pi}} \int_{l-d}^{l+d} \exp\left[-\frac{(l-l_a)^2}{2\sigma_a^2}\right] dl, \quad (4-4)$$

where length bin l has mid-point length l , minimum length $l-d$, and maximum length $l+d$. These probabilities can be thought of as a matrix with rows corresponding to length bins and columns as ages. As is obvious from equation (4-4), entries within a particular column (age) can be thought of as resulting from the integral over each length bin of a normal probability density with mean l_a and variance σ_a^2 . The mean length-at-age is computed from the temperature-dependent growth model (Chapter 3) and the variance of length-at-age is $\sigma_a^2 = l_a cv_l$, assuming that coefficient of variation in length (cv_l) is constant among ages.

With $P(l|a)$ available, one option to compute $P(a|l)$ would be to normalize each matrix cell by the sum of its row as:

$$p(a|l) = \frac{P(l|a)}{\sum_{i=1}^A P(l|i)}. \quad (4-5)$$

However, Taylor et al. (2005) suggest that this procedure will induce bias if the population has experienced size-dependent mortality such as size selective fishing or size-dependent changes in natural mortality. This results because within a particular age class, fast growing individuals (i.e., large L_∞) may experience either higher or lower mortality rate than their cohorts, and therefore be either over- or under-represented in the population. This “sorting” by growth rate can favor either slow growing individuals, as in the case of increasing vulnerability to exploitation with size, or fast growing individuals, as in the case of reduced natural mortality with size. Therefore, Taylor et al. (2005) suggest that an adjustment for mortality must be made to accurately predict the proportion of individuals in each age and length bin. Accordingly, I define the numbers of fish in each age and length bin as

$$N_{l,a} = N_a P(l|a), \quad (4-6)$$

where N_a is the abundance of fish at each age. If the age specific mortality rate (M_a) is available and recruitment (R) is assumed constant, abundance-at-age is given by

$$N_a = R e^{-\sum_{i=1}^{a-1} M_i}. \quad (4-7)$$

With abundance at each age and length bin thus available, the proportion in each age and length bin can then be calculated as

$$P_{l,a} = \frac{N_{l,a}}{N_T}, \quad (4-8)$$

where $N_T = \sum_l \sum_a N_{a,t}$. The probability of age given length is then calculated as

$$P(a | l) = \frac{P_{l,a}}{\sum_{i=1}^A P_{l,i}}. \quad (4-9)$$

Taylor et al. (2005) focus on age-specific mortality driven by vulnerability to exploitation. For the unexploited humpback chub, age-specific mortality as a function of changes in natural mortality was included. Lorenzen (2000) demonstrated that much variation in natural mortality can be explained by size of fish. Thus, Lorenzen's allometric relationship between natural mortality and length was used to calculate a declining mortality rate with age as

$$M_a = \frac{M_\infty L_\infty}{l_a}, \quad (4-10)$$

where M_∞ is the mortality rate suffered by an adult fish of size L_∞ . This mortality schedule was calculated with M_∞ specified as 0.148, as estimated by ASMR 3 considering tag-cohort specific data (see Results).

I computed four seasonal $P(a|l)$ matrices that I used to assign age to fish captured at different times of year. Growth during the year could thus be accounted for by recalculating $P(l|a)$ such that length-at-age was computed as either $l(a)$, $l(a+.25)$, $l(a+0.50)$, or $l(a+0.75)$. The resulting seasonal $P(a|l)$ matrices were then used to assign age to a fish depending on the quarter of the year in which it was captured.

To incorporate the uncertainty in assigning age based on length into the overall assessment, I used a Monte Carlo procedure where age was stochastically assigned to each fish based on the seasonal $P(a|l)$ matrices. To understand this procedure, it is first helpful to recognize that given a fish with length in bin l , the probability of belonging to each age is

multinomial with number of categories equal to the number of ages. I used the multinomial random number generator within program R (R Development Core Team 2007) to randomly assign age to marked fish. Recapture age was calculated as the sum of age-at-tagging and time-at-large.

I then stochastically assigned age to each fish using this procedure. For each resulting dataset of captures- and recaptures-at-age, I estimated adult (age-4+) abundance and recruitment using ASMR 3. Additionally, I used AD Model Builder (Fournier 2000) to compute the 95% profile confidence interval for adult abundance and recruitment. I repeated this procedure to generate and analyze 1,000 datasets (i.e., Monte Carlo trials).

Results

Index-Based Assessments

Between 1987-1999 and 2002-present, the Arizona Game and Fish Department sampled humpback chub using hoop nets in the lower 1,200 m section of the LCR. Examination of this index suggests that the abundance of both sub-adult (150-199 mm TL) and adult (≥ 200 mm TL) humpback chub declined during 1987-1992 and remained relatively constant through much of the 1990s (Figure 4-1). Since 2003, there is a slight upward trend in the catch rates of sub-adult fish. Note that several data points in this index are shifted slightly relative to those reported by Coggins et al. (2006a). This adjustment is due to additional standardization of the data used to construct this index (D. Ward, Arizona Game and Fish Department, Personal Communication). The trammel net catch rate of adult abundance in the LCR inflow reach of the Colorado River suggests a similar trend in adult fish (≥ 200 mm; Figure 4-1). In general, this index shows a stable to declining trend through the 1990s with a slight indication of increased abundance in most recent years. All monthly trammel net samples from the LCR inflow reach for 1990–2006 are presented in Figure 4-1. However, only samples from 1990-1993, 2001, and 2005-2006 (i.e.,

dark circles in Figure 4-1) represent robust sampling coverage throughout the entire reach. Annual sample sizes in 1994–2000 and 2002–2003 (i.e., hollow circles in Figure 4-1) were between 2% and 50% of the 1990–1993 average sample size, and in some years effort was focused near the LCR confluence where humpback chub density may have been highest. Thus, the 1990–1993, 2001, and 2005–2006 data are likely to best depict the overall trend of relative abundance within this reach. Simple linear regression analyses provide estimated slopes that are not significantly different from zero ($p = 0.16$ for all data, and $p = 0.26$ for the preferred data; Figure 4-1).

Tagging-Based Assessments

As described above, the data required for the ASMR models are numbers of fish marked and recaptured each year and for each age. For the results contained in this section, all ages are assigned based on the standard von Bertalanffy growth curve as described in Coggins et al. (2006b). With that in mind, examination of the age distribution of fish marked and recaptured since 1989 provides insight into the trends in sampling effort, and also provides important information related to humpback chub mortality (Figure 4-2). The top panel of figure 4-2 shows the numbers of newly marked fish and is influenced by both trends in sampling effort and numbers of un-marked fish alive. The most consistent period of sampling has been since about 2001 with about 1,100 fish marked annually (numbers of fish collected at the top of the bubble columns). Because a large fraction of the population was marked in sampling periods 1 and 2, the majority of fish marked in recent years are young fish and the number of new fish marked each year declines with fish age. The bottom panel of figure 4-2 represents the numbers of fish recaptured each year. Some of the same patterns related to sampling effort are evident, but there are some very interesting patterns that result from the high sampling effort in the early to mid 1990s (Figure 4-2). For example in 1995, a total of 1,244 humpback chub were collected and

902 of these fish had been marked in previous years. This pattern is evident for several years of data indicating that the high sampling effort in the early 1990s resulted in marking upwards of 70% of the humpback chub population. It is also apparent that because few age-3 to age-5 fish were marked during period 3, there were few age-8 to age-10 fish recaptured in the early 2000s five years later. This contributes to the “spoon” shapes to the lower panel of figure 4-2, where there were relatively large numbers fish < age-10 recaptured in period 4, lower catches of age-10 to age-15, and relatively stable numbers of fish > age-15.

Another finding is the extreme longevity of these fish. This is evident by examining the number of humpback chub of each age marked in each year and recaptured in subsequent years (Figure 4-3a through Figure 4-3e). Figure 4-3a shows the number of humpback chub of each age marked in 1989-1992 and recaptured in subsequent years. There is a remarkable number of old fish (> age-15) first marked in the early 1990s that continue to be recaptured into 2006. This slow decay pattern of marked fish demonstrates the low mortality rate suffered by older humpback chub.

Closed Population Models

The time series of abundance estimates for humpback chub ≥ 150 mm TL in the LCR during spring implies a decline in abundance from the early 1990s to present (Figure 4-4). However, as is apparent in the data, these estimators are very imprecise with corresponding poor ability to detect significant trends. Additionally, preliminary analyses of data collected in this program suggest that the 2007 estimate may be up to twice as large as the 2006 estimate (R. Van Haverbeke, U.S. Fish and Wildlife Service, Personal Communication).

ASMR Without Tag Cohort Specific Data

The three ASMR formulations generally agree that adult (age-4+) humpback chub abundance has been gradually increasing since about 2001 (Figure 4-5). For the three models,

the 2006 adult abundance estimate is 6,690 (95% CI 6,403-6,994), 6,768 (95% CI 6,397-7,131), and 6,648 (95% CI 6,222-7,102) for models ASMR 1, ASMR 2, and ASMR 3, respectively.

These results suggest that this population has increased from an estimated low of approximately 4,800-5,000 during 2000-2001. Estimated recruitment (age-2) among models is also in agreement (Figure 4-6). Following low recruitments for brood years during the early 1990s, all the models suggest that recruitment increased through the latter part of the 1990s. The biggest discrepancy among the three models is that ASMR 1 suggests a decline in recruitment following the 2001 brood year, while the other two models suggest stability. The structural assumptions of model ASMR 3 (see Coggins et al. 2006b) do not permit a reliable recruitment (age-2) estimate for brood year 2003. An additional difference in the models results are the estimates of instantaneous adult mortality (M_{∞}) where adult mortality ranges from 0.119 (ASMR 1) to 0.133 (ASMR 3).

Model Evaluation and Selection

With these results in hand, the question becomes which model is best? Stated another way, which model produces results most consistent with or best supported by the data? The discrepancies among model results related to adult abundance are not large, so from a management or conservation perspective, selecting the “best” model is probably not critical. However, the models do suggest rather different recruitment trends. Model ASMR 1 supports the hypothesis that recruitment has declined following the 2000 brood year, while the other two models suggest relative stability. Therefore, selecting which model is most consistent with the data is desirable. The patterns in Pearson residuals for both ASMR 1 (Figure 4-7) and ASMR 2 (Figure 4-8) demonstrate systematic lack of fit for particular sets of cohorts. This is best seen in the recapture residuals where it is apparent that there were more fish observed than predicted for

about eight pre-1990 cohorts, particularly for observations after 2000. Additionally, there were fewer recaptures associated with the 1992 cohort than predicted. These systematic trends likely impose bias in the model results for ASMR 1 and ASMR 2. In contrast, there is much less systematic lack of fit in the residual patterns for ASMR 3 (Figure 4-9). Among the three models, the Pearson residual standard deviation was smallest for ASMR 3.

The finding that ASMR 3 has the best fit among the three models is not surprising since it has the largest parameter set. Although ASMR 3 only varies 13 parameters in the direct numeric search, the conditional maximum likelihood estimates are used for each age- and time-specific capture probability (Coggins et al. 2006b). Therefore, and assuming a liberal maximum longevity of 50 years, ASMR 3 has 895 parameters. The question then becomes whether these additional parameters are justified. To provide insight into this question, I estimated relative K-L distance using AIC (Table 4-1). These results strongly indicate that model ASMR 3 is superior to ASMR 1 and 2.

Since the fundamental difference between ASMR 1-2 and ASMR 3 is the amount of flexibility in age- and time-specific capture probabilities, I examined the pattern in ASMR 3 estimated capture probabilities (Figure 4-10). The patterns in age-specific capture probabilities during sampling period 2 (i.e., 1991-1995; heavy gray lines) and sampling period 4 (i.e., 2000-2006; heavy black lines) differ markedly. These findings suggest that there was a major shift in the gear selectivity; sampling since 2000 appears to be much less effective at capturing fish between ages 9-20 than was sampling during the second period. Since structural assumptions in ASMR 1 and ASMR 2 require that vulnerability is asymptotically related to age, it is not surprising that these models are not able to account for this unexpected pattern, and thus display poor model fit.

ASMR with Tag Cohort Specific Data

In addition to repeating the analyses by Coggins et al. (2006a) above, I also fit the ASMR models to the tag cohort specific data using the log-likelihood in equation (4-2). The trends in adult abundance and recruitment are similar to those found using the simpler log-likelihood (Figures 4-11 and 4-12). In general, adult abundance estimates are slightly higher at the beginning of the time series and slightly lower at the end. Adult abundance estimates for 2006 were 6,057 (95% CI 5,797-6,308), 6,138 (95% CI 5,842-6,458), and 5,893 (95% CI 5,554-6,242) for the ASMR 1, ASMR 2, and ASMR 3 models, respectively. Adult mortality (M_{∞}) estimates from the models fit to the stratified data indicate slightly higher adult mortality than when fit to the pooled data and ranged from 0.128 (ASMR 1) to 0.148 (ASMR 3). This finding is consistent with the more rapid decay observed in the time series estimates of adult abundance.

Model Evaluation and Selection

Examination of Pearson residuals for the tag cohort specific models suggests similar patterns in model misspecification for ASMR 1 and ASMR 2 (Figures 4-13 and 4-14) relative to ASMR 3 (Figure 4-15). As with the pooled tag cohort data, ASMR 3 displays better fit. Model evaluation using AIC methods again suggests that ASMR 3 is preferable (Table 4-2) in general agreement with the residual evaluation. Finally, the estimated capture probability from ASMR 3 suggests a similar mechanism to explain the poor performance of models ASMR1 and ASMR 2 (Figure 4-16) as was found for the without tag cohort specific analysis.

Incorporation of Ageing Error in ASMR Assessments

I used the temperature-dependent growth model (Chapter 3) and the procedures identified above to construct seasonal $P(a|l)$ matrices. I then plotted the resulting probability distributions as surfaces to allow examination of the uncertainty in predicting age given length

(Figure 4-17). The most obvious feature of these probability surfaces is the increasing uncertainty in age assignment with increasing length. For instance and considering the April-June $P(a|l)$ surface (Figure 4-17), one can see that a 150 mm TL fish is age-2 with highest probability, but there is some chance that it is all ages between age-1 and age-4. In contrast, a 300 mm fish is approximately age-7 with highest probability but could be as young as age-4 or as old as age-18. It is precisely this uncertainty that I sought to incorporate in the assessment.

I stochastically assigned age to each fish using the appropriate $P(a|l)$ matrix depending on the time of year the fish was first captured. Using this procedure, I generated a total of 1,000 input datasets and fit the ASMR 3 model to each. For each model fit, I retained the estimated annual adult abundance and 95% profile likelihood confidence bounds. I also retained the estimated brood year recruitment and 95% confidence bounds. Note that because of the uncertainty in assigning age to even the smallest fish, newly tagged fish had the possibility of being assigned age-1. As a result, I expanded the age range of the model such that recruitment estimates were for age-1 fish.

Estimated adult abundance (age-4+) from model ASMR 3 ranged from 9,322 (95% CI 8,867-9,799) in 1989 to 6,017 (95% CI 5,369-6,747) in 2006 (Figure 4-18). As expected, these estimates have lower precision than those from ASMR 3 ignoring ageing error. The coefficient of variation in adult abundance estimates considering ageing error ranges from approximately 1%-7% in contrast to 0.5%-3% if uncertainty in assignment of age is ignored. The recruitment trend considering the new growth function and the incorporation of ageing error is much less precise than when ageing error is ignored (Figures 4-12 and 4-19). Although the point estimates from the two models are in agreement that recruitment has been increasing since about the mid

1990s, the uncertainty in the recruitment estimates from the latter assessment makes statements about differences among years quite tenuous.

Results Summary

The adult portion of the LCR humpback chub population has increased in recent years as a result of increased recruitment particularly associated with brood years 1999 and later. Model evaluation procedures indicate that the results from model ASMR 3 are most consistent with the data. Utilizing data stratified by tagging cohort appears to add little additional information to the assessment as indicated by overall similarity in abundance and recruitment estimates and residual analyses considering both pooled and stratified data. Inclusion of ageing error increases the uncertainty about individual annual estimates, but gross trends remain the same.

Discussion

The overall result of the mark-recapture-based open population model assessment is that the adult portion of the LCR humpback chub population appears to have increased in abundance since 2001. The assessment model best supported by the data is ASMR 3 with a corresponding 2006 adult abundance estimate of approximately 5,900-6,000 fish. In addition, this model suggests that there has been an increase in the adult abundance of approximately 20%-25% since 2001. This increase appears to be related to an increasing recruitment trend beginning perhaps as early as 1996, but likely no later than 1999. Recruitment of juvenile humpback chub since 2000 appears stable, but the precision of these estimates is quite low when ageing error is included in the assessment.

The LCR hoop net abundance index suggests a modest increase in the abundance of juvenile fish and stability in the abundance of adult fish. In addition, the LCR inflow reach trammel net abundance index indicates stability with a slight indication of increased abundance in 2005 and 2006. Though there would be increased confidence in the mark-recapture-based

open population model results if the catch rate metrics indicated similar trends, it is not surprising that these index measures are not able to detect a 25% increase in abundance. The basic assumption of catch rate indexes is that capture probability must remain constant for the index to be well correlated with abundance (MacKenzie and Kendall 2002). There is good reason to suspect that this assumption is violated for the index data series presented in this update due to the influence of turbidity on catchability (Arreguin-Sanchez 1996). Turbidity appears to influence humpback chub catchability in the Little Colorado River (Dennis Stone, U.S. Fish and Wildlife Service, Personal Communication) and turbidity varies greatly in the mainstem Colorado and Little Colorado Rivers as a function of tributary freshets and dam operations.

A more significant concern is the lack of correlation between ASMR 3 results and the mark-recapture closed population model estimates in the LCR. However, since the number of fish in the LCR during sampling is influenced by migration magnitude and timing, this source of variability may obfuscate expected correlations with the ASMR 3 results. It is also clear that the low precision of these annual closed population model estimates may not permit detection of a 25% increase in adult abundance. Additionally, preliminary analyses of data collected during 2007 suggest that the abundance estimate for 2007 may be twice as large as the 2006 estimate (R. Van Haverbeke, U.S. Fish and Wildlife Service, Personal Communication). Though this result would provide support for the ASMR 3 results, it would also call into question the ability of the LCR program to provide a consistent measure of overall population size. One would have to reconcile whether that level of change was related to a very large age class entering the sampled population, a larger than normal fraction of the population entering the LCR during the sampling period, or some other factor.

Though the GCDAMP is fortunate to have such a large mark-recapture database for these high-profile endangered animals, significant changes in sampling protocol over time continue to cause ambiguity in these analyses. As identified by Melis et al. (2006), retrospective analyses of the data suggest a continual updating of the adult mortality rate as additional information has been collected since 2000. Following addition of the 2006 data, this updating is again apparent (Figure 4-20). It appears that adult mortality rate may be stabilizing as more data are collected, but it is difficult to be certain. I believe that the likely cause of this updating is the sampling program essentially having to “catch-up” following the low sampling effort during period 3. When focused analysis of this dataset began with open population models in 2000 (GCMRC unpublished data), there had been so little sampling in the mid to late 1990s that the models interpreted the lack of old fish captures as a relatively high adult mortality rate. As additional data was collected through a more rigorous sampling program during 2000-2006, each time the model “saw” a recent old fish recapture, mortality rate was adjusted downward. The hope is that if the GCDAMP continues with a fairly uniform sampling program over time, adult mortality rate will stabilize and only abundance estimates in the last few years of the dataset will be subject to much updating.

An additional finding, identified by Martell (2006) and in this assessment, is the major change in gear selectivity between periods 2 and 4. I am uncertain what is driving the trend to lower the capture probability for the middle aged fish. However, it has been suggested that the high capture probability for middle aged fish was due to extensive trammel netting effort in the LCR inflow reach of the Colorado River during period 2. It is apparent from Figure 4-1 that there is a large difference in the amount of trammel netting effort in period 2 versus period 4. To investigate this possibility, I fit the ASMR 3 model to a subset of the database containing only

LCR data. The results indicated an almost identical pattern in age-specific capture probability as is observed with the full dataset. This is not surprising since fish captured in the LCR inflow reach of the Colorado River represent only about 10% of the entire humpback chub mark-recapture database. It has also been suggested that reducing the use of large hoop nets in the LCR during period 4 has reduced the catch rate of the largest fish. Though this is possible, the net throat openings are the same size on all nets used during both sampling periods. It has also been suggested that sampling in the LCR only 4 months of the year during period 4 as opposed to 10 to 12 months of the year during period 2 may be the cause. This is also possible, particularly if there is some differential migration timing for the middle aged fish relative the oldest individuals.

Large changes in sampling protocol should be approached with caution in light of how those changes may affect ability to infer population change. This is particularly true for populations that are in low abundance and individuals difficult to capture. I suggest that careful simulation of considered changes may help to expose potential problems or, at the very least, help to clarify thinking related to proposed changes in sampling protocol. Finally, those considering implementing a mark-recapture-based monitoring program should plan to expend considerable sampling effort using similar protocols for the duration of the monitoring program. I echo the recommendation of Williams et al. (2002) that the objectives of the monitoring program with regard to issues such as precision of measured quantities should not only be clearly identified, but that the measured quantities should be directly linked to the management objectives.

A major criticism of the ASMR technique as previously applied is that it does not explicitly account for uncertainty in the assignment of age to individual fish (Kitchell et al.

2003). As a result, abundance, recruitment, and mortality estimates may contain excessive bias. Additionally, estimates of precision are likely overstated by not incorporating this important source of uncertainty. This analysis attempts to address these concerns by incorporating uncertainty from age assignments into estimates of abundance and recruitment. Coggins et al. (2006b) conducted sensitivity analyses on the effect of random ageing error and found little systematic bias in reconstructed recruitment trends. However, the current analysis is a more rigorous treatment of the problem and has two major implications.

First, model results of estimated adult abundance are still very precise even when uncertainty in the assignment of age is accounted for in the assessment. Following review by Kitchell et al. (2003), this assessment lends additional credibility to results from ASMR indicating that it provides a rigorous measure of the state of the adult portion of the Little Colorado River humpback chub population. I recommend that this assessment be considered “best available science” for use in contemplating management decisions both within the GCDAMP and the U.S. Fish and Wildlife Service.

Second, this analysis points out the difficulty that open population models have generally in the precise estimation of recruitment (Williams et al. 2002; Pine et al. 2003). Because many of the most critical management questions for humpback chub center around how best to improve humpback chub recruitment, particularly considering improved rearing conditions in the mainstem Colorado River, it will be difficult for ASMR to detect statistically significant changes in recruitment unless those changes are quite large. As a result, design of experimental adaptive management actions intended to increase recruitment should consider first and foremost how to achieve large changes in recruitment. Small scale experimental treatments of short time duration or so called “mini-experiments” should be summarily discounted recognizing that the monitoring

program is unlikely to detect small recruitment change even if it occurs. Additionally, multi-year experiments should be strongly favored in order to help offset not only unexpected and uncontrollable effects, but the low precision in recruitment estimates.

Table 4-1. AIC model evaluation results among ASMR models fit to data pooled among tag cohort.

Model	AIC	# Parameters	Rank	Δ AIC
ASMR1	-216274	18	3	2492
ASMR2	-217132	30	2	1634
ASMR3	-218766	895	1	0

Table 4-2. AIC model evaluation results among ASMR models fit to data stratified by tag cohort.

Model	AIC	# Parameters	Rank	Δ AIC
ASMR1	-196278	18	3	2577
ASMR2	-197183	30	2	1672
ASMR3	-198856	895	1	0

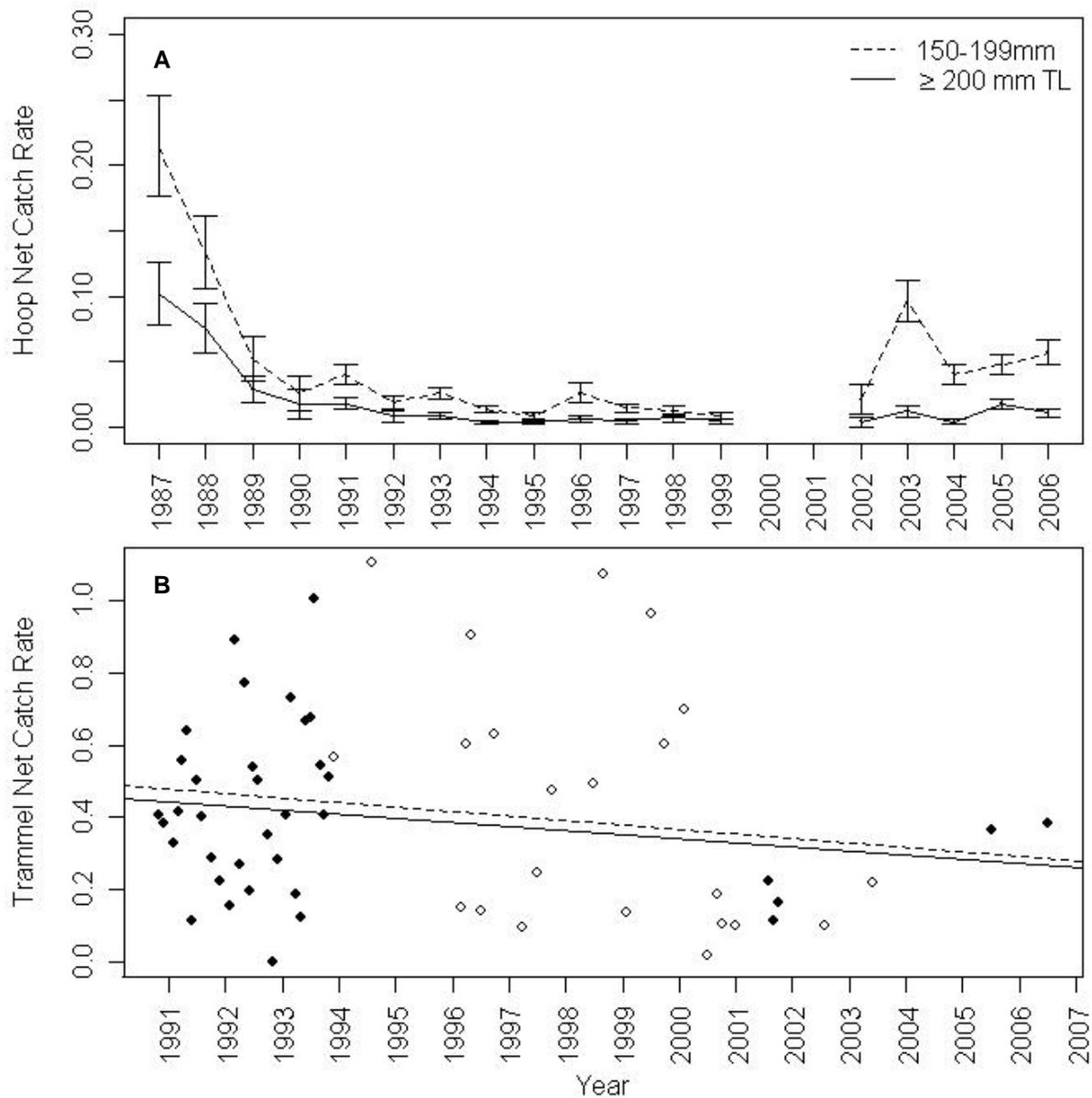


Figure 4-1. Relative abundance indices of sub-adult (150-199 mm total length; TL) and adult (≥ 200 mm TL) humpback chub based on hoop net catch rate (fish/hour) in the lower 1,200 m section of the Little Colorado River (A) and trammel net catch rate (fish/hour/100 m) of adult humpback chub in the Little Colorado River inflow reach of the Colorado River (B). Error bars in panel (A) are 95% confidence intervals. In panel (B), the solid line represents a regression model fit to the subset of data representing robust sampling (solid circles) and the dashed line represents a regression model fit to the entire dataset (all circles).

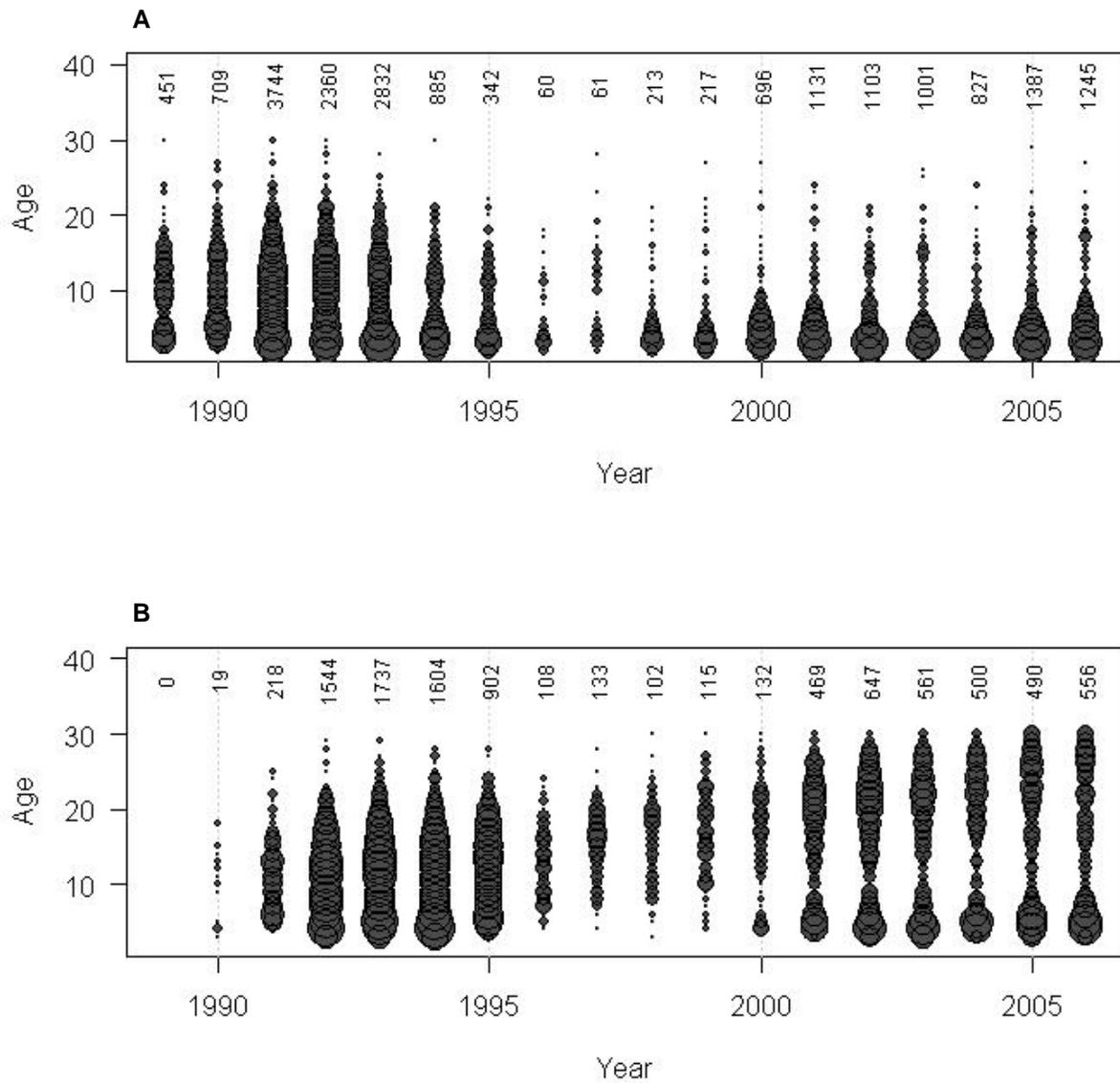


Figure 4-2. Numbers of humpback chub marked (A) and recaptured (B) by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages indicated by relative size of bubbles within each column.

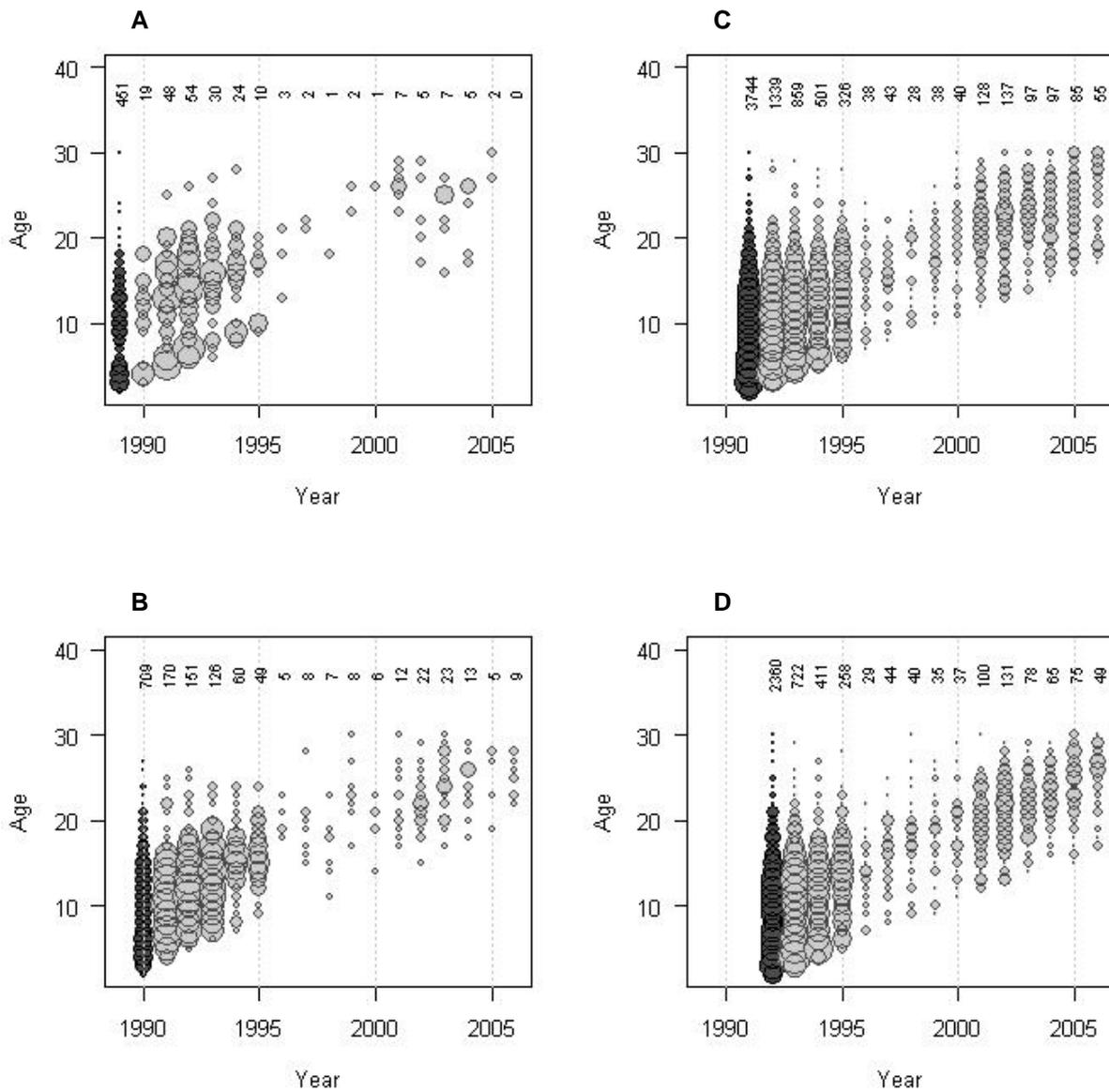


Figure 4-3a. Numbers of fish marked by age in years 1989 (A), 1990 (B), 1991 (C), and 1992 (D) indicated by dark circles and subsequently recaptured (light circles) by age and years. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages indicated by relative size of bubbles within each column.

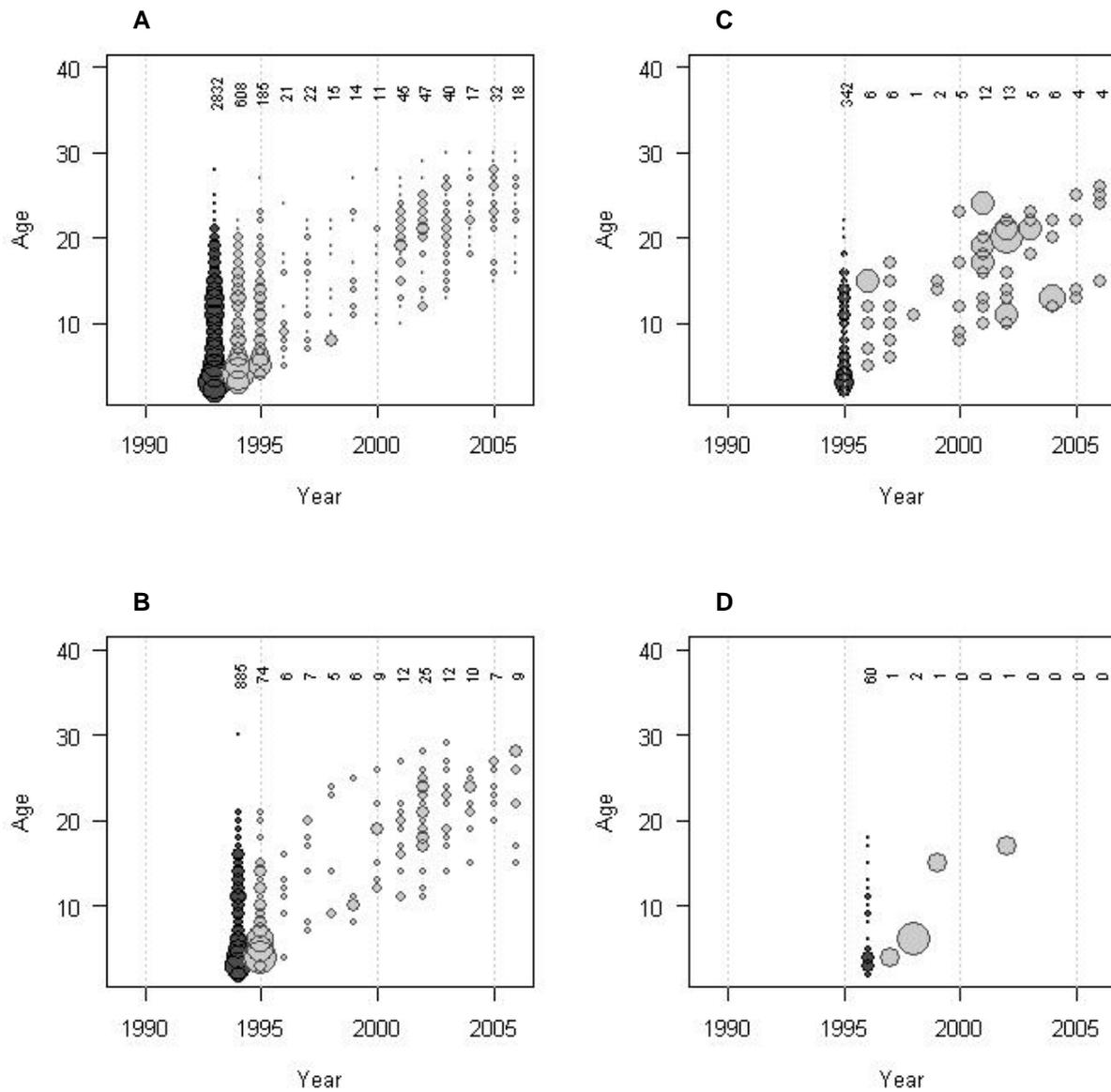


Figure 4-3b. Numbers of fish marked by age in years 1993 (A), 1994 (B), 1995 (C), and 1996 (D) indicated by dark circles and subsequently recaptured (light circles) by age and years. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages indicated by relative size of bubbles within each column.

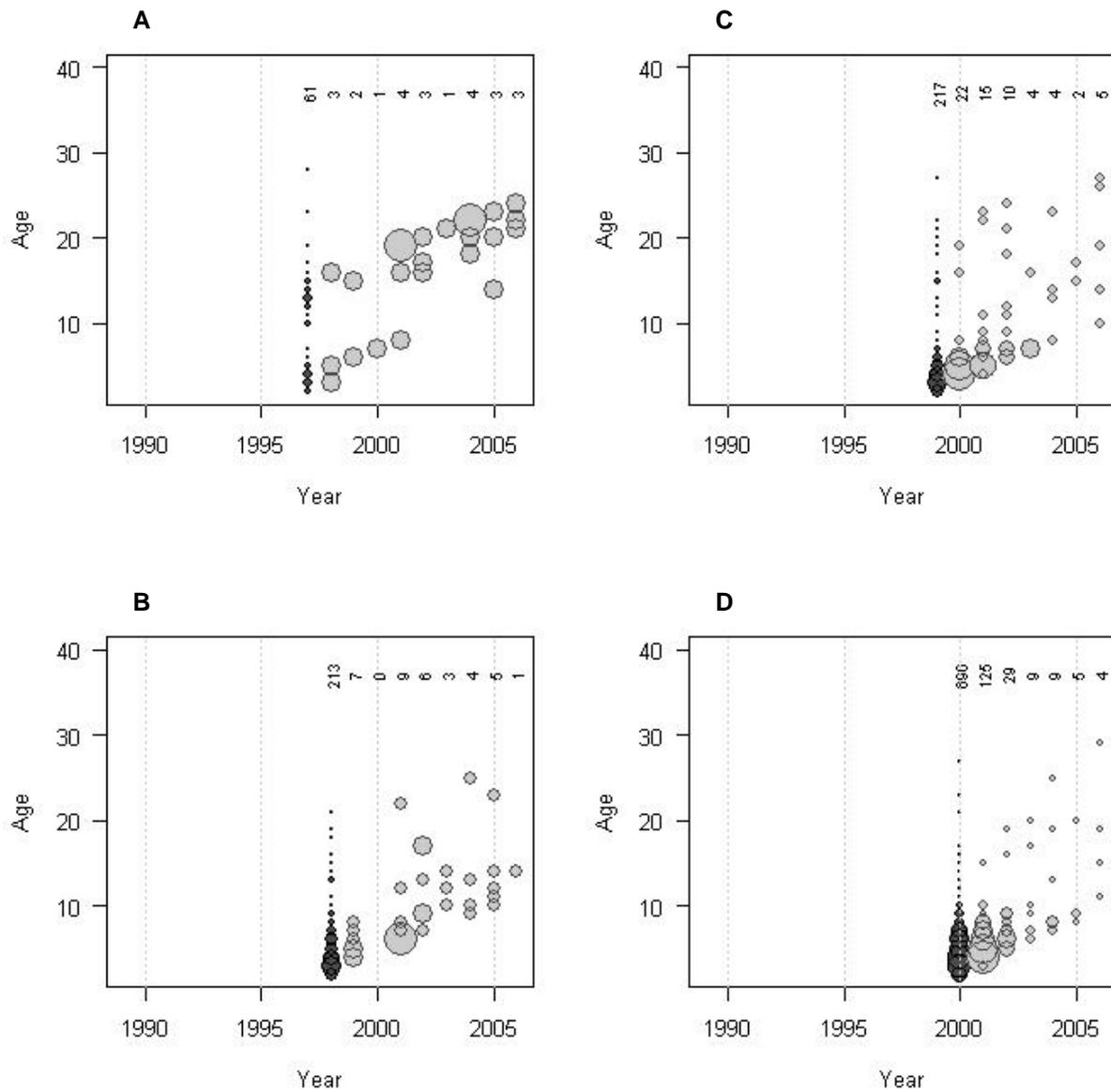


Figure 4-3c. Numbers of fish marked by age in years 1997 (A), 1998 (B), 1999 (C), and 2000 (D) indicated by dark circles and subsequently recaptured (light circles) by age and years. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages indicated by relative size of bubbles within each column.

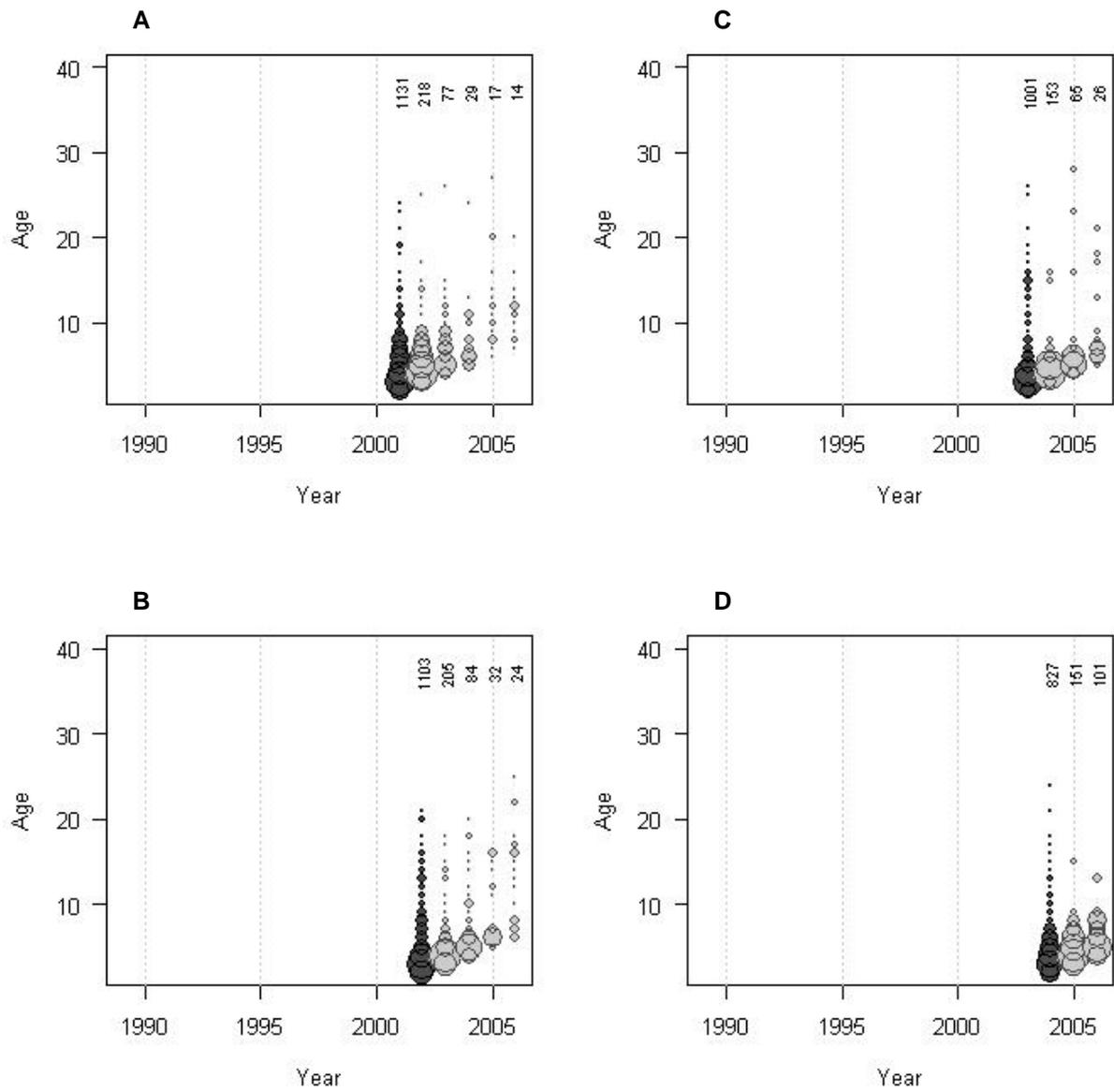


Figure 4-3d. Numbers of fish marked by age in years 2001 (A), 2002 (B), 2003 (C), and 2004 (D) indicated by dark circles and subsequently recaptured (light circles) by age and years. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages indicated by relative size of bubbles within each column.

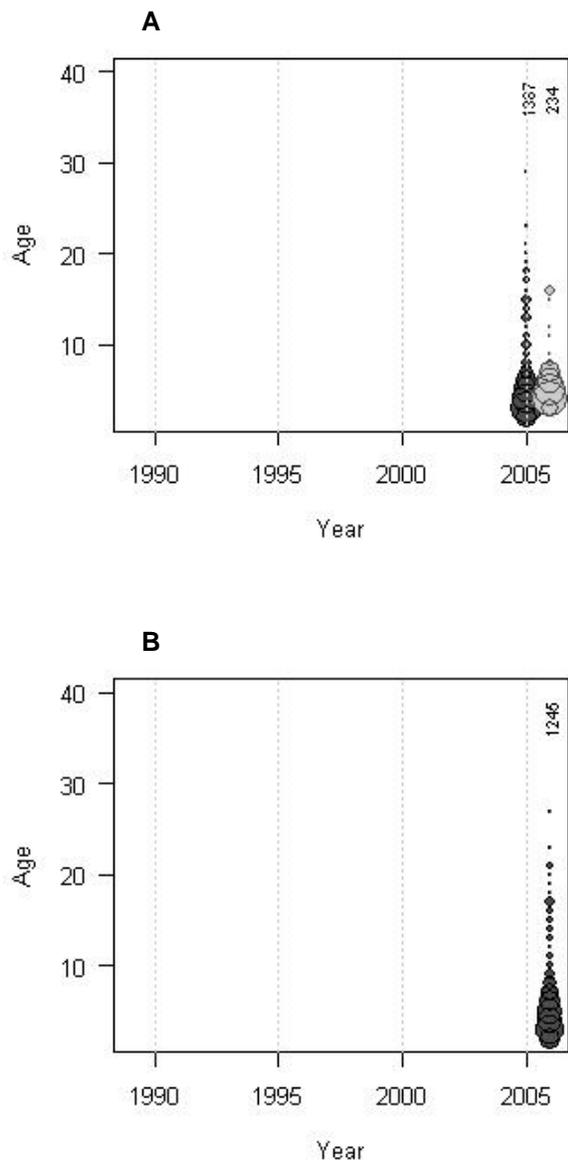


Figure 4-3e. Numbers of fish marked by age in years 2005 (A) and 2006 (B) indicated by dark circles and subsequently recaptured (light circles) by age and years. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages indicated by relative size of bubbles within each column.

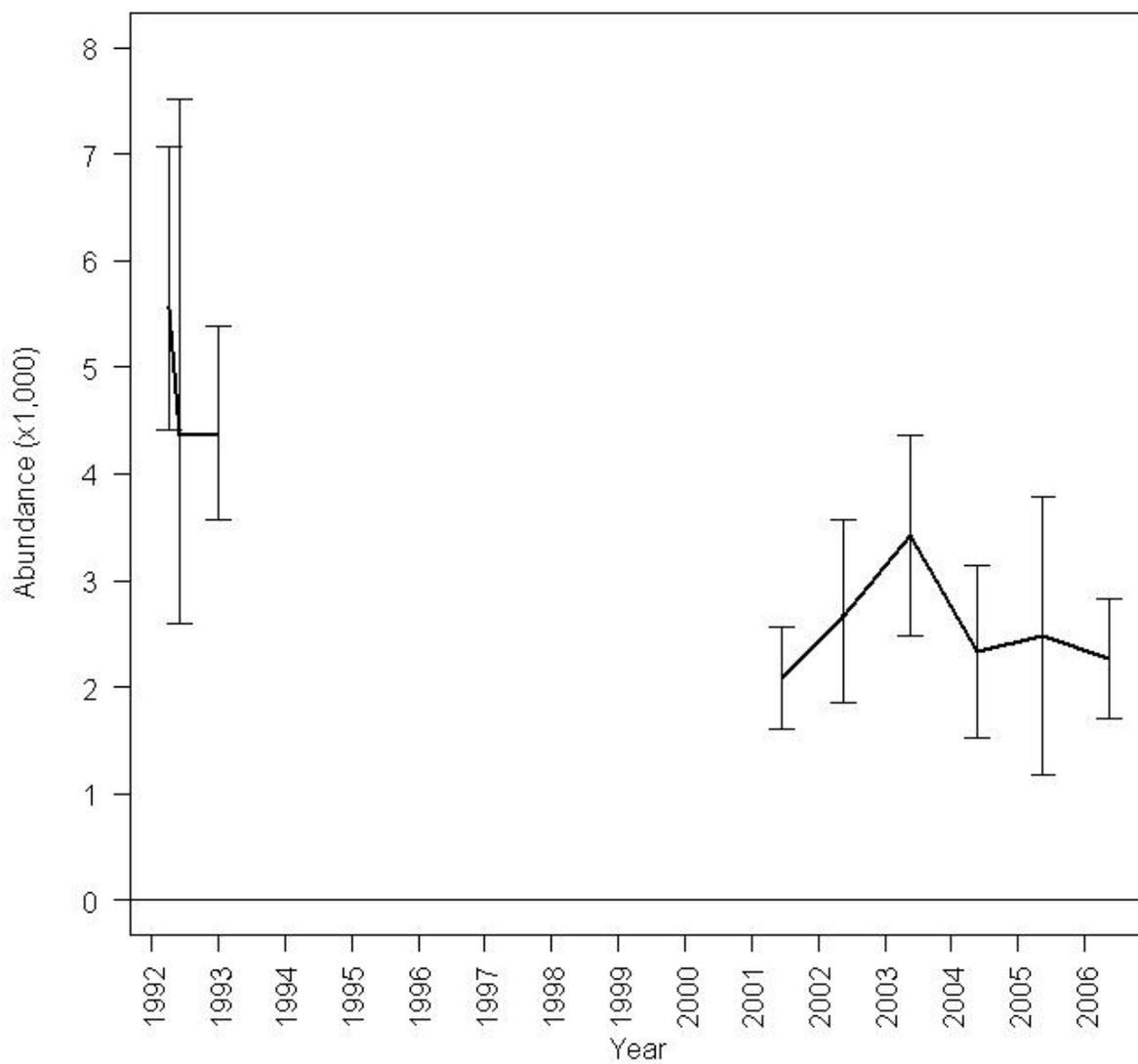


Figure 4-4. Mark-recapture closed population model estimates of humpback chub abundance \geq 150 mm total length in the Little Colorado River. Error bars represent 95% confidence intervals.

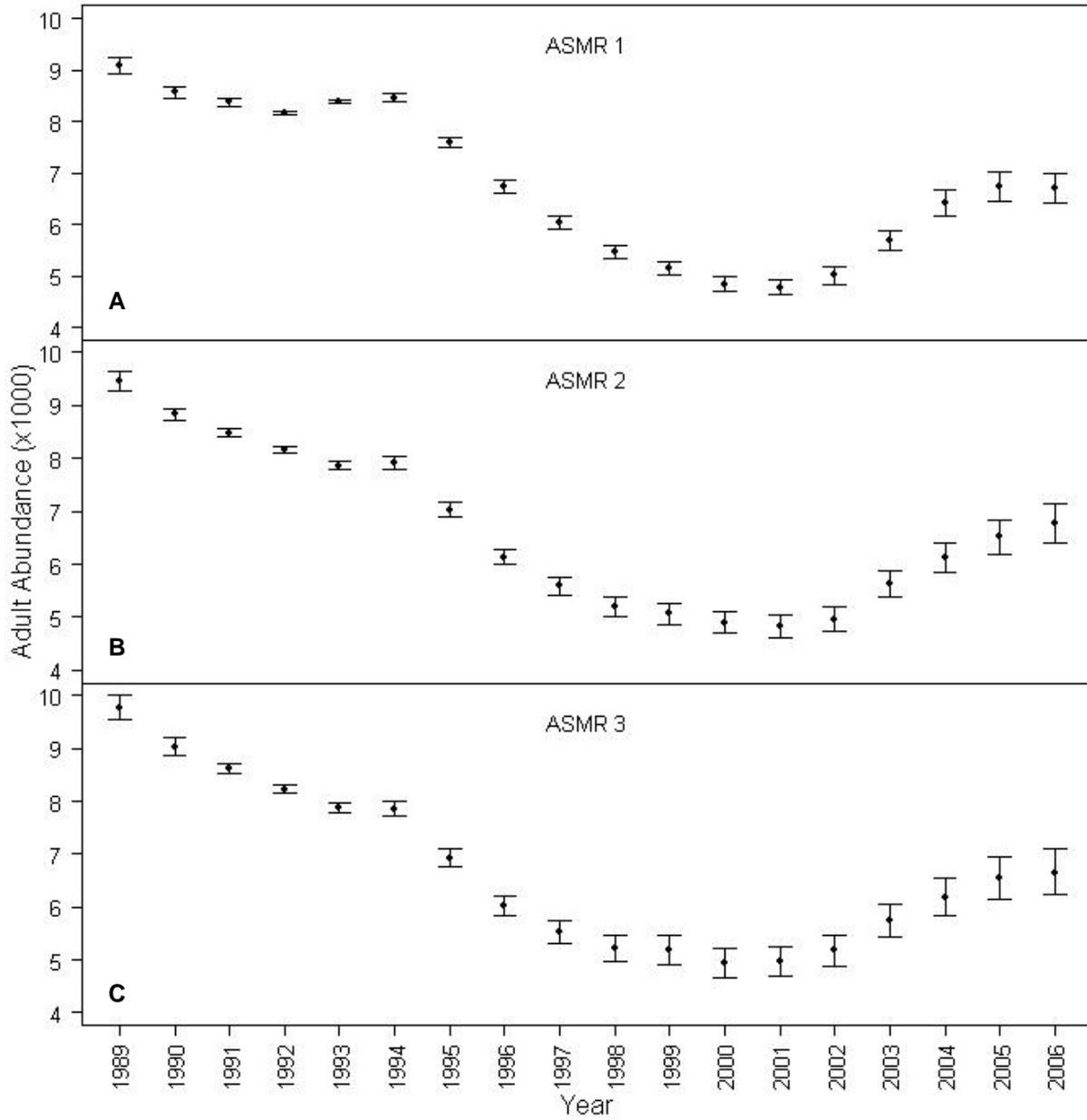


Figure 4-5. Humpback chub adult abundance (age-4+) estimates from the ASMR 1 (A), ASMR 2 (B), and ASMR 3 (C) models using data pooled among tag cohorts. Error bars are 95% credible intervals from 200,000 Markov Chain Monte Carlo trials.

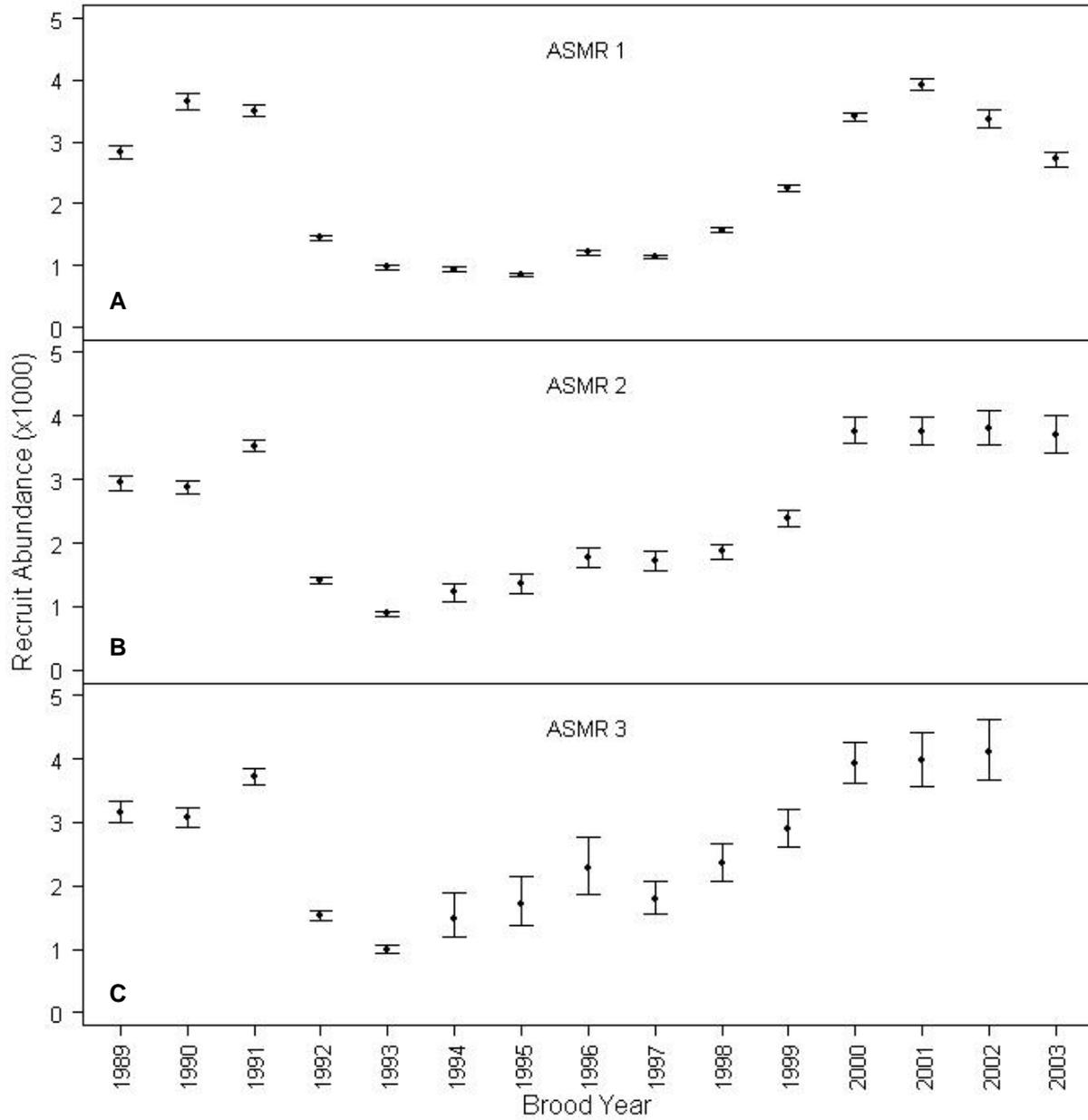


Figure 4-6. Humpback chub recruit abundance (age-2) estimates from the ASMR 1 (A), ASMR 2 (B), and ASMR 3 (C) models using data pooled among tag cohorts. Error bars are 95% credible intervals from 200,000 Markov Chain Monte Carlo trials.

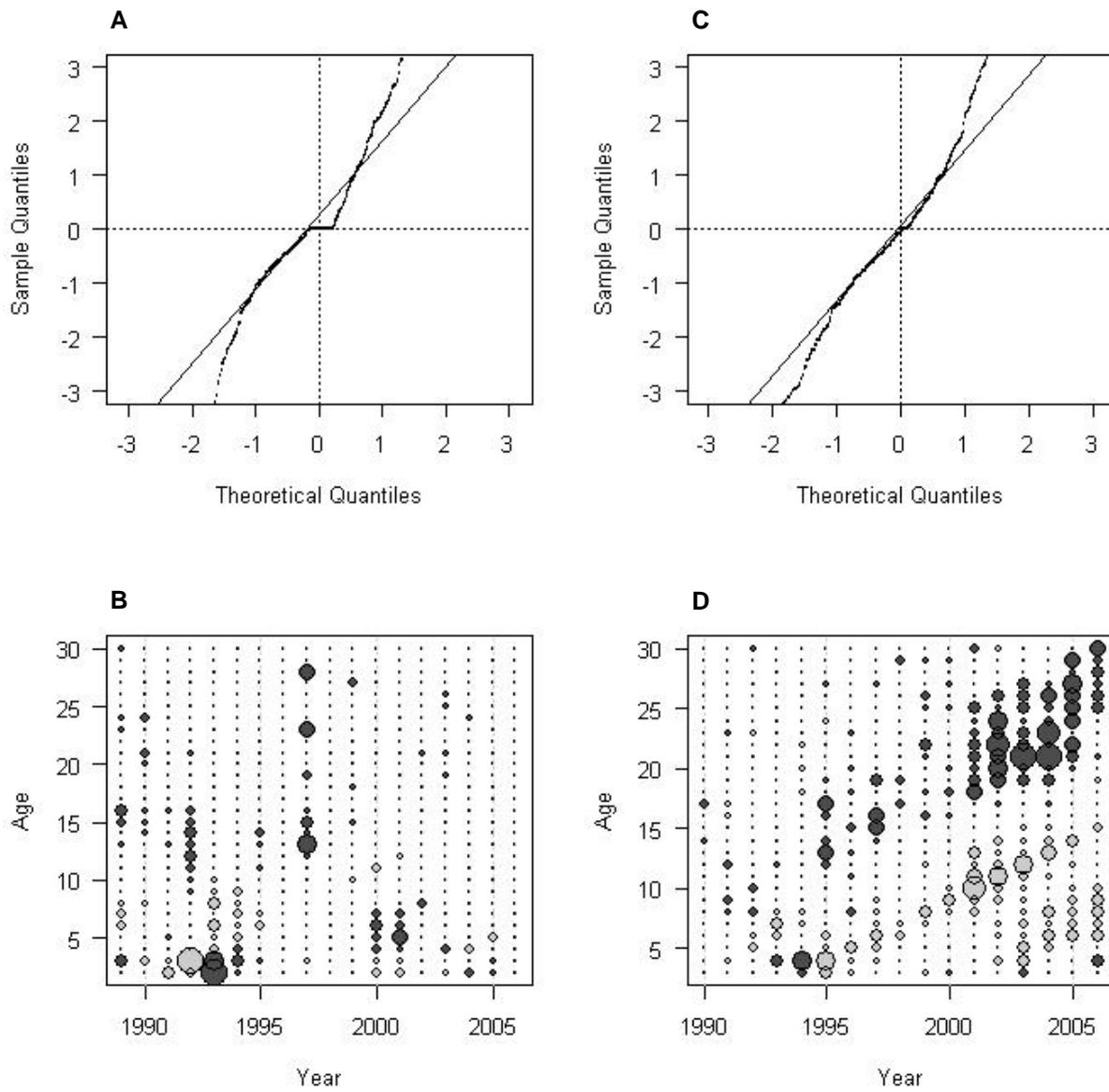


Figure 4-7. Pearson residual plots for model ASMR 1 using data pooled among tag cohorts. Individual plots are: Quantile-Quantile plots for marked (A) and recaptured (C) fish and Pearson residuals-at-age and at-time for marked (B) and recaptured (D) fish.

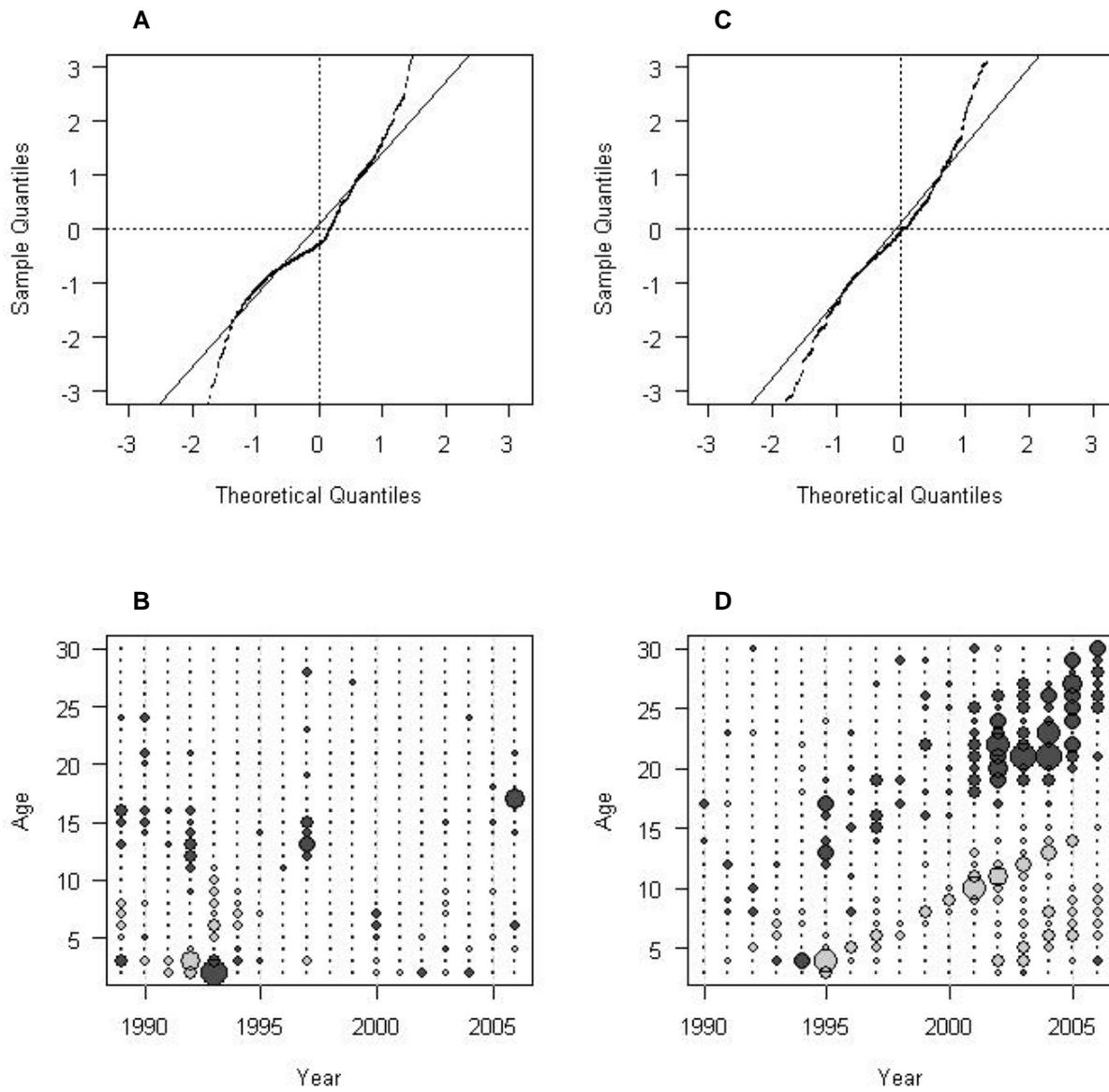


Figure 4-8. Pearson residual plots for model ASMR 2 using data pooled among tag cohorts. Individual plots are: Quantile-Quantile plots for marked (A) and recaptured (C) fish and Pearson residuals-at-age and at-time for marked (B) and recaptured (D) fish.

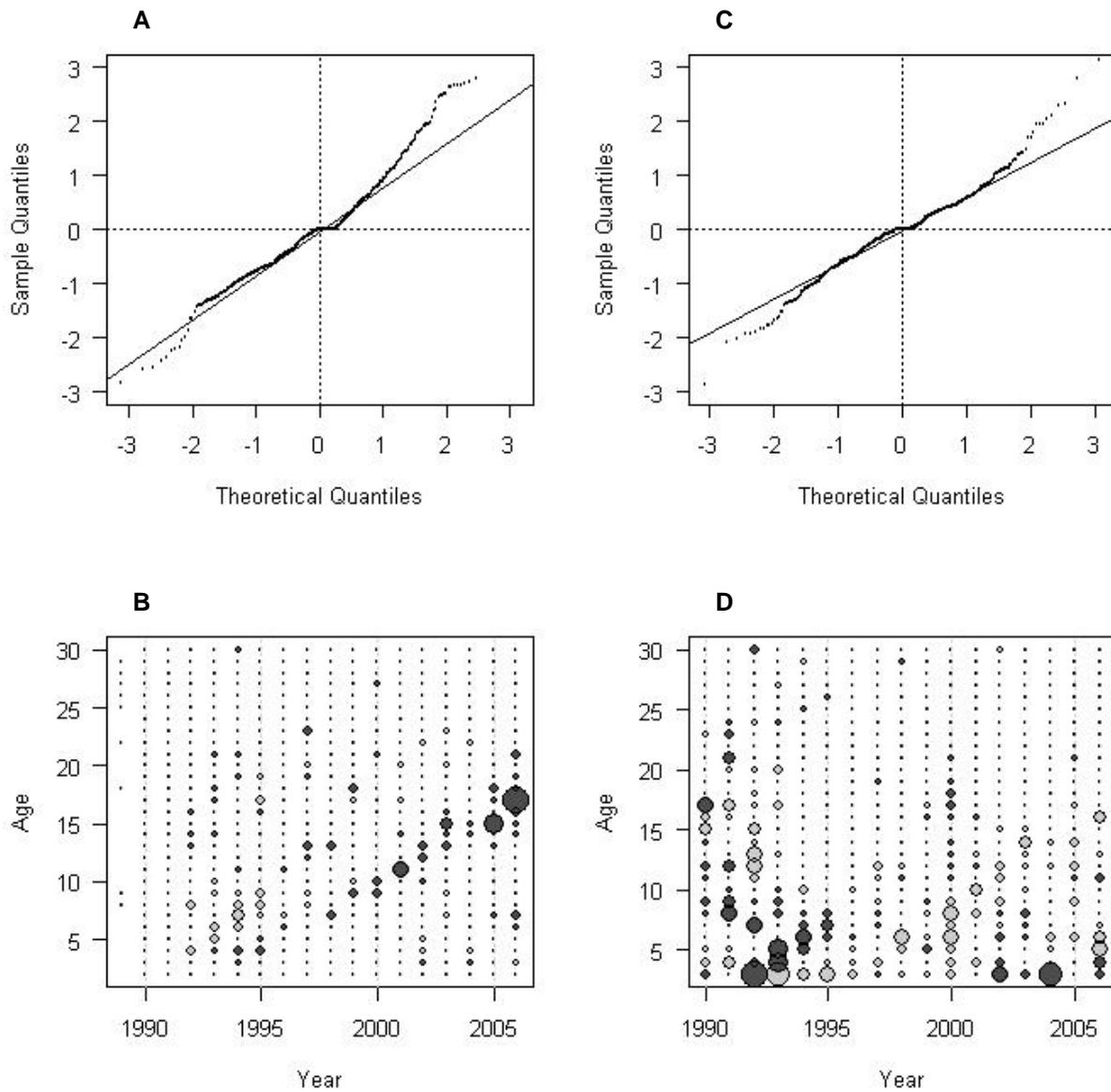


Figure 4-9. Pearson residual plots for model ASMR 3 using data pooled among tag cohorts. Individual plots are: Quantile-Quantile plots for marked (A) and recaptured (C) fish and Pearson residuals-at-age and at-time for marked (B) and recaptured (D) fish.

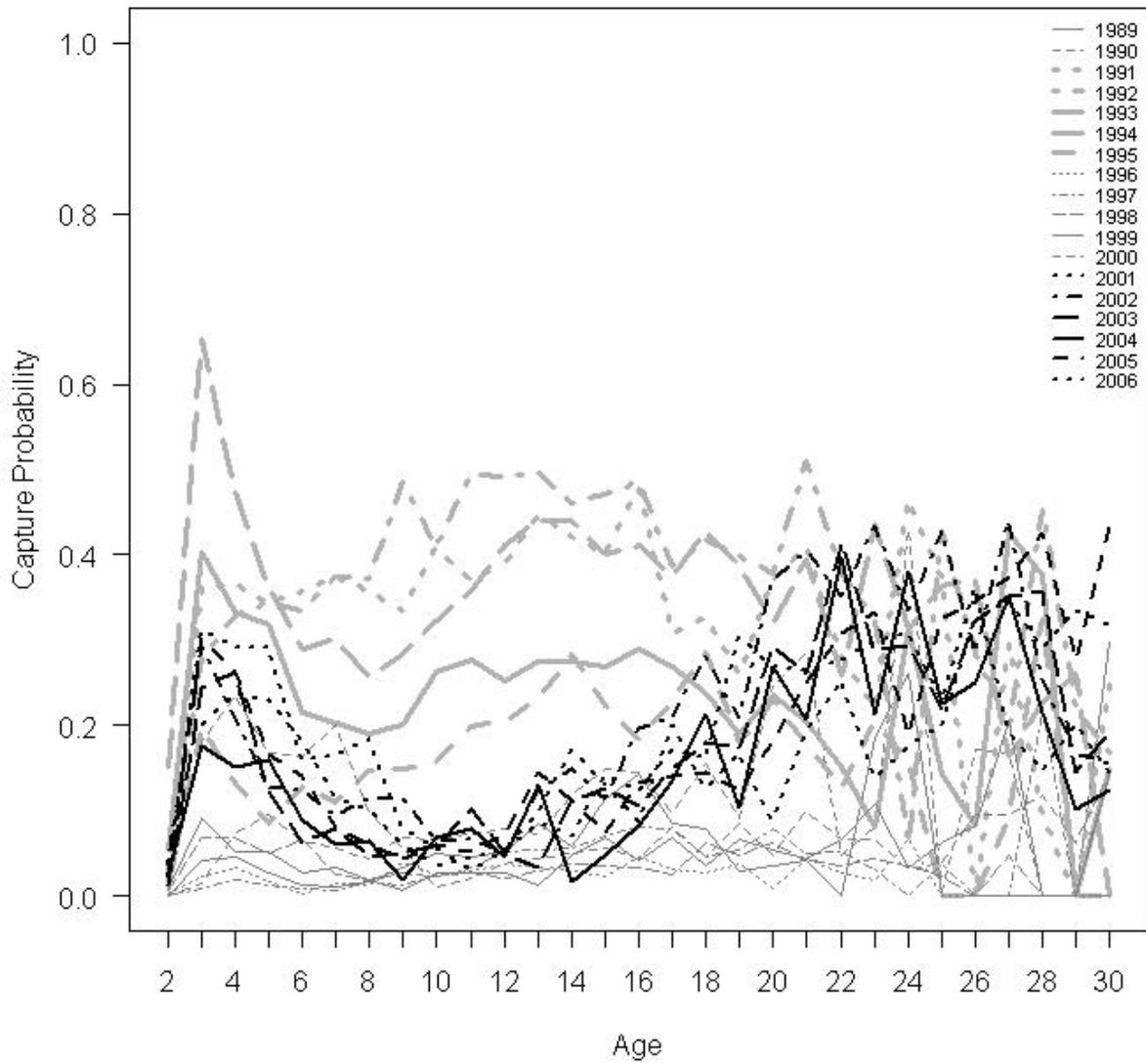


Figure 4-10. Capture probability by age and year estimated from model ASMR 3 using data pooled among tag cohorts.

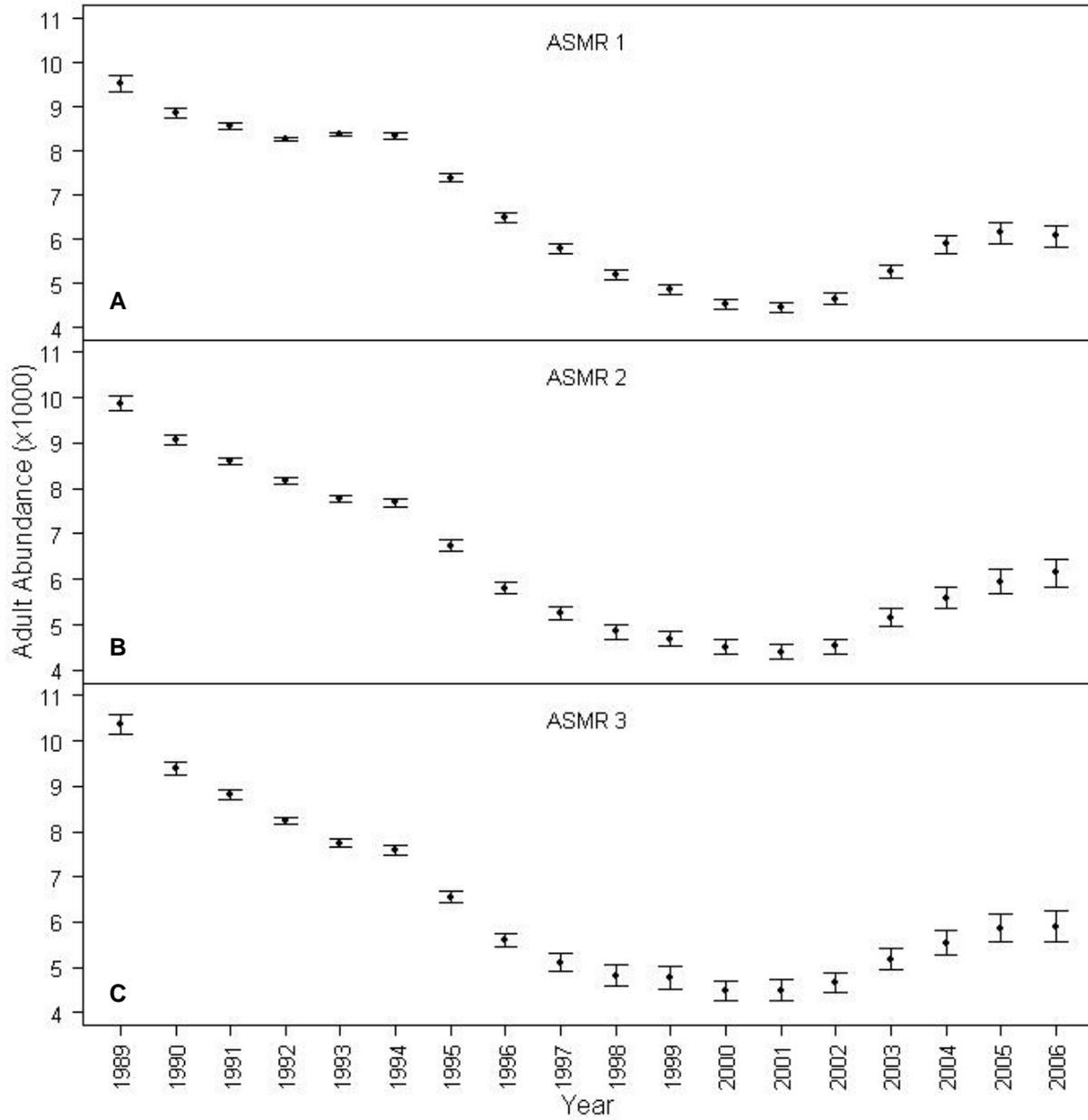


Figure 4-11. Humpback chub adult abundance (age-4+) estimates from the ASMR 1 (A), ASMR 2 (B), and ASMR 3 (C) models using data stratified by tag cohort. Error bars are 95% credible intervals from 200,000 Markov Chain Monte Carlo trials.

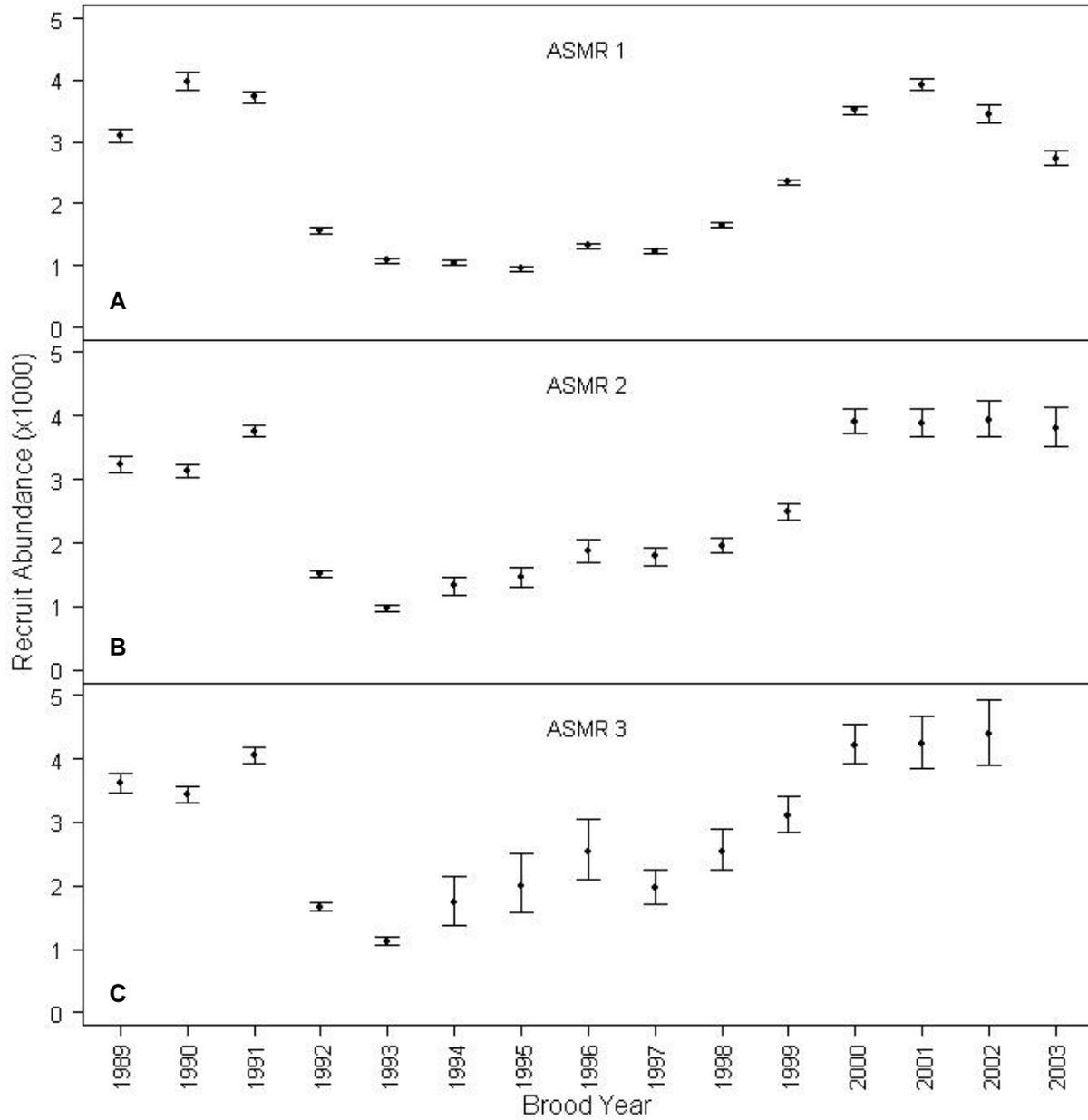


Figure 4-12. Humpback chub recruit abundance (age-2) estimates from the ASMR 1 (A), ASMR 2 (B), and ASMR 3 (C) models using data stratified by tag cohort. Error bars are 95% credible intervals from 200,000 Markov Chain Monte Carlo trials.

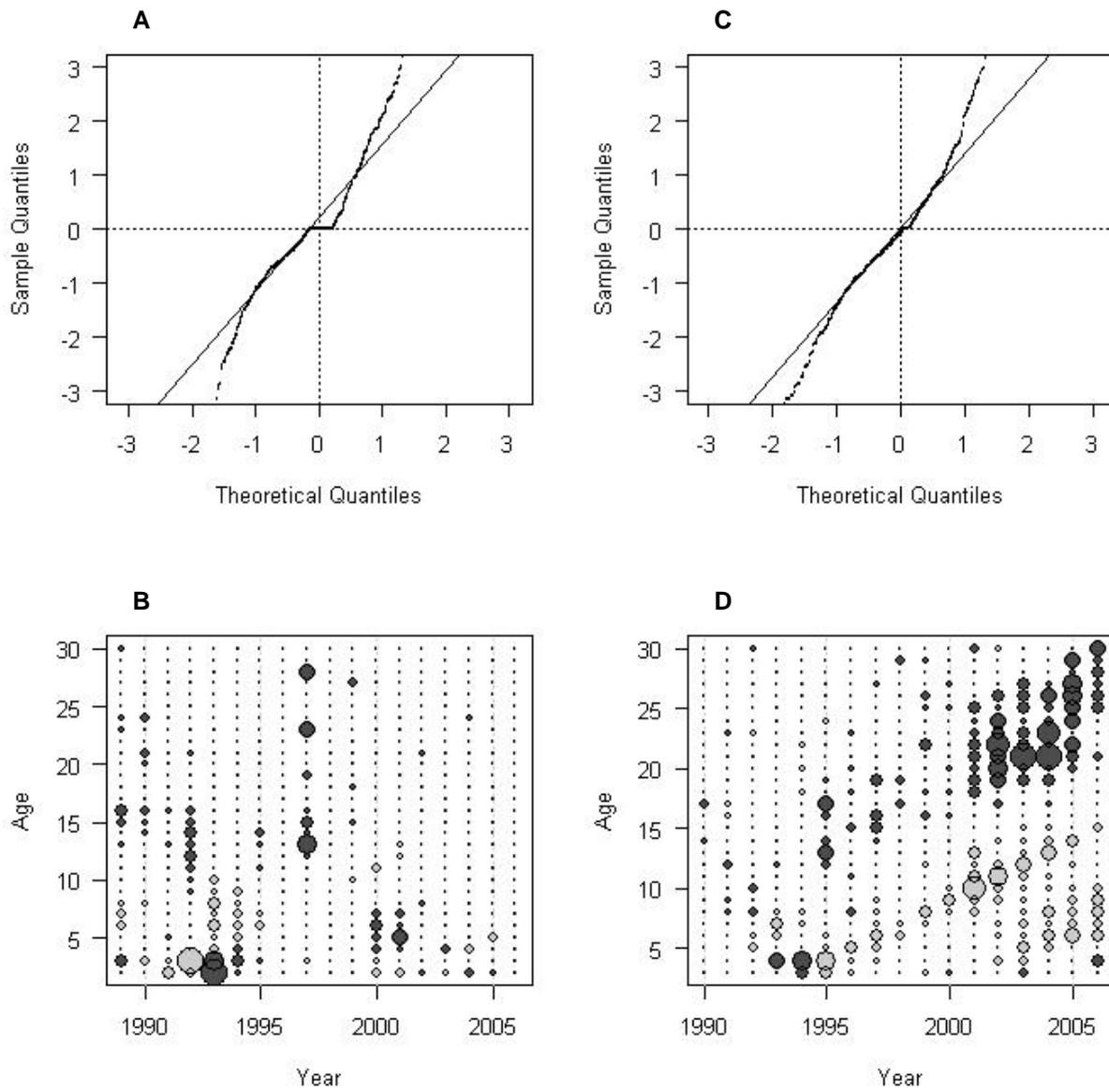


Figure 4-13. Pearson residual plots for model ASMR 1 using data stratified by tag cohort. Individual plots are: Quantile-Quantile plots for marked (A) and recaptured (C) fish and Pearson residuals-at-age and at-time for marked (B) and recaptured (D) fish.

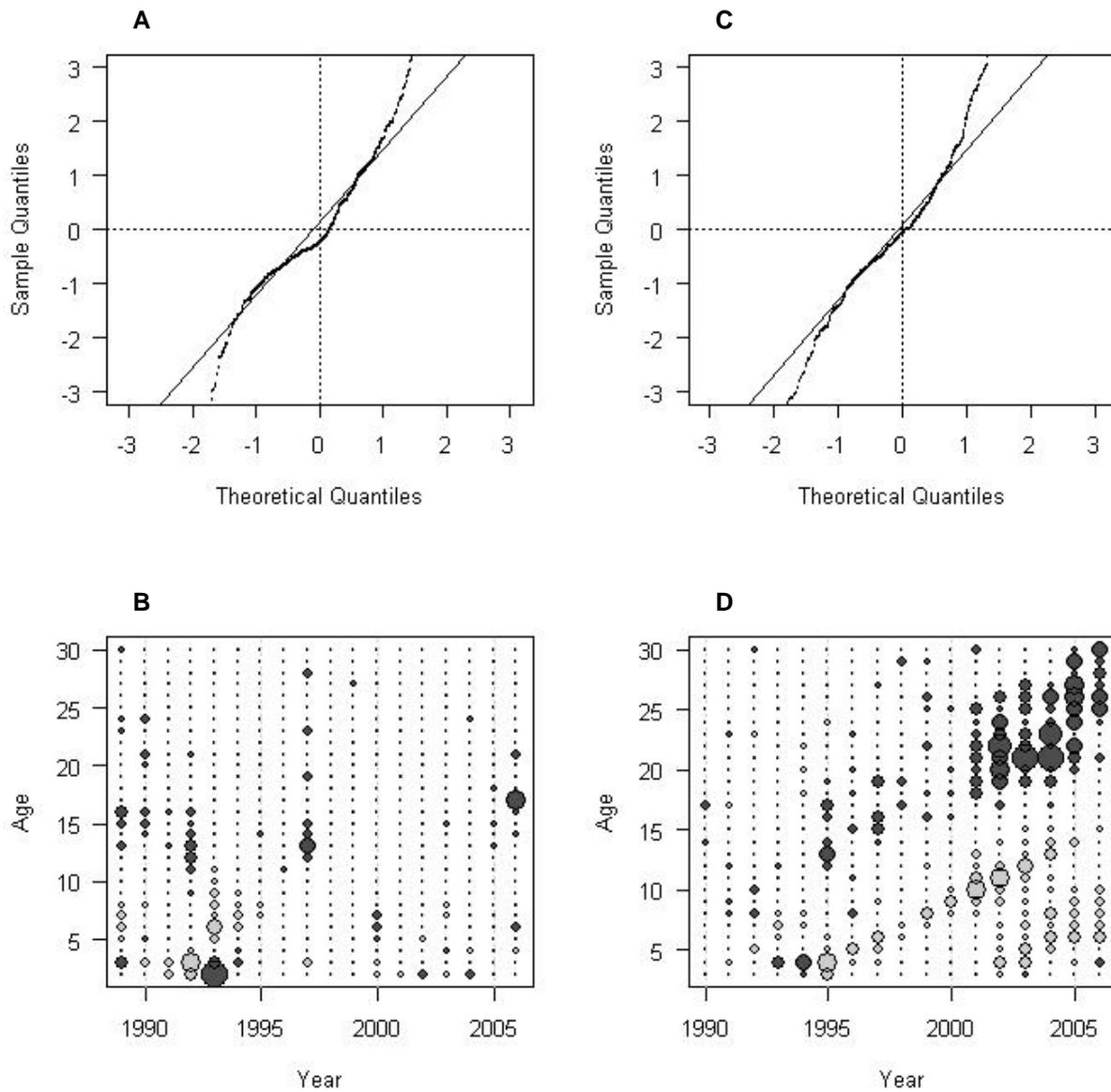


Figure 4-14. Pearson residual plots for model ASMR 2 using data stratified by tag cohort. Individual plots are: Quantile-Quantile plots for marked (A) and recaptured (C) fish and Pearson residuals-at-age and at-time for marked (B) and recaptured (D) fish.

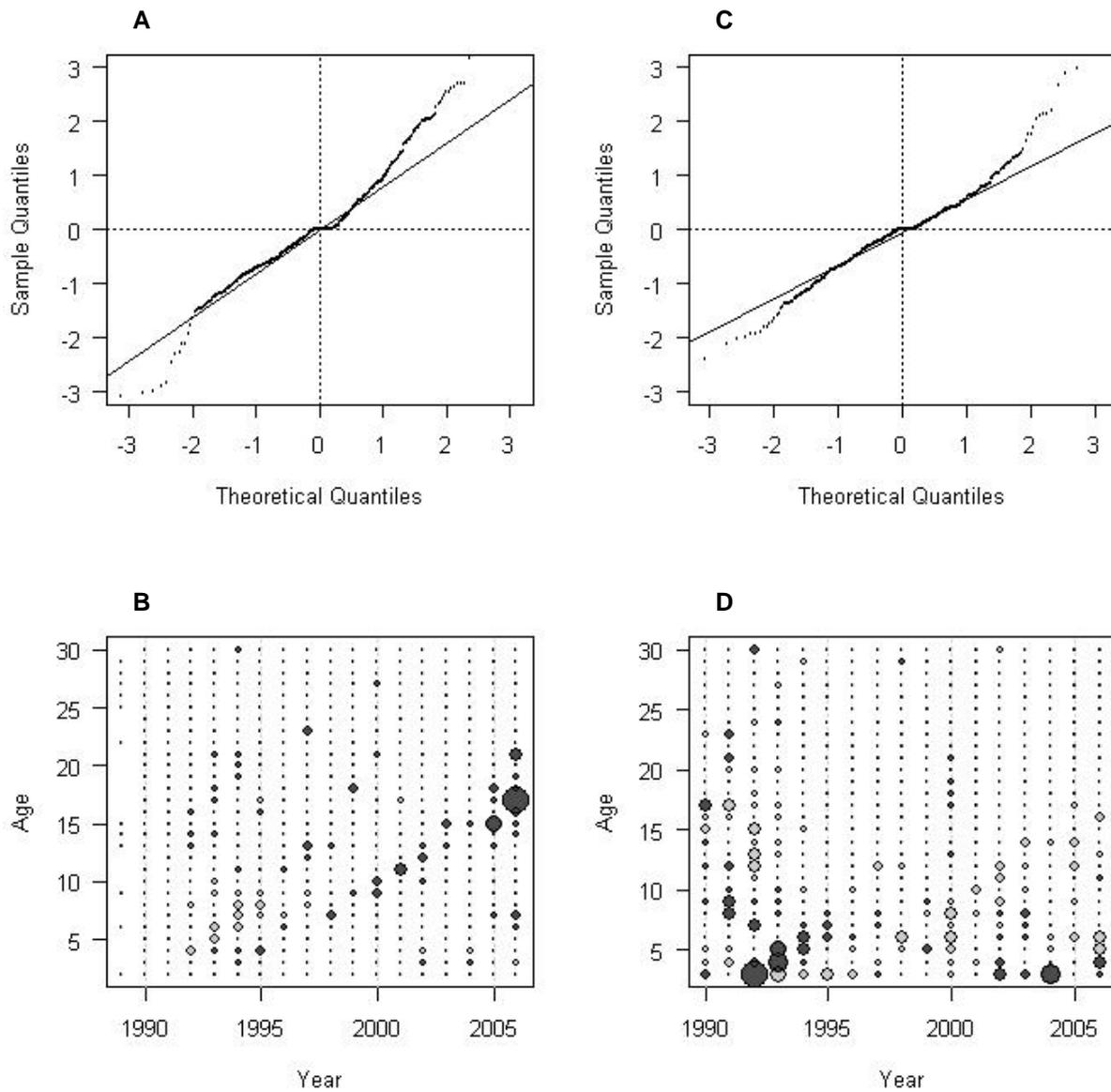


Figure 4-15. Pearson residual plots for model ASMR 3 using data stratified by tag cohort. Individual plots are: Quantile-Quantile plots for marked (A) and recaptured (C) fish and Pearson residuals-at-age and at-time for marked (B) and recaptured (D) fish.

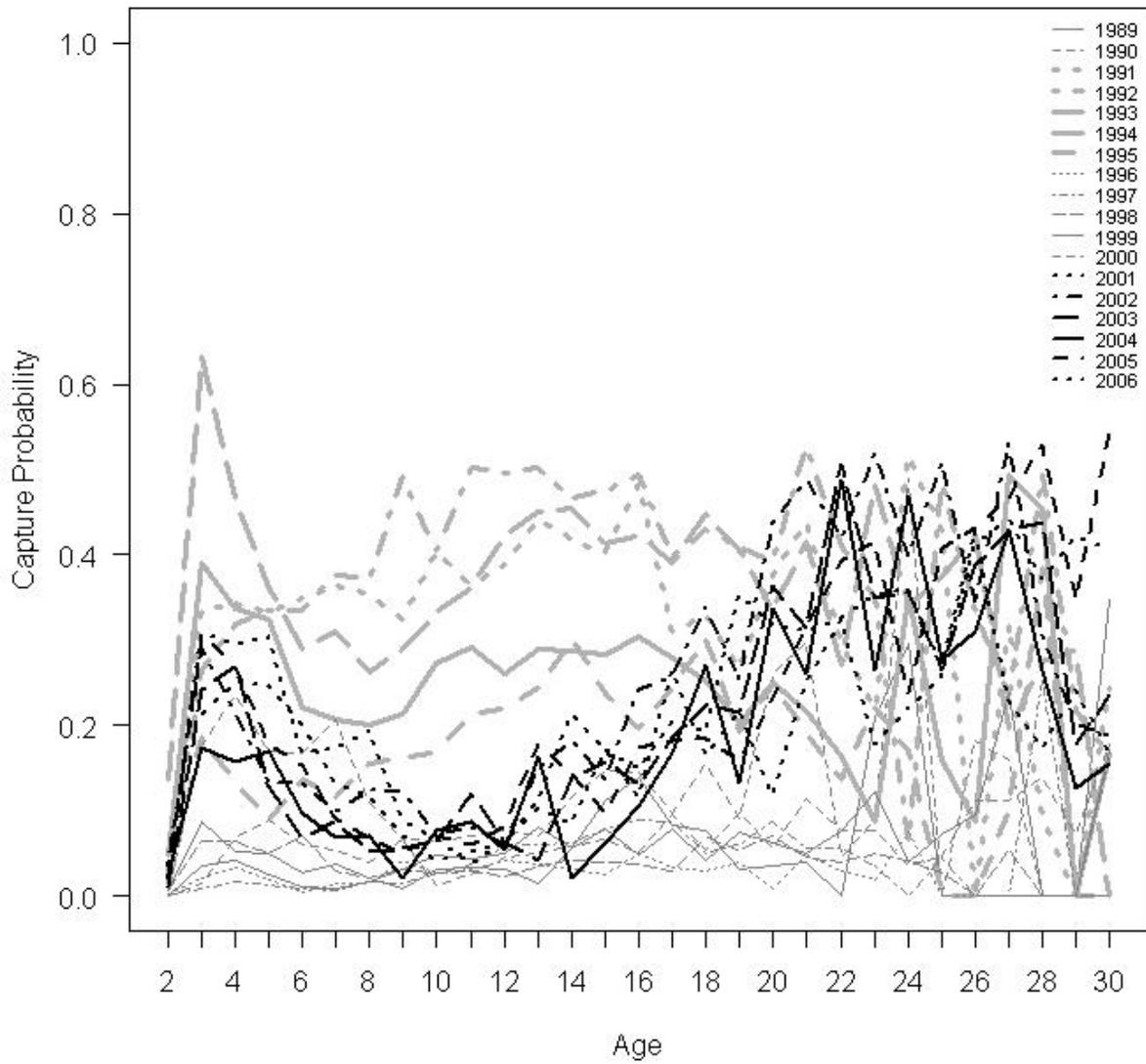


Figure 4-16. Capture probability by age and year estimated from model ASMR 3 using data stratified by tag cohort.

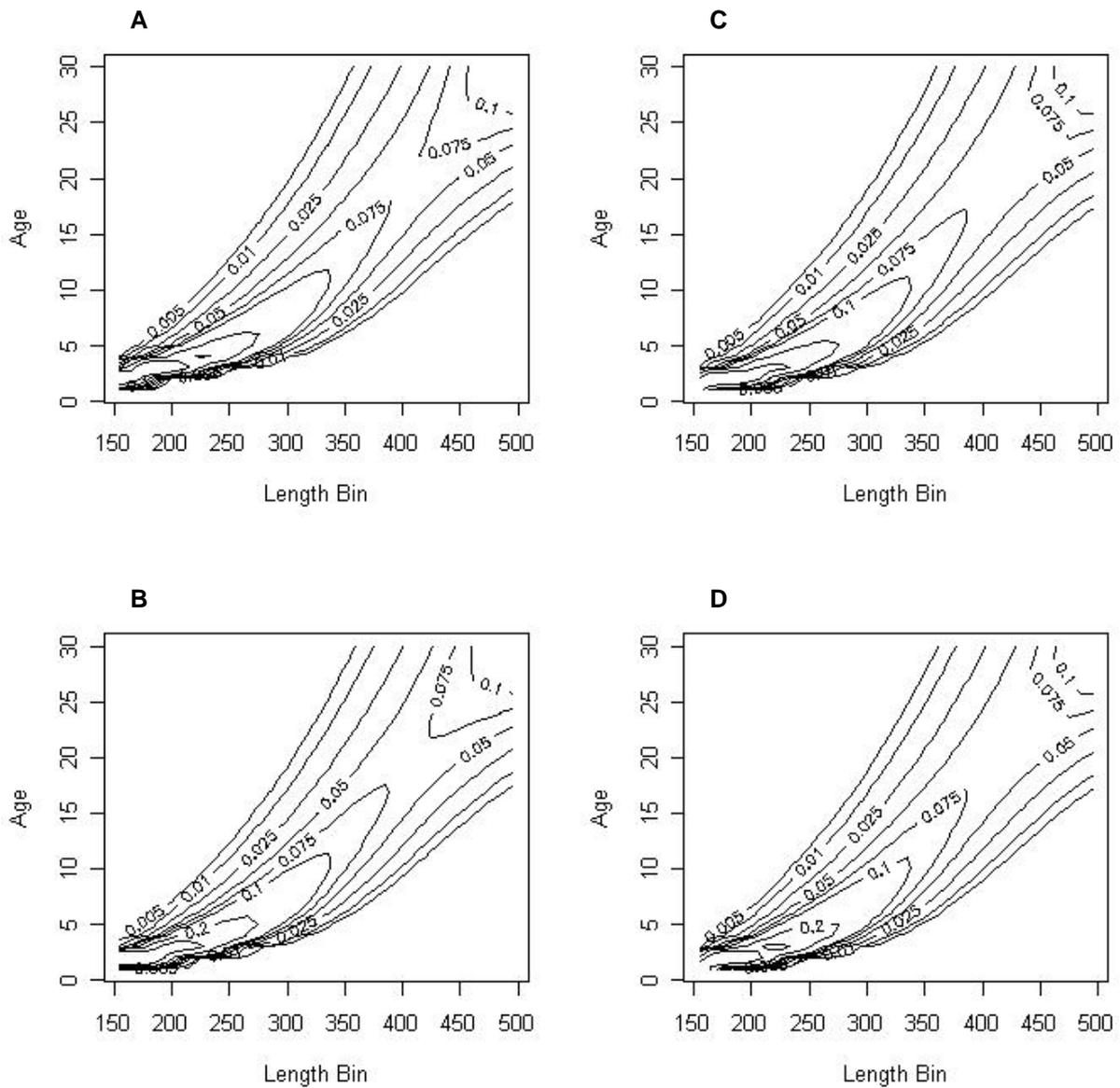


Figure 4-17. Seasonal probability surfaces of age for a particular length bin. These surfaces sum to unity in the vertical dimension (i.e., for each length bin) with the height of the surface indicating the probability of a particular age given a particular length bin, $P(a|l)$. Individual plots are for April-June (A), July-September (B), October-December (C), and January-March (D).

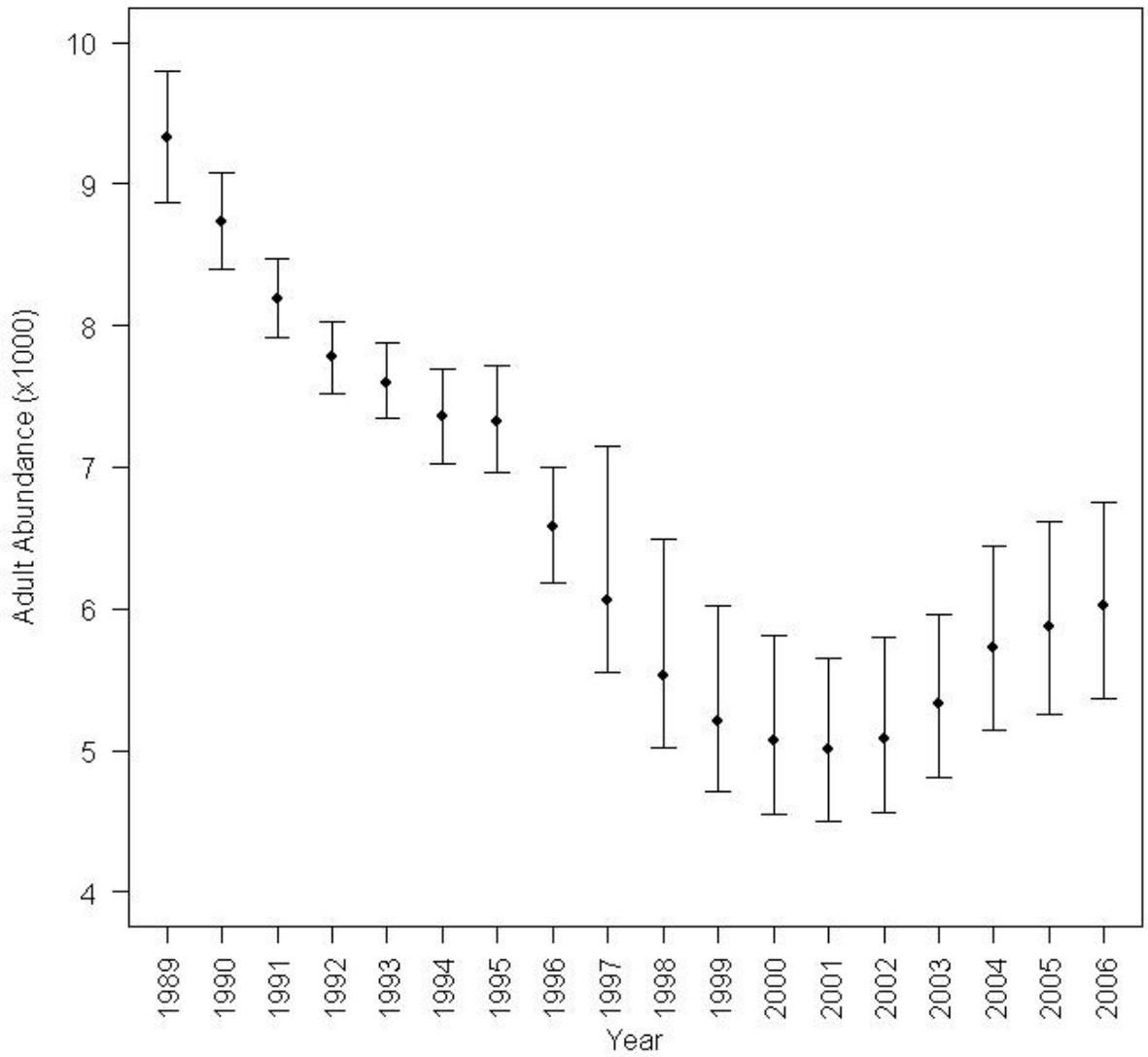


Figure 4-18. Estimated adult abundance (age-4+) from ASMR 3 incorporating uncertainty in assignment of age. Point estimates are mean values among 1,000 Monte Carlo trials and error bars represent maximum and minimum 95% profile confidence intervals among 1,000 Monte Carlo trials.

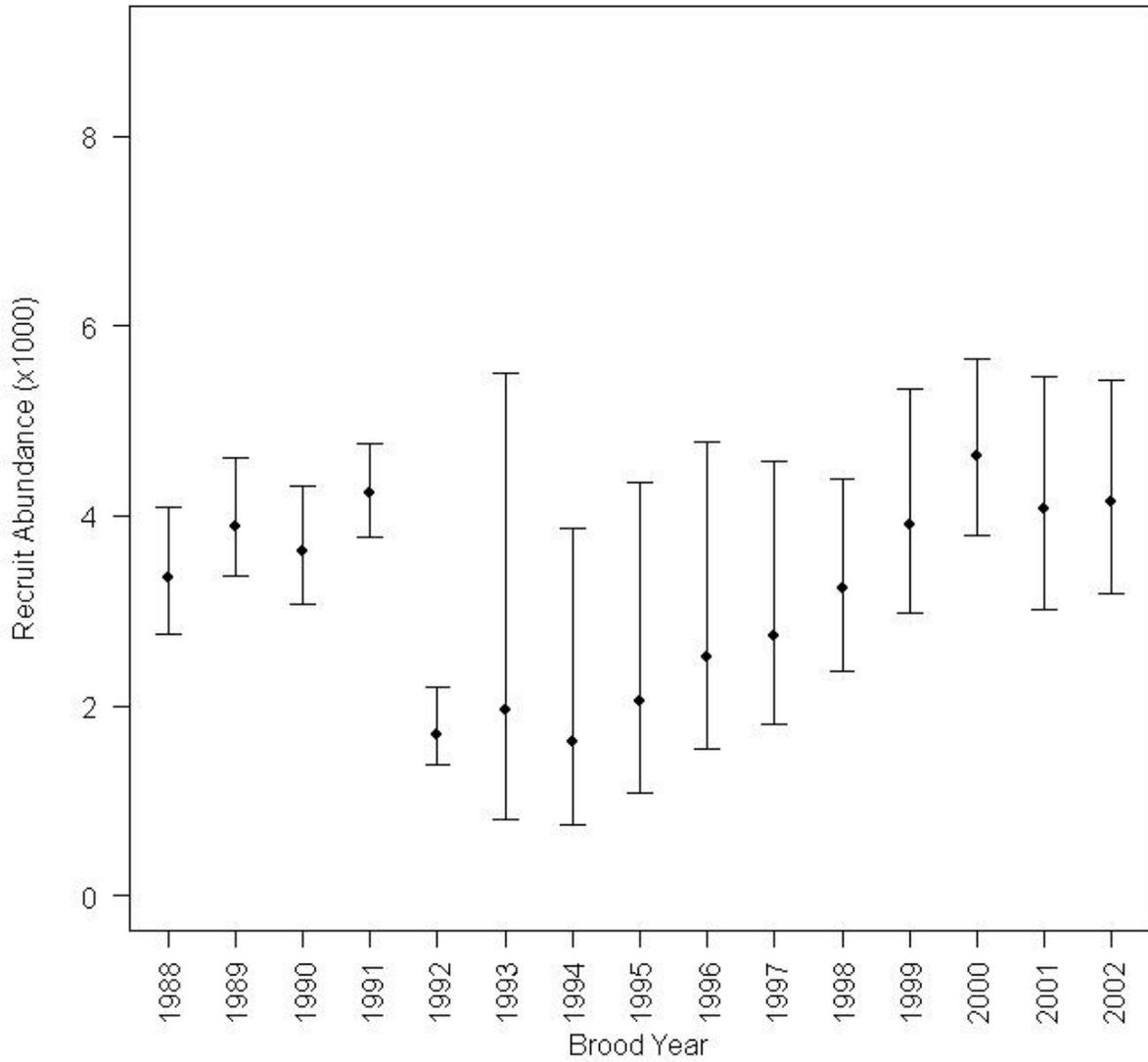


Figure 4-19. Estimated recruit abundance (age-1) from ASMR 3 incorporating uncertainty in assignment of age. Point estimates are mean values among 1,000 Monte Carlo trials and error bars represent maximum and minimum 95% profile confidence intervals among 1,000 Monte Carlo trials.

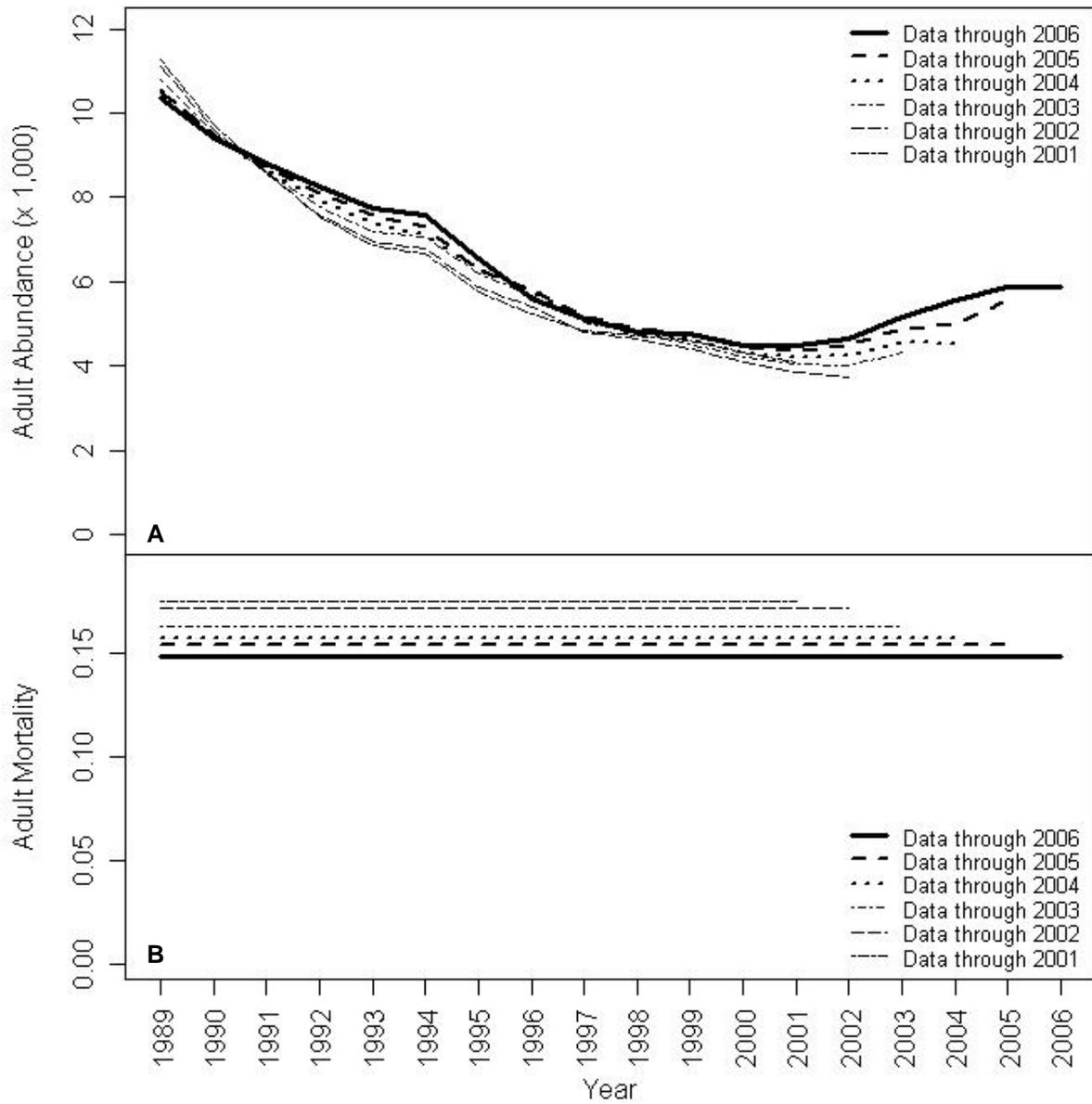


Figure 4-20. Retrospective analysis of adult abundance (A) and mortality rate (B) considering datasets beginning in 1989 and ending in the year indicated in the figure legend.

CHAPTER 5
LINKING TEMPORAL PATTERNS IN FISHERY RESOURCES WITH ADAPTIVE
MANAGEMENT: WHAT HAVE WE LEARNED AND ARE WE MANAGING
ADAPTIVELY?

With increased public awareness of the altered and degraded conditions prevalent in many U.S. rivers over the last two decades, river restoration activities have increased exponentially (Palmer et al. 2007). In the southwest, motivations for river restoration activities are varied and include riparian zone and water quality management, in-stream habitat improvement, flow modification, and concern over federally listed endangered species (Baron et al. 2002; Gloss et al. 2005; Follstad-Shah et al. 2007). A recent review of U.S. river restoration activities discovered that in many cases (>90%) little information was available from monitoring or other activities to assess the success of these efforts (Bernhardt et al. 2005). Though this finding is troubling considering the associated financial expenditures (>7.5 billion dollars between 1990 and 2003; Bernhardt et al. 2005), the science of river restoration and associated measures of ecological “success” are yet in formative stages (Palmer et al. 2005). Nevertheless, this finding shows that clear project goals and monitoring systems to evaluate progress towards those goals are often lacking.

The Glen Canyon Dam Adaptive Management Program (GCDAMP) was formed as a provision of the Record of Decision following the Final Environmental Impact Statement on the operation of Glen Canyon Dam (USDOJ 1995). Though the overarching goal of the GCDAMP could be described as assisting the U.S. Secretary of Interior to comply with the body of law governing the management of Colorado River water resources and Grand Canyon National Park and Glen Canyon National Recreation area, this program has significant river restoration intent as described in the Grand Canyon Protection Act of 1992 (Act). The geographic scope of the GCDAMP is the Colorado River within Glen and Grand Canyons and associated riparian and

terrace zones influenced by dam operations (GCDAMP 2001). Additionally, the Act refers to improving resources in Grand Canyon Nation Park and Glen Canyon National Recreation Area, and the majority of the GCDAMP goals refer directly to aquatic or riparian resources (GCDAMP 2001).

The GCDAMP is generally viewed as a successful example of a large-scale adaptive management and river restoration program (Ladson and Argent 2002; Poff et al. 2003), but specific criteria defining resource goals are generally lacking in the foundational and working documents of the program (GCDAMP 2001). Although the GCDAMP has attempted to develop goals shared by all of the participating stakeholders, the result has been an unfocused set of ambiguous resource goals that are neither well prioritized nor organized within an ecosystem or “guiding image” perspective (NRC 1996; Palmer et al. 2005). According to the U.S. Department of Interior technical guide on adaptive management (Williams et al. 2007), a requirement of adaptive management is a statement of explicit and measurable goals. Therefore, and according to guidance from the U.S. Department of Interior, this program is not operating within an optimum adaptive management framework.

To meet agency guidelines from Williams et al. (2007), further program development is clearly needed, but the GCDAMP has initiated several large-scale adaptive management experiments since inception in 1996 and the program continues to attempt to learn as much as possible from those efforts. This chapter provides an overview of past experimental actions, uncontrolled factors, and attempts to evaluate the effects of these actions on Colorado River fish populations. I describe trends in uncontrolled, but possibly important factors such as: (1) Colorado River and major tributary hydrology, (2) release water temperature from Glen Canyon Dam, and (3) variable production of native fish from the Little Colorado River (LCR).

Description of Adaptive Management Actions

Below I summarize the major management actions implemented by the GCDAMP since inception. These actions are potentially biologically significant to Colorado River fish populations (Chapter 2).

1996 Experimental High Flow

Prior to the construction of Glen Canyon Dam, annual spring flood discharges in the Colorado River often exceeded 50,000 ft³/s (cfs) with infrequent events exceeding 210,000 cfs (Topping et al. 2003). Following construction of Glen Canyon Dam, flows rarely exceeded 30,000 cfs. For seven days in April 1996, a widely publicized experimental high flow (hereafter 1996 EHF) was released from Glen Canyon Dam with a peak discharge of 45,000 cfs (Webb et al. 1999). Though a discharge of this magnitude represents a minor pre-dam flood event with recurrence interval < 1.25 years, it represented a post-dam event with recurrence interval of 5.1 years (Schmidt et al. 2001). The overarching restoration goal of the 1996 EHF was to redistribute fine sediment within the channel to build shoreline sandbars, a primary program objective. However, a broad set of physical and biological studies were undertaken in concert with the 1996 EHF and are thoroughly documented in the literature (e.g., Webb et al. 1999; Patten and Stevens 1999).

2000 Low Summer Steady Flow

A program of experimental flows (hereafter LSSF) from Glen Canyon Dam (Valdez et al. 2000) was initiated in 2000 to benefit native fish resources and to comply with the reasonable and prudent alternatives of the U.S. Fish and Wildlife Service Biological Opinion on the operation of Glen Canyon Dam (USFWS 1994). The hydrograph for this treatment is thoroughly described elsewhere (Trammell et al. 2002), but consisted primarily of a period of constant 8,000 cfs discharges from June 1, 2000 to September 30, 2000 with the intent of promoting improved

native fish rearing conditions through increased temperature and hydraulically stable near-shore environments. Preceding this prolonged constant 8,000 cfs discharge, there was a 52-day block of high (17,000 to 30,000 cfs) and generally constant discharge to mimic spring flooding during April and May. During the constant 8,000 cfs discharge in September, there were several spike flows to 16,000 and 30,000 cfs for up to four days with the intent of disadvantaging non-native fish.

Sampling during the LSSF indicated higher abundance of speckled dace *Rhinichthys osculus*, flannelmouth sucker *Catostomus latipinnis*, bluehead sucker *Catostomus discobolus*, and fathead minnow *Pimephales promelas* in backwater areas, particularly in the lower portions of Grand Canyon (Trammel et al. 2002). These results suggested some benefit to warm water fishes associated with LSSF. Unfortunately, few juvenile humpback chub were captured during LSSF, perhaps related to low production of young of year fish in the LCR during 2000 (Dennis Stone, U.S. Fish and Wildlife Service, Personal Communication).

2004 Experimental High Flow

Following large sediment inputs to the Colorado River from the Paria River in late summer and fall of 2004, a second experimental high flow was implemented from Glen Canyon Dam (hereafter 2004 EHF; Wright et al. 2005). In contrast to the 1996 EHF, the 2004 EHF occurred during November and with slightly lower discharge (41,000 cfs) and shorter duration (60 hours; Topping et al. 2006). As with the 1996 EHF, this management action was primarily focused on restoring shoreline sandbars. Much of the data analysis and reporting for this effort are still ongoing.

2003-2005 Non-native Fish Suppression Flows

Coupled with removal of non-native fish (see below), a program of increased flow fluctuations (termed NNFSF, non-native fish suppression flows) from Glen Canyon Dam was

implemented during January-March, 2003-2005 to suppress rainbow trout *Oncorhynchus mykiss* on a systemic basis by disrupting spawning and rearing. Korman et al. (2005) conducted extensive studies on the spawning and rearing success of rainbow trout during the NNFSF. These studies also investigated the extent of spawning in the Colorado River and tributaries between River Mile 0 (RM 0) at Lees Ferry and RM 62 near the confluence of the LCR. Korman et al. (2005) concluded that these flows were likely ineffective at substantially reducing rainbow trout recruitment because of sub-optimal timing (i.e., too early-in the year) and possible compensatory survival at older ages. Based on surveys of available spawning habitat and density of young of year rainbow trout between RM 0 and RM 62, they further concluded that NNFSF likely did not affect rainbow trout reproduction downstream of RM 0 since there was little to no evidence of reproductive activity in this reach during 2004.

2003-2006 Mechanical Removal of Non-native Fish

This effort removed over 23,000 non-native fish between RM 56.3 and 65.7 between January 2003 and August 2006. Concurrent with these removals, the fish community composition within this reach shifted from one being numerically dominated by rainbow trout (>90%) in 2003, to one dominated by native fishes and the non-native fathead minnow (>90%) in 2006. Though trends in the abundance of rainbow trout in both the removal and the control reaches imply a systemic decline in rainbow trout unrelated to removal efforts, mechanical removal also contributed to the shift in community composition. Motivation, methodology, and results of the non-native fish removal program are presented in Chapter 2.

Description of Uncontrolled Factors

Below I summarize some of the uncontrolled factors influencing both fish population dynamics and the ability to detect potential fish population responses.

Paria, Little Colorado, and Colorado River Hydrology

Variability in the Paria, Little Colorado, and Colorado Rivers hydrology all potentially affect fish populations in the Colorado River. Seasonal and episodic freshets in the Paria River are of much smaller discharge than the Colorado River (Figure 5-1), yet in the post GCD system, the Paria River is the largest source of fine sediment (Wright et al. 2005). As a result, flooding in the Paria River is a dominant driver of turbidity in downstream portions of the Colorado River. Because turbidity decreases primary and secondary production (Kennedy and Gloss 2005), the Paria River is a major factor structuring the downstream aquatic community both in terms of food resources (Carothers and Brown 1991) and foraging efficiency for sight feeders such as rainbow trout (Barrett et al. 1992). Examination of the Paria River hydrograph (Figure 5-1) demonstrates the “flashy” character of this system and reveals major fall flooding during 1997-2000, 2004, and 2006. Conversely, 1995-1997 and 2001-2003 were periods of relatively less flooding and with corresponding lower turbidity downstream from the Paria River confluence.

The LCR is also a major source of fine sediment to the system with a corresponding influence on turbidity. In contrast to the Paria River, large floods in the LCR are frequently of equal or greater discharge than the post-dam Colorado River (e.g., 1992 and 2002 events; Figure 5-1). These events not only increase turbidity, they also transport large numbers of native and non-native fish to the Colorado River (Valdez and Ryel 1995; Stone et al. 2007). In turn, results of fish sampling (e.g., species and length composition and catch rate) downstream of the confluence can be highly influenced by recent LCR hydrology.

Annual release volume from Glen Canyon Dam is influenced by storage capacity in Lake Powell, annual inflow volume to Lake Powell, and a set of laws and regulations aggregately termed “The Law of the River”. During periods of high storage capacity and low annual inflow,

relevant policies guarantee a minimum annual release volume of 8.23 million acre feet (maf) of water. During periods of lower reservoir storage and larger annual inflows, annual release volumes may exceed this amount. Since 1990, annual release volume exceeded 8.23 maf in 1995-2000 (Figure 5-1). Though the relationship between annual release volume and fish population dynamics remains unclear, Paukert and Rogers (2004) found a positive relationship between annual release volume and flannelmouth sucker condition factor. These authors hypothesized that greater annual volumes provide increased euphotic volume and therefore greater primary and secondary production.

Release Water Temperature from Glen Canyon Dam

Water temperature released from Glen Canyon Dam is largely dependent on the reservoir elevation in relation to the dam penstock depth. By 1973, the last vestige of the pre-dam thermograph disappeared as the reservoir filled to an elevation promoting annual hypolimnetic releases of between 7° and 12° C (Vernieu et al. 2005). The reservoir water levels fell during a drought in 2000-2005 prompting partial epilimnetic releases and the warmest release water temperatures since the before the reservoir filled. These warmer water releases, coupled with further downstream warming during the summer months, resulted in significantly increased water temperature in the Colorado River near the LCR confluence during 2003-2006 as compared to 1990-2002 (Figure 5-2). Though water temperatures during 2003-2006 were still below pre-dam values, they are much closer to those required for successful spawning and rearing by warm-water adapted native fishes (Hamman 1982; Valdez and Ryel 1995), and should be conducive to increased growth of humpback chub *Gila cypha* (Chapter 3).

Juvenile Native Fish Production in the Little Colorado River

Native fish production in the LCR is influenced by a host of factors controlling egg, larval, and juvenile survival. Dominant factors likely include: hydrology, temperature, food resources,

parasite infestation, and predation risk. As mentioned above, freshets in the LCR tend to increase the abundance of young fish in the mainstem downstream of the confluence, particularly associated with late summer rainstorms (Valdez and Ryel 1995). Valdez and Ryel (1995) suggest that survival rates of these young native fish attempting to rear in the mainstem is extremely low given post-dam conditions. It is, therefore, easy to conceive how LCR freshets may affect year class strength if a significant portion of a cohort must attempt to rear in the mainstem. Conversely, that portion of the cohort remaining in the LCR may experience a compensatory increase in survival and ultimately contribute significantly to recruitment.

Valdez and Ryel (1995) hypothesized that flooding activity in the LCR tends to disadvantage non-native fish and cleanse spawning gravels. This is the argument provided to explain the very large number of young of year humpback chub observed from the 1993 brood year (Valdez and Ryel 1995) following extensive flooding in late 1992-early 1993. Furthermore, these authors hypothesized that the 1993 brood year consisted of such large numbers of young humpback chub that LCR resources were insufficient for juvenile fish rearing – leading to reduced growth rates and condition, and prompting large numbers of fish to emigrate to the mainstem during July 1993 base flow conditions. Clearly, it is difficult to predict how LCR hydrology may affect native fish production and recruitment.

Another factor potentially influencing native fish production in the LCR is infection by the non-native Asian Tapeworm *Bothriocephalus acheilognathi* and the copepod *Lernaea cyprinacea*. These parasites are present in the LCR and both humpback chub and speckled dace appear to be particularly susceptible to infection (Choudhury et al. 2004). Hoffnagle et al. (2006) demonstrated diminished condition of humpback chub infested with these parasites and suggested sub-lethal and lethal effects.

How Are Fish Populations Affected by Adaptive Management Actions and Uncontrolled Factors?

The GCDAMP is fortunate to have long-term time series measures of the relative abundance of native and non-native fish as indexed by electrofishing catch rate in the mechanical removal reach (Figures 5-3 and 5-4), and by hoop net catch rate in the mainstem downstream from the LCR confluence (RM 63.7-64.2; Figure 5-5). These measures, along with average size (Figures 5-6 through 5-8), provide relatively good information to infer changes in population demography over time.

Has Increased Turbidity Affected Fish Populations in Grand Canyon?

Turbidity is hypothesized to affect fish populations via a suite of direct and indirect mechanisms. Decreased water clarity should generally result in reduced autochthony (Yard 2003) potentially limiting food resources for some fishes. However, increased tributary discharge may also result in increased detritus available for consumption by simuliids – a dominant food item for fish species downstream of the Paria River and LCR (Kennedy and Gloss 2005). Turbidity may also affect foraging efficiency, particularly for rainbow trout (Barrett et al. 1992). Thus, turbidity may mediate negative interactions between non-native and native fish (Gradall and Swenson 1982; Gregory and Levings 1998; Johnson and Hines 1999) and possibly represent a mortality source for rainbow trout (Chapter 2).

With these hypotheses in mind and given minimal flooding activity from the Paria River during 1995-1997 and 2001-2003, I would predict that the abundance of rainbow trout in the mechanical removal reach should be highest during these time periods. Examination of the catch rate data indicates that rainbow trout abundance was high during 2001-2003, but not during 1995-1997 (Figure 5-3). Similarly, if native fish are advantaged by high turbidity conditions, their abundance should be lower during these time periods. Available data indicate no strong

trends in native fish abundance in these time periods as indexed by either electrofishing or hoop net catch rate (Figure 4-5). Humpback chub recruitment estimates from the age-structured mark-recapture model (Chapter 4) suggest an increasing recruitment trend beginning with the 1995 brood year. Though turbidity may affect rainbow trout abundance in downstream reaches, there are clearly other controlling mechanisms such as immigration from the Lees Ferry reach (Chapter 2; Korman et al. 2005). Additionally, there does not appear to be a simple relationship between turbidity and native fish populations.

The preceding discussion illustrates the challenges involved in evaluating the impact of adaptive management experiments and uncontrolled factors on fish populations in Grand Canyon. For nearly every credible hypothesis suggesting a positive influence from turbidity, an equally credible contradictory hypothesis can be generated. Additionally, correlative analyses to assess various *a posteriori* hypotheses of cause and effect relationships provide weak inference at best (Yoccoz et al. 2001; MacKenzie et al. 2007). This is particularly true with regard to the highly variable and uncontrolled factors (e.g., tributary hydrology) and short duration adaptive management experiments (i.e., 1996 and 2004 EHF and LSSF).

Has Reduced Non-native Fish Abundance and Increased Temperature Affected Native Fish Populations in Grand Canyon?

The GCDAMP initiated the mechanical removal of non-native fish program (Chapter 2) in response to the increases in the abundance of non-native rainbow and brown *Salmo trutta* trout near the confluence of the LCR during 1996-2002 (Figure 5-3). Implicit in the action was the hypothesis that native fish are negatively impacted by non-native fish. More specifically, that juvenile native fish survival was negatively impacted by non-native fish via predatory and competitive interactions. If this hypothesis is correct, the abundance of juvenile native fish in the mechanical removal reach would increase after non-native removal. Additionally, the

removal effort was predicted to promote increased humpback chub recruitment associated with the 2003-2006 brood years.

Examination of electrofishing catch rate in the mechanical removal reach suggest an order of magnitude increase in the relative abundance of flannelmouth sucker and bluehead sucker between 2003 and 2006 (Figure 5-4). Increases in humpback chub and speckled dace are also apparent, though not as large. Hoop net catch rates of humpback chub also increased, particularly in late 2004-2006 (Figure 5-5). Additionally, the relative abundance of non-native fathead minnow increased markedly in 2005 and 2006 (Figure 5-3). Though these responses are consistent with predictions, it is not clear that these responses were caused in whole or part by diminished abundance of rainbow and brown trout.

The mechanical removal of non-native fish coincided with the warmest water temperatures in the mainstem Colorado River near the LCR confluence observed since before 1990 (Figure 5-2). Since there is near perfect temporal correlation between these factors both hypothesized to control native fish survival, it is difficult to evaluate their effects separately. Indeed, these factors acting in combination likely have a multiplicative effect on juvenile fish survival through increased growth of native fish, increased food resources, and decreased predation risk (Paukert and Petersen 2007).

Paukert and Petersen (2007) used bioenergetics models to evaluate the effects of increased water temperature on the growth, food consumption, and rainbow trout predation on juvenile humpback chub. Their results indicated that an 8g humpback chub could realize a 287% greater annual increase in mass under the 2005 thermograph as compared to mean 1993-2002 water temperatures. They further predicted that the 2005 thermograph would reduce the time juvenile chub were vulnerable to predation by 2-3 months. Paukert and Petersen (2007) also predicted

that the rainbow trout population in the mechanical removal reach annually consumed more than 18,000 kg of invertebrates. If food availability is a limiting factor for native fishes in Grand Canyon, liberation of these resources may have significantly increased their growth and survival.

The average length of native fish captured with electrofishing provides some evidence of increased growth and survival consistent with the predictions of Paukert and Petersen (2007). The declining trend in both flannelmouth sucker and humpback chub TL is a result of a larger fraction of smaller fish in the electrofishing catch during 2005 and 2006 than previous years (Figure 5-7). This is particularly evident for flannelmouth sucker as the 2006 length frequency distribution displays multiple modes consistent with several successful year classes (Figure 5-9). The increasing trend in speckled dace TL is consistent with the hypothesis of increased growth in 2005 and 2006 (Figure 5-7). The sudden appearance of adult bluehead sucker in 2002-2006 electrofishing samples is puzzling and is most consistent with immigration of adults from the LCR (Figures 5-4 and 5-7). Sampling by U.S. Fish and Wildlife Service personnel in the LCR has indicated large increases in bluehead suckers during 2006 (Van Haverbeke and Stone 2007) in support of this hypothesis. Increased size of humpback chub captured in hoop nets in 2005-2006 also supports the hypothesis of increased growth and survival, as this gear seldom captures adult fish in the mainstem Colorado River (Figure 5-8). However, as described above, interpreting patterns of relative abundance or length composition of juvenile fish is complicated by LCR hydrology and associated fish migration.

Conclusions and Recommendations

Index data from electrofishing and hoop net sampling in the mechanical removal reach indicate an increase in native fish abundance in 2005-2006, particularly for the sucker species. These changes in abundance are consistent with the predicted response to removal of non-native fish in this reach, but are also consistent with predictions of increased water temperature. Thus,

it is not possible to determine which factor is most responsible for the changes. Nevertheless, from an adaptive management perspective, there is good evidence that a successful policy with respect to native fish conservation may involve at least one of these factors.

A strategy that could be employed to determine the relative influence of these factors is to manipulate the system so that one of the factors remained at the present state while the other was varied. Perhaps the most tenable option to achieve this circumstance would be for the GCDAMP to continue non-native fish control and wait for wetter hydrology to raise reservoir levels and decrease release temperatures (though such hydrology may not soon occur according to Seager et al. 2007). If under these conditions native fish abundance and subsequent recruitment remained high, the conclusion would be that interactions with native fish were the dominant factor. In contrast, if native fish resources suffered, the conclusion would be that water temperature was the dominant factor. This latter conclusion would lend support to construction of a selective withdrawal structure on Glen Canyon Dam in order to provide control of release water temperature. If warmer release water conditions persist, there would be limited ability to discriminate among these two factors, but additional evidence might accumulate supporting the success of the combined factor policy. This would also have the benefit of achieving the primary program objective of native fish conservation.

However, two GCDAMP review panels have concluded that the risk to native fish may be compounded by warmer water releases by favoring non-native fishes (Mueller et al. 1999; Garret et al. 2003). This advice might be interpreted to be wary of transitory behavior of native fish populations following onset of warmer water conditions. Initial signs of native fish benefit could be short lived as the non-native fish community shifted to favor warm-water species potentially capable of even more detrimental interactions with native fishes than the present assemblage.

Additionally, such a shift in fish community composition might not be easily reversible in a short period of time, particularly with limited control of release water temperature.

The ultimate success of a native fish conservation policy should be evaluated in light of increased native fish recruitment. A policy that increased native fish survival for some life stage, but failed to promote recruitment to adulthood, could not be deemed successful. This observation highlights the importance of the humpback chub stock assessment program (Chapter 4). However, evaluating policy success solely on recruitment estimates may not allow critical insights into policy performance since recruitment to adulthood is the integration of conditions faced by a cohort for multiple years. Differential recruitment from both the LCR and the mainstem Colorado River is a further complication. Consider a situation where a management action is undertaken in the mainstem concurrent with uncontrolled factors benefiting rearing conditions in the LCR. If recruitment for those brood years is determined largely by the LCR and the management activity in the mainstem is ineffective, evaluation of the recruitment time series might erroneously lead managers to believe that activities in the mainstem represented a successful policy.

Because of these complications, I contend that a more rigorous mainstem monitoring program to estimate growth and survival of native fish is needed in order to fully evaluate adaptive management experiments. Such a program would need to monitor immigration of juvenile native fish from the LCR into the mainstem and the abundance of native fish in the mainstem near the LCR confluence. These data could then be used in a balance framework to estimate time specific apparent survival rate. Korman et al. (2005) have successfully implemented a similar framework to study the effect of dam operations on juvenile rainbow trout in the Lees Ferry reach. Though the Lees Ferry program benefits from having high densities of

fish and is not confounded by tributary hydrology, it might be possible to modify their approach and implement it to study native fish survival and growth dynamics in the mainstem Colorado River. This information, coupled with the ongoing stock assessment program, would significantly increase the ability of the GCDAMP to evaluate adaptive management experiments.

Williams et al. (2007) argue that critical elements of an adaptive management program require specification of explicit and measurable program goals and the ability to predict policy performance relative to those goals. The GCDAMP would benefit from additional specificity in program goals so that it is clear if and when a policy could be judged successful. As an example, the native fish index data suggests recent improved conditions for native fish, but without specific goals the program cannot judge whether the policy should be pronounced successful. The program could also benefit from additional predictive capability both to screen policy options and to formalize and evaluate alternative hypotheses of system behavior. As discussed by Anderson et al. (2006), predictive models of fish population dynamics in riverine systems should recognize and model the dynamic feedbacks among various trophic components and the forcing factors mediating such interactions. Apparently without recognizing it, these authors have described many of the elements contained in the Ecopath/Ecosim modeling framework (Christensen and Walters 2003). I recommend that the GCDAMP rely more heavily on these types of quantitative approaches to predict native fish population dynamics under alternative management policies.

With improved monitoring and predictive capabilities to evaluate explicit and measurable goals, I believe the GCDAMP will be well placed to better conceive and implement future adaptive management experiments. Such planning should recognize the uncontrolled variability in the system and select experimental design options to most effectively alleviate potential

confounding factors, while attempting to implement experimental policies most likely to achieve program goals. I contend that one of the biggest obstacles in this effort is the inability to implement experiments of sufficient duration and magnitude to provide measurable results. The mechanical removal effort combined with multi-year temperature modification has the potential to elicit effective learning and improved resource condition. The ultimate success of this effort will depend heavily on the commitment to subsequent well planned experimentation and monitoring.

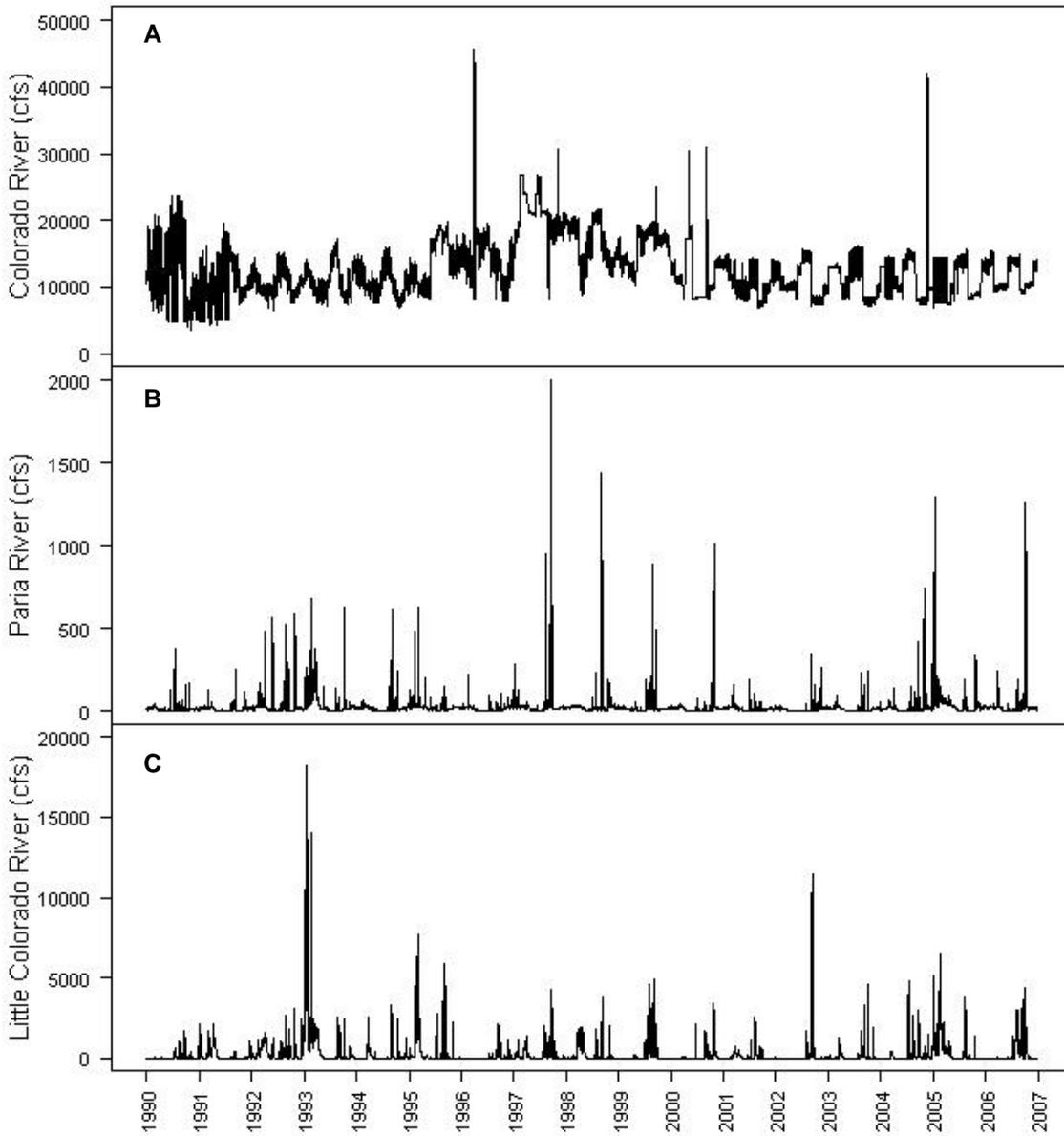


Figure 5-1. Discharge in ft^3/s (cfs) for the Colorado River at Lees Ferry (A), the Paria River at Lees Ferry (B), and the Little Colorado River at Cameron, AZ (C), 1990-2006.

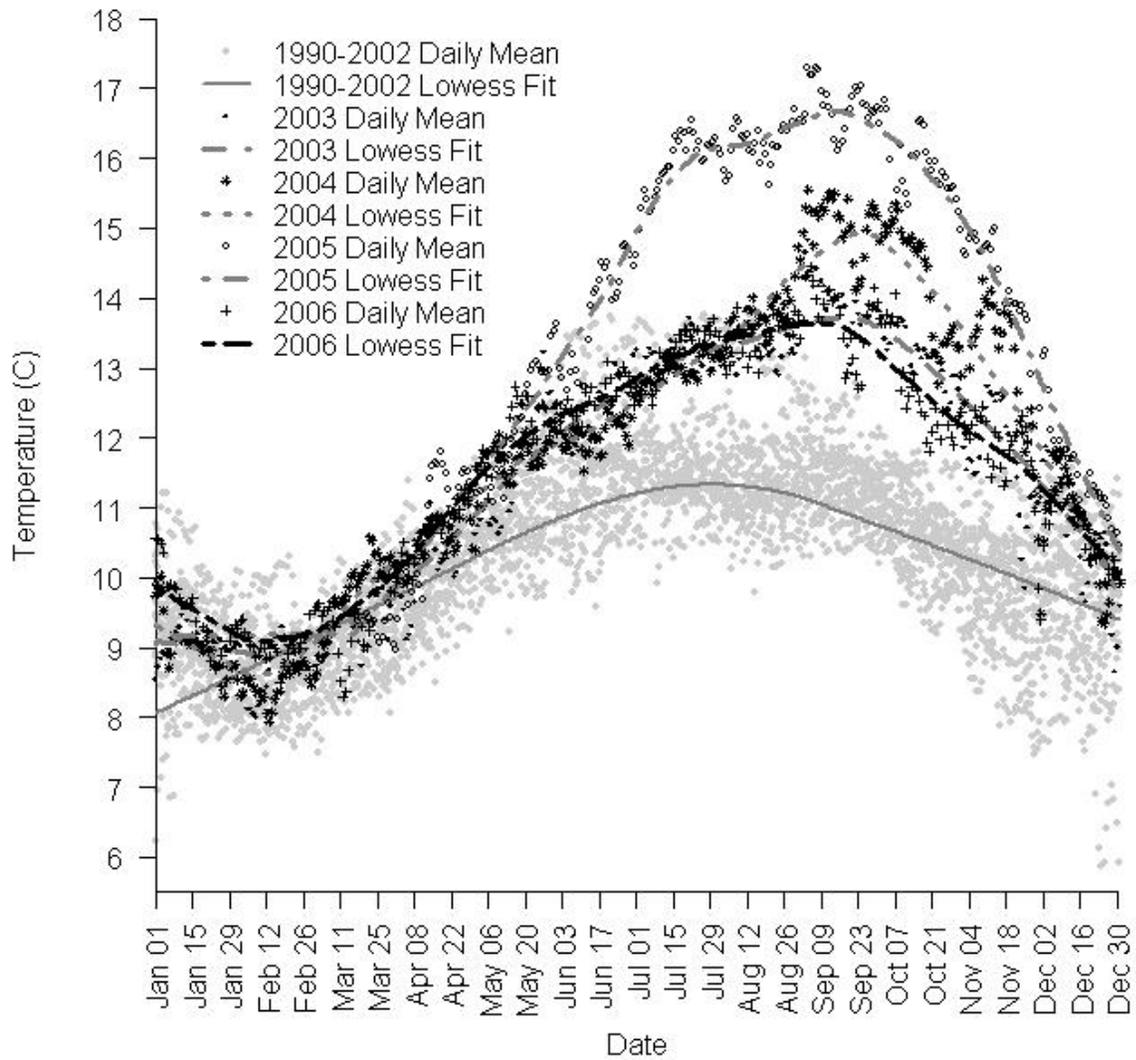


Figure 5-2. Daily mean water temperatures observed in the Colorado River at approximately river mile 61, 1990-2006. Lines indicate locally weighted polynomial regressions (Lowess) fits to the indicated data set.

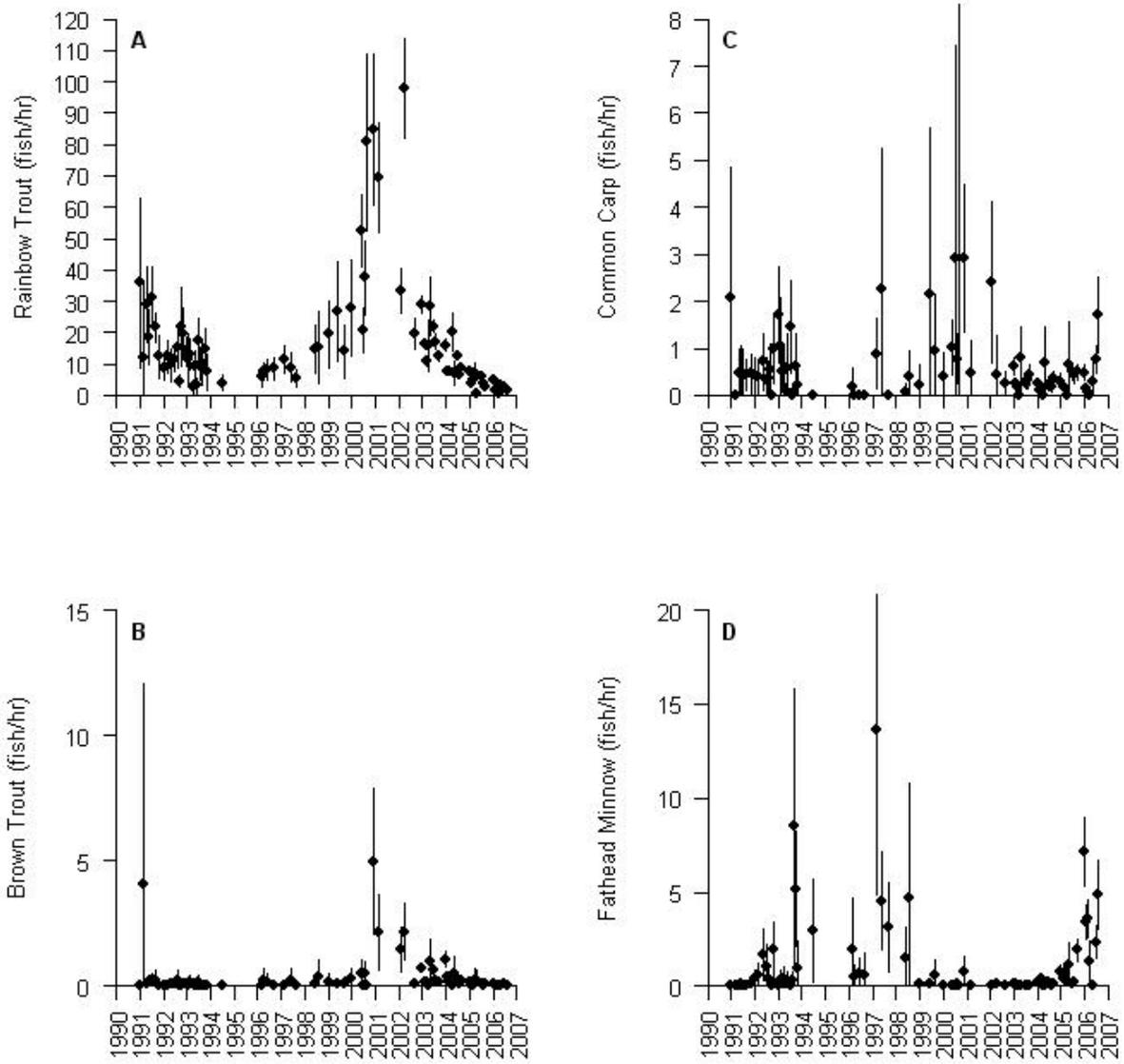


Figure 5-3. Monthly electrofishing catch rate (fish/hour) in the Colorado River between river mile (RM) 56.3 and RM 65.7 for rainbow trout (A), brown trout (B), common carp (C), and fathead minnow (D). Error bars represent 95% confidence intervals.

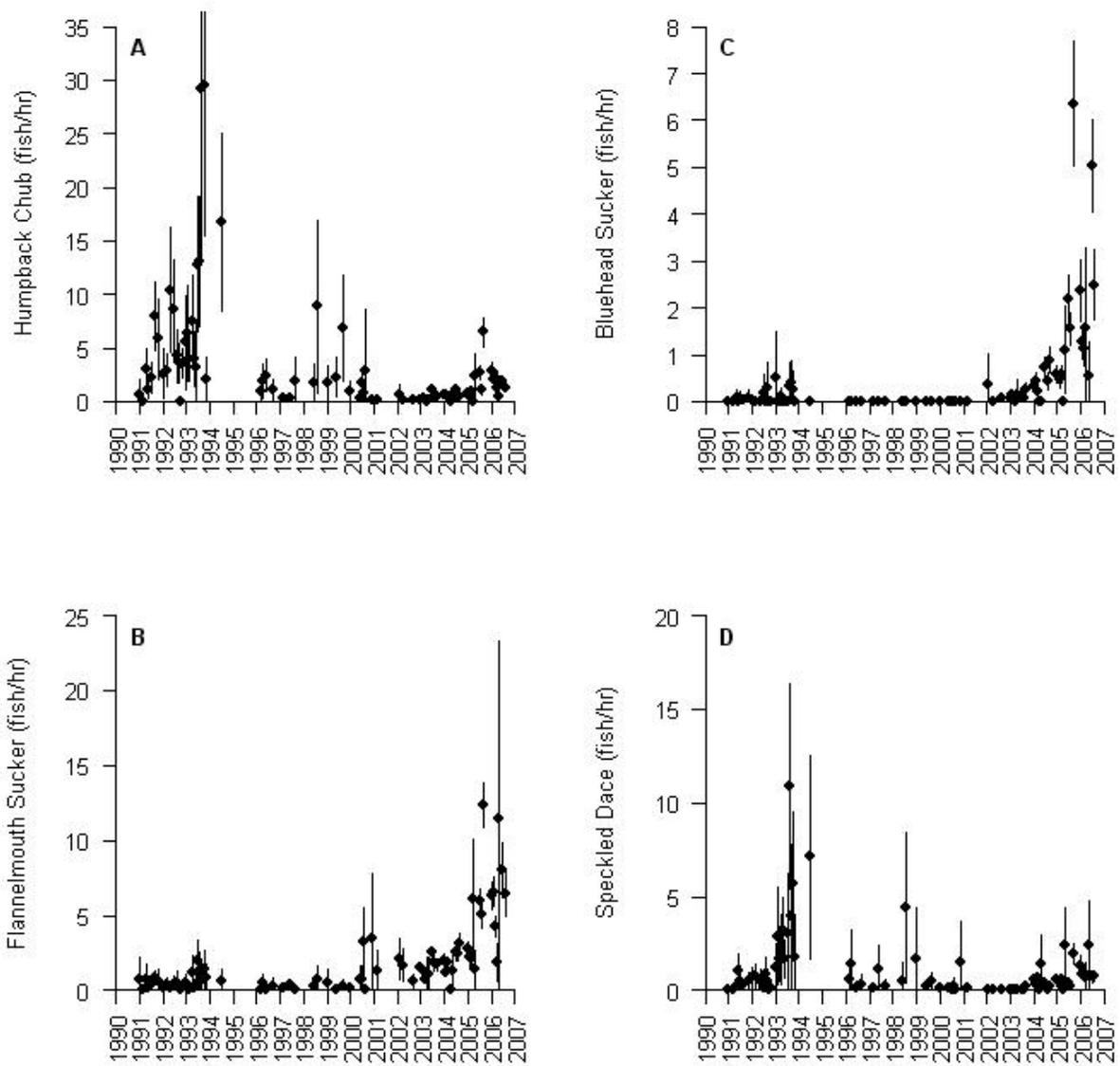


Figure 5-4. Monthly electrofishing catch rate (fish/hour) in the Colorado River between river mile (RM) 56.3 and RM 65.7 for humpback chub (A), flannemouth sucker (B), bluehead sucker (C), and speckled dace (D). Error bars represent 95% confidence intervals.

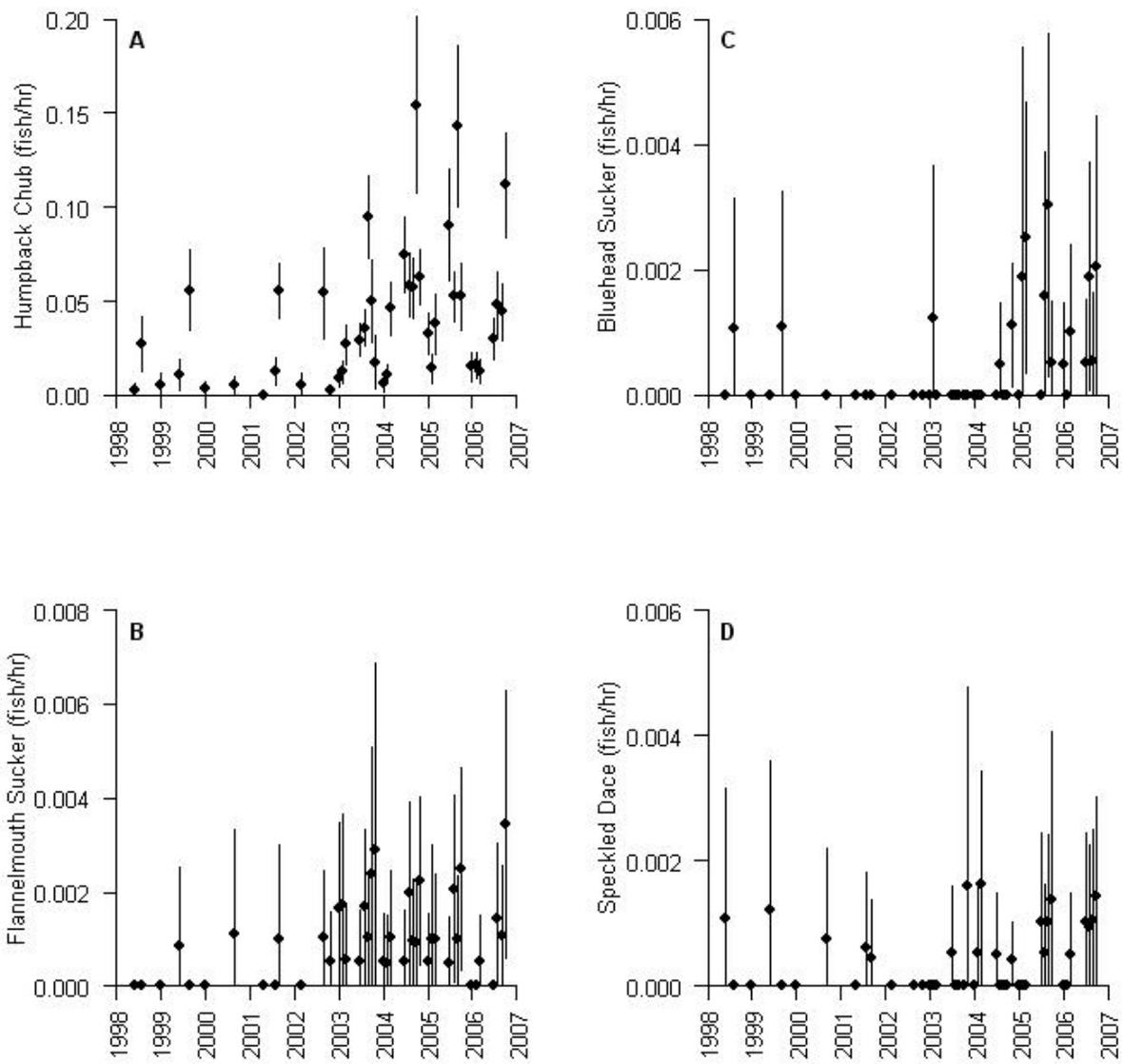


Figure 5-5. Monthly hoop net catch rate (fish/hour) in the Colorado River between river mile (RM) 63.7 and RM 64.2 for humpback chub (A), flannelmouth sucker (B), bluehead sucker (C), and speckled dace (D). Error bars represent 95% confidence intervals.

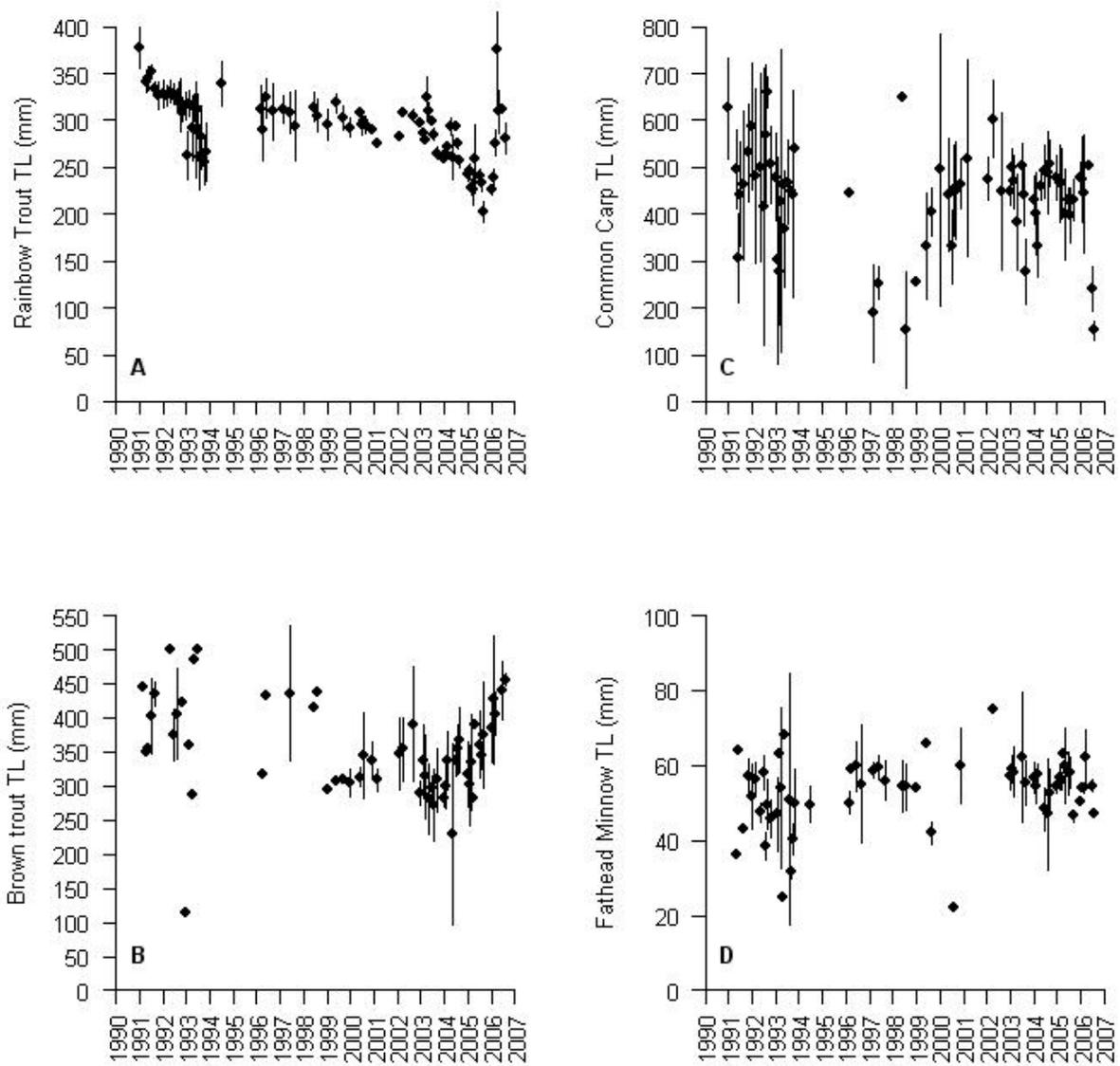


Figure 5-6. Monthly average total length (TL; mm) observed in electrofishing sampling in the Colorado River between river mile (RM) 56.3 and RM 65.7 for rainbow trout (A), brown trout (B), common carp (C), and fathead minnow (D). Error bars represent 95% confidence intervals.

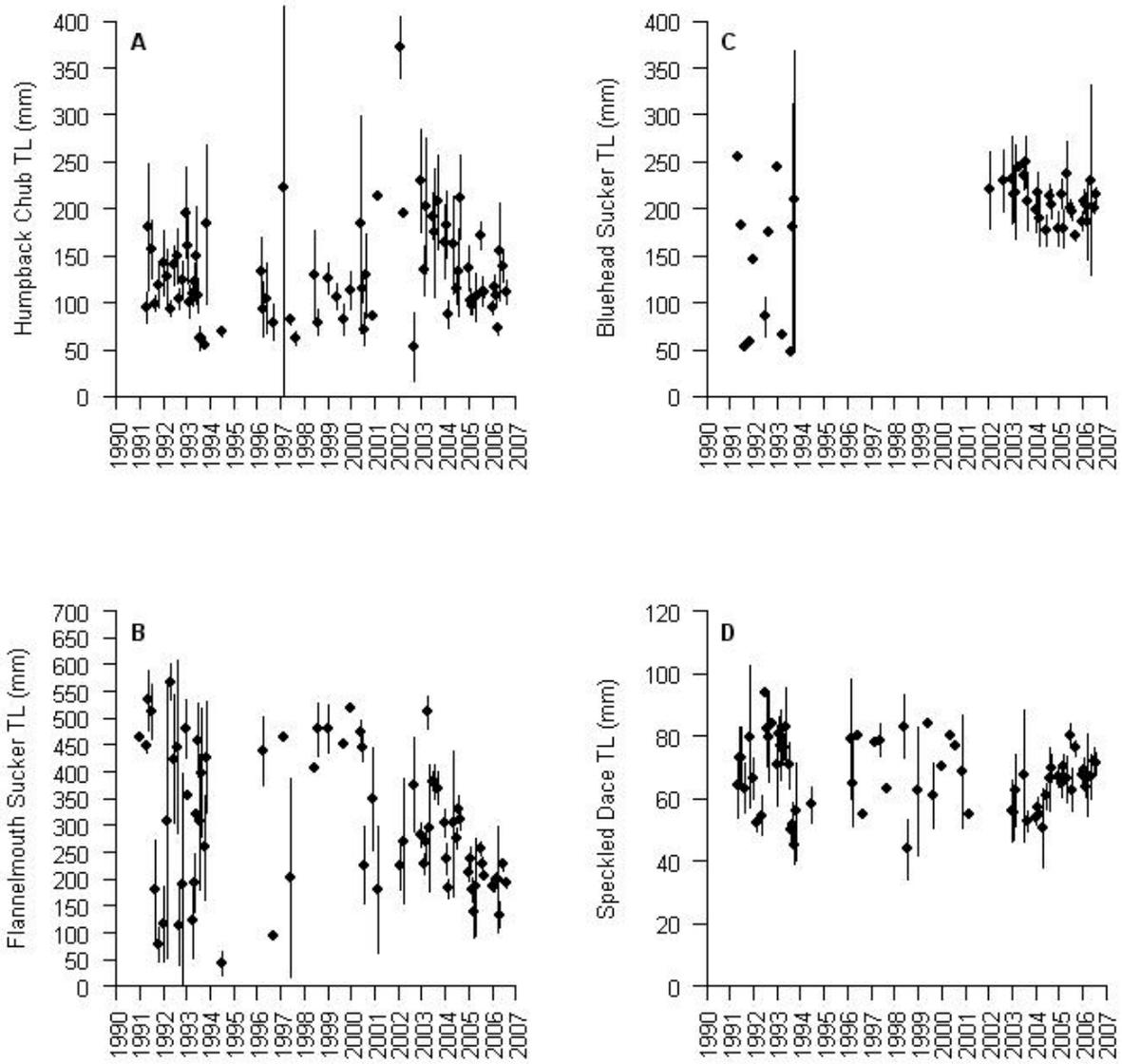
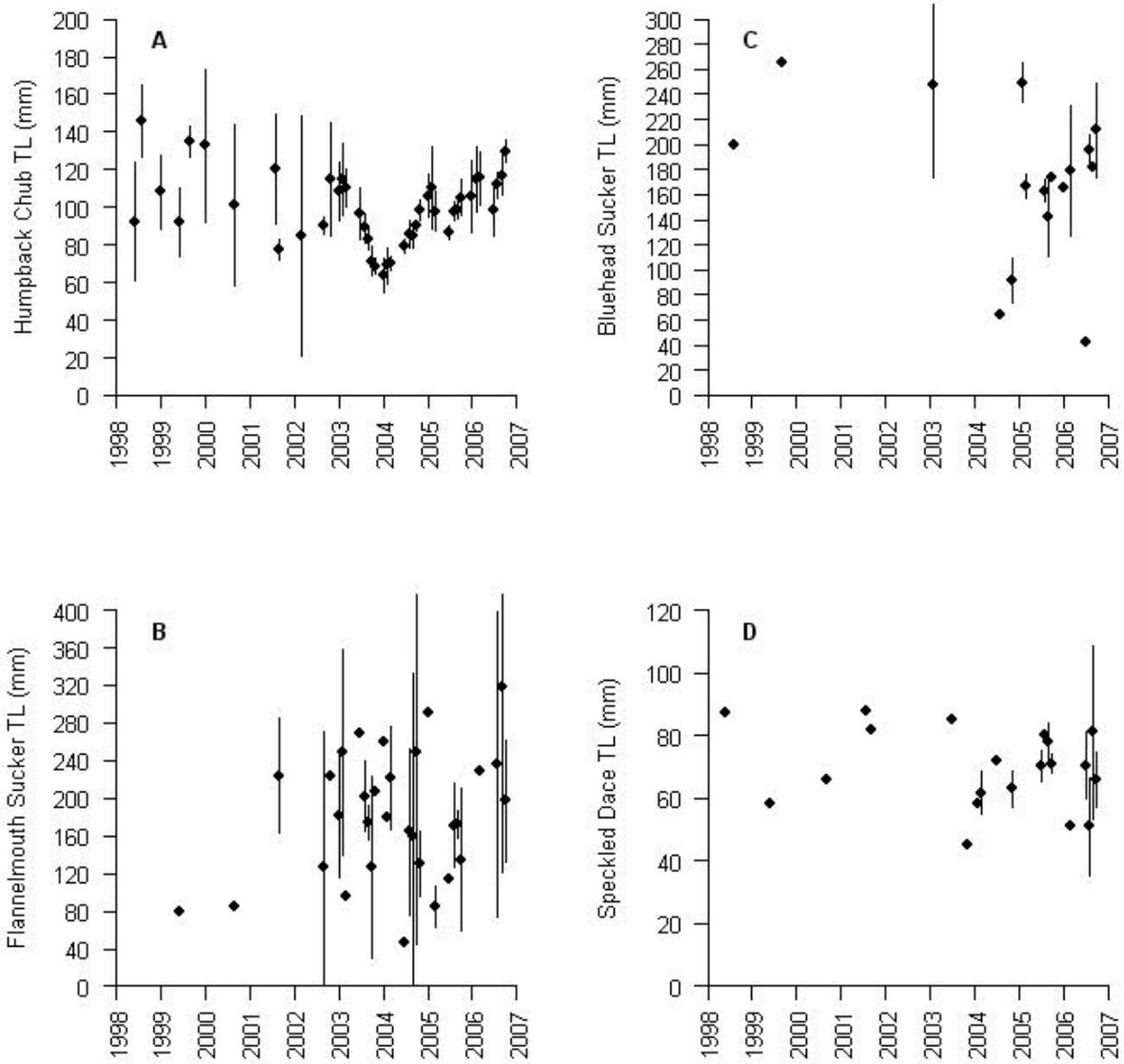


Figure 5-7. Monthly average total length (TL; mm) observed in electrofishing sampling in the Colorado River between river mile (RM) 56.3 and RM 65.7 for humpback chub (A), flannelmouth sucker (B), bluehead sucker (C), and speckled dace (D). Error bars represent 95% confidence intervals.



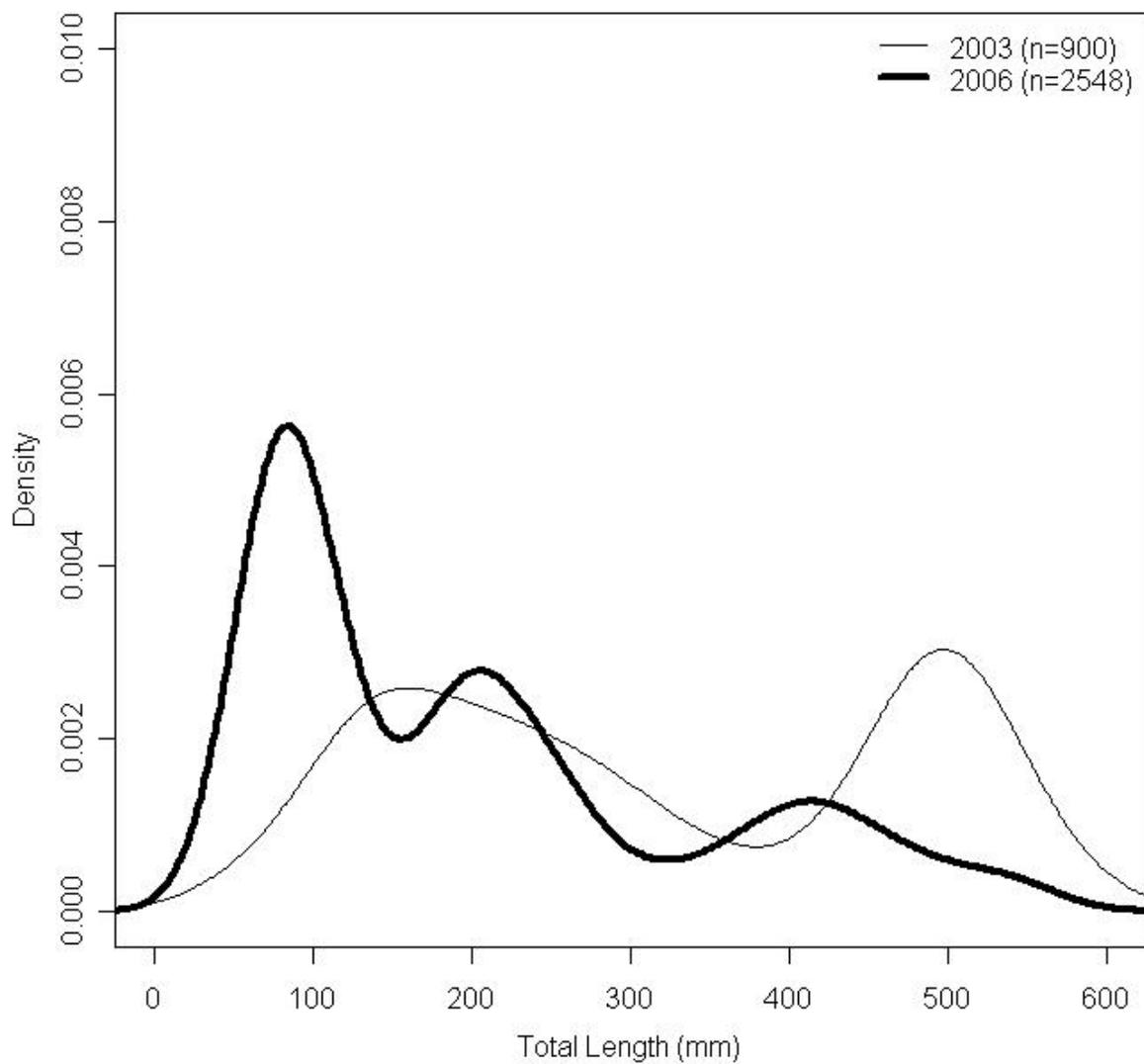


Figure 5-9. Smoothed kernel density plot of the total length of flannelmouth sucker captured with electrofishing in the mechanical removal reach during 2003 and 2006. Numbers in the legend represent total number (n) of fish captured.

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BIOGRAPHICAL SKETCH

I was born in Phoenix, AZ in 1967 to Lewis and Jan Coggins. After attending primary school in both Phoenix and in Tuba City on the Navajo Reservation in Northern AZ, I graduated from Coconino High School in Flagstaff, AZ in 1985. During these formative years, I was fortunate to have a father who loved exploring Northern Arizona and particularly Marble and Grand Canyons. Our explorations and his teachings of the natural world had a profound effect on my career choices. After graduating from the University of Arizona in 1990 with a degree in ecology and evolutionary biology, I moved to Alaska where I worked as a fisheries biologist for the Alaska Department of Fish and Game in Bristol Bay and Kodiak. I married Jennifer (Gape) Coggins in December 1993 and our first child, Elizabeth Tate, was born in Kodiak, AK in 1997. While employed by the state, I was able to pursue and earn a master's degree in fisheries from the University of Alaska, Fairbanks, in 1997, under the guidance of Dr. Terry Quinn. I returned to Flagstaff in 1999 to study Grand Canyon fishes with the U.S. Geological Survey. In August 2002, our second child, Annie Rose, was born in Flagstaff, AZ.