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[Article]

Abundance Trends and Status of the Little Colorado River Population of Humpback Chub

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Abstract.—The abundance of the Little Colorado River population of federally listed humpback chub *Gila cypha* in Grand Canyon has been monitored since the late 1980s by means of catch rate indices and capture–recapture-based abundance estimators. Analyses of data from all sources using various methods are consistent and indicate that the adult population has declined since monitoring began. Intensive tagging led to a high proportion (>80%) of the adult population being marked by the mid-1990s. Analysis of these data using both closed and open abundance estimation models yields results that agree with catch rate indices about the extent of the decline. Survival rates for age-2 and older fish are age dependent but apparently not time dependent. Back-calculation of recruitment using the apparent 1990s population age structure implies periods of higher recruitment in the late 1970s to early 1980s than is now the case. Our analyses indicate that the U.S. Fish and Wildlife Service recovery criterion of stable abundance is not being met for this population. Also, there is a critical need to develop new abundance indexing and tagging methods so that early, reliable, and rapid estimates of humpback chub recruitment can be obtained to evaluate population responses to management actions designed to facilitate the restoration of Colorado River native fish communities.

The humpback chub *Gila cypha*, a cyprinid endemic to the Colorado River basin, was described in 1945 from a specimen captured near the mouth of Bright Angel Creek in Grand Canyon, Arizona (Miller 1946). This morphologically unique cyprinid has been characterized as the most specialized member of the genus *Gila* and is highly adapted to exist in turbulent canyon-bound reaches of the Colorado River basin (Minckley 1973). This species was included on the federal list of endangered species in 1967 (USOFR 1967) and is protected under the Endangered Species Act (ESA) of 1973. Presently, only six populations are known, five in the upper basin of the Colorado River (i.e., above Lees Ferry) and one in Grand Canyon (Valdez and Ryel 1995).

The humpback chub population in Grand Canyon is centered near the confluence of the Colorado and Little Colorado rivers (LCR) in Grand Canyon (36.19°N, 111.79°W; Kaeding and Zimmerman 1983; Douglas and Marsh 1996; Gorman and Stone 1999). Valdez and Ryel (1995) describe the humpback chub distribution as consisting of nine aggregations throughout Marble

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and Grand canyons. However, only the aggregation near the confluence of the LCR and Colorado River (hereafter referred to as the LCR population) is known to successfully reproduce. Because of abiotic and biotic changes in the Colorado River after the construction of Glen Canyon Dam in 1963, the LCR population relies on the LCR as its primary spawning and juvenile rearing habitat (Gorman and Stone 1999).

Humpback chub demonstrate potadromous spawning migrations between the Colorado River and the LCR (Gorman and Stone 1999). Recaptures of tagged animals suggest that the geographic extent of this population is the lower 15 km of the LCR and the Little Colorado River inflow reach of the Colorado River (LCR inflow reach, defined as approximately 9 km upstream and 11 km downstream of the confluence; Valdez and Ryel 1995). The spawning migration creates both difficulties and opportunities for monitoring the population. Typically, adult humpback chub stage near the mouth of the LCR in March and April, ascend into the LCR in April and May, and return to the LCR inflow reach over a protracted time period from June to September (Valdez and Ryel 1995; Gorman and Stone 1999). Though the existence of a spawning migration between the LCR inflow reach and the LCR is accepted, a number of uncertainties remain. The most important of these are the size or age at which fish begin to exhibit migratory behavior and whether a proportion of the adult population fails to migrate every year (i.e., skip spawn). Douglas and Marsh (1996) suggested that two populations exist: one resident population in the LCR and one that migrates between the LCR and LCR inflow reach. However, Gorman and Stone (1999) suggested that the majority of adult humpback chub larger than 300 mm total length (TL) live in the LCR inflow reach except during the spawning migration.

Because of ongoing management disputes related to water use issues within the Colorado River basin and the potential effect of these management actions on humpback chub population viability, a monitoring program coordinated by the U.S. Geological Survey, Grand Canyon Monitoring and Research Center (GCMRC), was developed to track changes in the abundance and recruitment of the LCR population. Information from this program is also potentially useful in evaluating the ESA recovery goals for humpback chub, which specify capture–recapture studies to estimate absolute population size and trend (USFWS 2002). The GCMRC program includes analyses of historical data, ongoing sampling, and external peer review (Kitchell et al. 2003). Here we describe a synthesis of data to characterize the dynamics of the population. We assessed humpback chub population status and trend using catch rate indices and capture–recapture-based abundance estimates from open and closed models. While each of these methods requires various assumptions, the results of the synthesis are clear: the LCR humpback chub population has steadily declined since at least 1989. We present these results and suggest strengths and weaknesses in the various approaches as related to stock assessment of the LCR population.

Methods

Field methods.—Repeated sampling for long-term population trends in native fish abundance began in 1987 with the initiation of standardized hoop net sampling in the lower LCR. During 1991–1995, intensive sampling was conducted both in the Colorado River and the LCR in conjunction with an environmental impact study of the operation of Glen Canyon Dam (USBOR 1995). Sampling in both the Colorado River and the LCR has continued from 1996 to the present, but at reduced intensity. Although sampling effort and research groups have varied across the study period, the methodologies and sampling personnel have remained fairly consistent (Table 1). Fish were predominately collected using hoop nets (0.5–1.0 m in diameter, 1.0–5.0 m long, 6-mm mesh, single or double 10-cm throat) and trammel nets (7.6–45.7 m long, 1.8 m deep, 1.3–3.8-cm inner mesh and 30-cm outer mesh) in the LCR (Douglas and Marsh 1996; Gorman and Stone 1999) and hoop nets, trammel nets, and pulsed DC electrofishing (Coeffelt Mark XXII CPS) in the Colorado River (Valdez and Ryel 1995).

Index-based assessments.—We analyzed two long-term catch rate data sets for trends in the abundance of the LCR population. The first data set consists of the hoop net catch rate in the lower LCR, which was collected annually for 20–30 consecutive days in April and May during the years 1987–1999 and 2002–2003. Hoop nets were deployed at 13 standardized locations in the LCR within 1,200 m of the confluence with the Colorado River. The nets were fished daily for about 24 h throughout the monitoring period. The second data set consists of the monthly trammel net catch rate in the LCR inflow reach. In various months between 1990 and 2003, trammel nets were deployed during crepuscular and night periods. Sample locations were chosen at slow-water and current separation points. We use the results of these two analyses as gross indices of long-term population trends with which to compare the estimated population sizes from the capture–recapture models described below.

Tagging-based assessments.—Between 1989 and 2002, over 14,500 unique humpback chub (TL $>$ 150 mm) were measured and implanted with passive

TABLE 1.—Sample sizes of humpback chub by year, gear type, and location. Values for nets are the numbers of net sets; values for electrofishing are the numbers of shoreline sections (typically 100–400 m in length) sampled. The Colorado River samples were collected in the Little Colorado River inflow reach (approximately 9 km upstream and 11 km downstream of the confluence with the Little Colorado River). The Little Colorado River samples were collected within 15 km of the confluence with the Colorado River.

	Colorado River			Little Colorado River	
Year	Electrofishing	Trammel netting	Hoop netting	Trammel netting	Hoop netting
1987				85	142
1988				179	399
1989				177	454
1990	20	142		73	356
1991	231	1,076	4	319	2,826
1992	407	847		198	3,712
1993	558	1,104	15	146	4,602
1994	37	19	2	103	3,885
1995	137			71	2,371
1996	89	122		4	1,114
1997	89	163		20	936
1998	70	42	372	27	1,435
1999	106	54	550	12	1,046
2000	225	344	284	7	2,700
2001	47	1,098	605	64	2,651
2002	168	120	199	1	2,998
2003	119	100	108	8	2,786
Total	2,303	5,231	2,139	1,494	34,413

integrated transponder (PIT) tags to provide a unique, long-term identification mark. Capture–recapture data were used in a simple, two-sample closed-population model to estimate population size ($\hat{N}$) and two Jolly–Seber-type open-population models to generate estimates of capture probability ($\hat{p}$), rate of population change ($\hat{\lambda}$), and population size (Seber 1982; Williams et al. 2002). We used an extension of the Jolly–Seber population model to incorporate information on age at first capture (Pollock 1981) to estimate mortality, capture probability, and LCR population size with the program MARK (White and Burnham 1999). We also used methods presented by Pradel (1996) to estimate the rate of population change directly without having to estimate population size.

In addition, we developed a new age-structured, open-population capture–recapture model (ASMR) similar to the Jolly–Seber models but developed specifically to address analysis needs related to this robust capture–recapture data set. The ASMR model predicts age at first capture from length, the numbers of marked and unmarked fish at risk of capture from the age-specific survival rate, and age- and time-specific capture probabilities. Details of the ASMR model are provided in the companion paper in this issue (Coggins et al. 2006, this issue).

Model background.—Capture–recapture methods have rigorous assumptions and are broadly defined as "closed" or "open" depending on whether the population is allowed to change over the sample interval (open models) or not (closed models). Short-term capture–recapture studies are usually closed-population estimates and are based on the assumption that all members of the population are vulnerable to sampling and that no animals leave or enter the population between sampling occasions. Open-population models allow for changes in the population due to births, deaths, and movement into and out of the area and are generally more suited for longer-term studies (Pine et al. 2003).

Most multiyear capture–recapture studies use some variation of the classic open Jolly–Seber model to estimate population size, recruitment, and survival (Jolly 1965; Seber 1965; Pollock et al. 1990). A key assumption of open-population models is that every animal (both marked and unmarked) present in the population during a sampling period has the same probability of being captured. Parameter estimates from open-population models can be biased if capture probabilities are heterogeneous (Pollock et al. 1990). In many fisheries applications, much of this heterogeneity in capture probability is related to animal age. Incorporating age information into the Jolly–Seber model reduces estimation bias by accounting for this heterogeneity in capture probability (Pollock 1981; Pollock et al. 1990).

Closed-population models.—Between 2001 and 2003, we made a series of two-pass, closed-population abundance estimates of humpback chub (TL $>$ 150 mm) in the lower 14.2 km of the LCR during two 12–14-d annual spring sampling trips. Population size and variance were estimated using a Chapman-modified,

TABLE 2.—Jolly–Seber and Pradel population trend models fit to humpback chub data, 1989–2002. The best-fitting model is the one with the lowest corrected Akaike information criterion (AIC_c) value.

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	Number of parameters
Jolly–Seber models					
Age-dependent survival; time-dependent capture probability	41,303.2	0.0	1.0	1.0	27
Time-dependent survival and capture probability	42,478.1	1,174.9	0.0	0.0	26
Fixed survival; time-dependent capture probability	42,718.8	1,415.6	0.0	0.0	14
Age-dependent survival and capture probability	45,072.5	3,769.3			28
Fixed survival and capture probability	47,188.8	5,885.6			2
Pradel models					
Time-dependent survival, capture probability, and rate of population change	99,755.7	0.0	1.0	1.0	38
Fixed survival; time-dependent capture probability and rate of population change	99,916.8	161.1	0.0	0.0	27
Time-dependent survival and capture probability; fixed rate of population change	100,014.6	258.9	0.0	0.0	28
Fixed survival; time-dependent capture probability; fixed rate of population change	100,441.1	685.3	0.0	0.0	16

length-stratified, Lincoln–Petersen abundance estimator (Seber 1982). Sampling for each abundance estimate consisted of a marking event (i.e., the first trip during each spring) and a recapture event (i.e., the second trip). We compare these recent estimates with earlier estimates presented by Douglas and Marsh (1996) and other closed-population estimates of humpback chub abundance (TL > 200 mm) in the LCR inflow reach (Valdez and Ryel 1995; Trammell and Valdez 2003).

Open-population models.—We used MARK (White and Burnham 1999) to estimate the mortality and capture probability for humpback chub (TL > 150 mm) from both age-structured (i.e., Jolly–age models; Pollock 1981) and non-age-structured models (i.e., traditional Jolly–Seber models; Seber 1982). Models were developed based on humpback chub life history (i.e., that they are long-lived fish with type III survival) and variability in sampling effort over time. We used the corrected Akaike information criterion (AIC_c; Burnham and Anderson 1998) as a guide in evaluating the fit of models built in MARK (Table 2). Each model was further evaluated to be the most biologically reasonable, parsimonious model. We compared age-independent models with the age-structured models (Table 2) to evaluate differences in the mortality estimates and capture probability trends resulting from the two model types. We estimated the population size of adult humpback chub as defined by the ESA recovery goals (i.e., TL > 200 mm, age-4 and older; USFWS 2002) using an age-structured Jolly–Seber model within MARK. Variance estimates were calculated using the Delta method, and confidence intervals were constructed following methods from Chao (1989) outlined in Williams et al. (2002). Because humpback chub are long lived and capture–recapture data were sparse for individuals greater than age 15, capture probabilities and mortality for fish older than age 15 were assumed to be equal to those of 15-year-old fish.

We estimated population change ($\hat{\lambda}$) across all ages (i.e., independent of age) in MARK using temporal symmetry models (TSMs) described by Pradel (1996; Table 2). Estimates of population growth are more robust to heterogeneity in capture probability than traditional Jolly–Seber models (Schwarz 2001; Hines and Nichols 2002). However, these models do assume that capture probability does not change radically over time. This approach to estimating $\hat{\lambda}$ is also dependent on the sampled area's remaining constant (e.g., if the sampling area expands during the study, biased population growth rate estimates are likely). To meet this assumption, the TSMs were fit with a subset of the data, namely, collections made only within the LCR. The population change estimates do not depend on the geographic closure of the sample area but do assume that the trends in the sampled population are indicative of the population as a whole. Previous investigations suggest extensive annual movement of fish between the LCR inflow reach and the LCR (see Introduction), so that trends generated from data collected in the LCR should be representative of the overall LCR humpback chub population.

We chose candidate TSMs to estimate population change based on the life history characteristics of humpback chub and sampling methodologies used throughout the study. The models had three parameters (survival, $\hat{\phi}$; capture probability, $\hat{p}$; and rate of population change, $\hat{\lambda}$), and each parameter was either time dependent or time independent. A value of λ in excess of one indicates a population increase, a value less than one indicates a population decrease, and a value equal to one indicates that the population is stable. When constraints (such as fixed time effects) are placed on either $\hat{\phi}$ or $\hat{p}$, part of the variation around each of these parameters is shifted to the model parameters without constraints. We followed the guidelines in Franklin (2001) to only place constraints

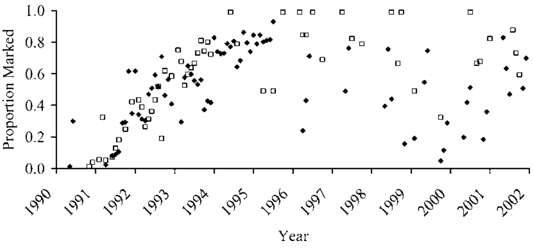

FIGURE 1.—Observed monthly mark rates of adult (age-4 and older) humpback chub captured in the Little Colorado River (diamonds) and the Little Colorado River inflow reach of the Colorado River (squares).

on the model parameter of interest. We again evaluated model fit using AIC_c (Table 2).

The annual ASMR model.—We used the ASMR model (Coggins et al. 2006) to estimate the age-specific mortality rate, the age- and time-specific capture probabilities, adult abundance, and recruit (age-2) abundance. Like the traditional Jolly–Seber type models, the annual ASMR model uses data aggregated within years and ignores multiple within-year recapture information. Three formulations (ASMR 1–3) of the overall model structure were used to explore alternatives in estimating time- and age-specific capture probabilities. We used a Markov chain–Monte Carlo algorithm to assess parameter uncertainty for each model formulation (Coggins et al. 2006).

Multistate movement models.—The ASMR and traditional Jolly–Seber models do not explicitly represent seasonal spawning movements between the LCR and the LCR inflow reach. Because sampling has historically been concentrated in the LCR (there were over 12,500 recapture events in the LCR versus about 1,100 in the LCR inflow reach), it is possible that the capture probabilities calculated from spatially aggregated data could lead to misleading population estimates (e.g., underestimates of the numbers of adult fish that are seasonally resident in the LCR inflow reach). To evaluate this possibility, we developed a spatially explicit model for individual recapture histories (Appendix), treating fish as being in two possible location states (the LCR or the LCR inflow reach) in each sampling month. The binomial likelihood function for this model was combined with the Poisson likelihood function for unmarked fish from the ASMR model (Coggins et al. 2006) to provide an overall model for the dynamics of both marked and unmarked fish. Our goal was to estimate age-specific mortality rates, monthly movement rates to and from the LCR, monthly capture probabilities in both locations, and the abundance of unmarked fish over time by maximizing this combined likelihood function. We also evaluated multistate movement models (Brownie et al. 1993; Hestbeck et al. 1991) in MARK that allow animals to move between strata and provide a probability of transitioning between strata.

Results

High mark rates (>80%) were achieved in the mid-1990s (Figure 1). Examination of the monthly mark rates among recapture locations (LCR versus LCR inflow reach) indicates that fish mix and move between the two areas, as there are similar patterns in overall mark rate with large changes in sampling intensity.

Index-Based Assessments

Long-term catch rate indices from the standardized hoop and trammel net sampling show 2–3-fold declines in catch rate from the late 1980s to the present (Figure 2). Although all monthly trammel net samples from the LCR inflow reach for 1990–2003 are presented, only samples from 1990–1993 and 2001 represent robust

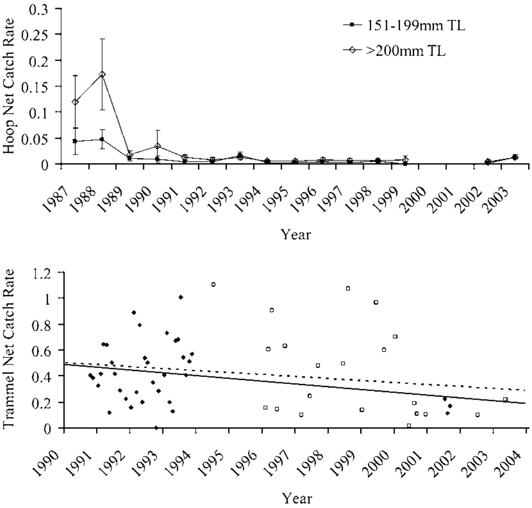

FIGURE 2.—Annual mean humpback chub catch rate using hoop nets (top panel; catch/h, with 95% confidence intervals) in the lower 1,200 m of the Little Colorado River (LCR) and mean monthly humpback chub (TL >200 mm) catch rate using trammel nets (bottom panel; catch $\cdot h^{-1} \cdot 100\ m^{-1}$) in the Little Colorado River inflow reach (LCR inflow reach) of the Colorado River. In the bottom panel, diamonds represent the extensive sampling that took place in 1990–1993 and 2001 and that was well distributed throughout the LCR inflow reach. Squares represent the limited sampling that took place in 1994–2000 and 2002–2003 and that, in some years, was concentrated near the confluence of the LCR. Though both regression lines (dashed, 1990–2003; solid, 1990–1993 and 2001) suggest a declining trend in abundance, the slope of neither regression is significantly different from zero ($P = 0.14$ for both regressions).

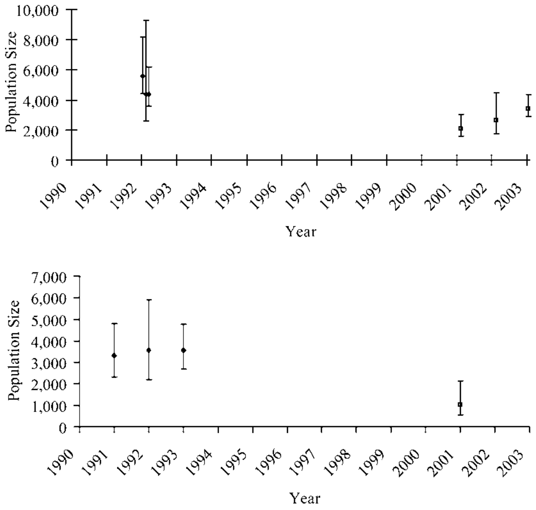

FIGURE 3.—Abundance estimates for humpback chub from closed-population capture–recapture models in the Little Colorado River (top panel; all estimates for fish larger than 150 mm total length) and the Little Colorado River inflow reach of the Colorado River (bottom panel; all estimates for fish larger than 200 mm total length). In the top panel, the estimates depicted as diamonds are from the studies of Douglas and Marsh (1996) and those depicted as squares are from this article. In the bottom panel, the estimates depicted as diamonds are from the studies of Valdez and Ryel (1995) and that depicted as a square are from the studies of Trammell and Valdez (2003). The error bars in both panels indicate 95% confidence intervals.

sampling coverage throughout the entire reach. Annual sample sizes in 1994–2000 and 2002–2003 were between 2% and 50% of the 1990–1993 average sample size, and in some years effort was focused near the LCR confluence. The lack of robust coverage and limited sampling in the mid to late 1990s suggest that comparing the 1990–1993 and 2001 data best depicts the overall trend of relative abundance. However, though both data sets suggest an overall decline in adult humpback chub abundance, simple linear regression analyses provide estimated slopes that are not significantly different from zero ($P = 0.14$ for both regressions; Figure 2).

Closed-Population Models

Population size estimates for fish (TL $>$ 150 mm) from the Chapman-modified, Lincoln–Petersen closed-population model ranged from about 2,000 in 2001 to about 3,400 in 2003, a decline from the 4,300–5,400 individuals estimated in the 1990s (Figure 3). Recent closed-population abundance estimates in both the LCR and the LCR inflow reach (Figure 3) suggest smaller population sizes in the early 2000s than in the early 1990s, although the precision for all Lincoln–Petersen estimates is low.

Open-Population Models

The bootstrap goodness-of-fit test in MARK was able to calculate a $\hat{c}$ to adjust for the overdispersion of the data. This estimate was used to evaluate the effects of overdispersion on AIC_c model selection. No changes in model selection were found across the range of $\hat{c}$ values evaluated. The best (lowest AIC_c) Jolly–Seber model for estimating mortality and capture probability was the age-dependent mortality and time-dependent capture probability model (Table 2). Annual mortality decreased with age, from about 68% for age-2 fish to about 16% for fish over age 15 (Figure 4). Mortality estimates from each of the ASMR model formulations were similar to those of the Jolly–age methods; these estimates were age dependent and ranged from about 65% for age-2 fish to about 18% for fish over age 15 (Figure 4).

Annual capture probabilities were consistent across all models. Annual capture probability for the Jolly–age model ranged from 0.04 to 0.51 (Figure 4). Capture probability from the three ASMR model formulations was similar, ranging from about 0.04 to 0.47 (Figure 4). In both the ASMR and Jolly–age models capture probability was highest in the early 1990s, when

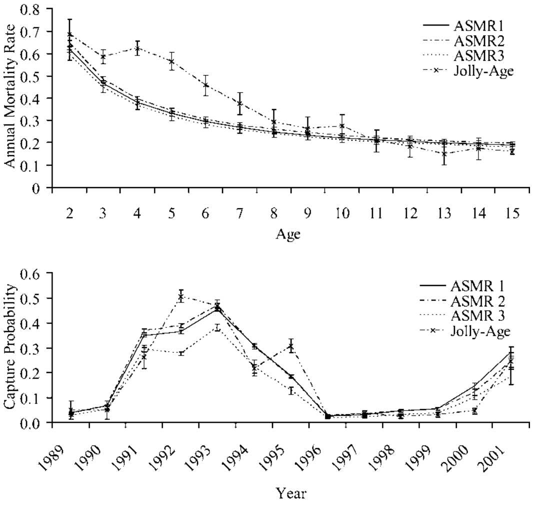

FIGURE 4.—Humpback chub annual mortality rates across ages (top panel) and capture probabilities across years (bottom panel) from the three formulations of the annual age-structured, open-population capture–recapture (ASMR) model and the age-structured Jolly–Seber model. The error bars on the ASMR estimates are 95% credible intervals from Markov chain–Monte Carlo sampling of posterior parameter distributions; those on the Jolly–Seber estimates are 95% confidence intervals.

sampling effort was high, and lowest in the late 1990s, when sampling effort was limited. More intensive sampling effort since 2000 has resulted in increased capture probability from about 0.10 to 0.25 (Figure 4).

Population Change

The best TSM model (Table 2) was a fully time-dependent model that did not place time constraints on any model parameter. The estimated annual rates of population decline across all years were variable because of poor model fit and imprecise estimates in 1996–1999, when sampling effort was low. Excluding these years, the geometric mean annual population change declined 14% annually ($\hat{\lambda} = 0.86$). In addition to using the fully time-dependent TSM model, we followed Franklin's (2001) suggestion to allow mortality and capture probability to remain time dependent and make population change time independent. The $\hat{\lambda}$ estimate for this model also indicates a negative trend in population growth of about 1% annually (SE = 0.006). Because humpback chub are a relatively large, long-lived species with few natural predators as adults, natural mortality should be relatively constant. To examine this, we fit a model with fixed survival and time-dependent capture probability and population change. The geometric mean of population change from this model was also negative, indicating a decline of about 4% annually. When the low sampling years of 1996–1999 are excluded, the overall findings for population growth indicate a decline of up to 14% annually.

Recruitment

As described in our companion paper (Coggins et al. 2006), the ASMR method allows for estimation of recruitment preceding the onset of sampling activities by utilizing back-calculation methods from virtual population analysis. The recruitment reconstructions among the three ASMR formulations suggest a peak in recruitment in the late 1970s to early 1980s of 13,500–18,500 age-2 fish (Figure 5). After that peak, an overall decline was evident to the early 1990s, when annual recruitment stabilized at about 2,000 age-2 fish. Recruitment may have stabilized or increased in the late 1980s before resuming its decline and again stabilizing through the 1990s.

Population Size

The best (i.e., biologically reasonable with a low AIC_c value) Jolly–age model for estimating the population size of age-4 and older humpback chub allowed mortality to vary with age and capture probability to vary with time. This model gave a better fit than non-age-structured models, demonstrating the strong affect of age on mortality (Table 2). Adult population estimates for this Jolly–Seber model ranged from about 14,500 in 1989 to about 2,400 in 2001 (Figure 5). Adult population estimates from the ASMR methods were similar across methods and ranged from 10,000–11,000 in 1989 to 3,100–4,400 in 2001 (Figure 5). Population estimates from both the Jolly–age and ASMR models were similar in magnitude and trend from the early 1990s through 2001.

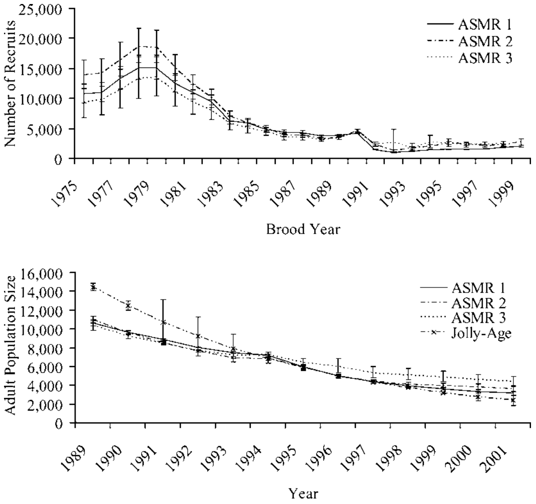

FIGURE 5.—Age-2 humpback chub recruitment by brood year estimated using the three formulations of the annual age-structured, open-population capture–recapture (ASMR) model (top panel) and adult (age-4 and older) humpback chub abundance estimates using the three formulations of the ASMR model and the age-structured Jolly–Seber model (bottom panel). The error bars on the ASMR estimates are 95% credible intervals from Markov chain–Monte Carlo sampling of posterior parameter distributions; those on the Jolly–Seber estimates are 95% confidence intervals.

Movement Model Results

Unfortunately, the combined movement and ASMR model is overparameterized and unable to provide reliable estimates of movement rates. For example, seasonal changes in the capture rates in the LCR can be explained equally well as the result of seasonal movement to the LCR inflow reach or seasonal changes in capture probability for fish still in the LCR. To complicate matters further, seasonal movement rates probably vary with age, younger fish being much less likely to migrate downstream after the spawning season (Gorman and Stone 1999).

To avoid the overparameterization problem, we used capture probabilities and population size from the ASMR models. We used this information to examine a series of seasonal movement rate scenarios designed to represent a range of possibilities for explaining the observed changes in catch rate in the LCR as well as the ontogeny of downstream migration. This is unsatisfactory as a long-term solution to the problem of disentangling movement and sampling intensity effects, but it allowed us to determine whether recognition of seasonal movement results in different abundance trend estimates than those obtained from the spatially aggregated methods. The results of these scenario tests were essentially the same as those of the annual ASMR and Jolly–Seber models shown in Figure 5. We were not able to fit multistate models in MARK for reasons similar to those described above for ASMR: low capture probabilities between states and the associated failure to estimate a transition probability.

Discussion

Population Trend and Abundance Assessments

All of our evidence implies that the adult humpback chub population in the LCR has experienced a large decline in abundance since 1989. Low sampling effort in the late 1990s (1996–1999), heterogeneity in capture probability related to age, and a large number of age-classes make complicated models with large numbers of parameters necessary to realistically estimate population parameters. However, population trend and annual population size estimates from all catch indices and methods indicate declines in population size of 30–60% since the early 1990s.

A comparison of the recent closed-population (Lincoln–Petersen) estimates with other closed-population estimates from the early 1990s indicates large declines in population size. The only published population estimates for humpback chub in the LCR are closed-population estimates of fish exceeding 150 mm TL by Douglas and Marsh (1996). Their estimates for the spring of 1992 ranged from about 4,300 to 5,500 (Figure 3). Our closed-population estimates from spring 2000–2003 ranged from about 2,000 to 3,400 fish (TL >150 mm; Figure 3). A comparison of closed-population estimates for fish occupying the inflow reach suggests a decline in adult abundance of about 60% between the early 1990s and 2001 (Valdez and Ryel 1995; Trammell and Valdez 2003). Although the assumptions of closed-population models (particularly the lack of animals moving into and out of the sampling area) may not have been met, Lincoln–Petersen estimates do allow some relaxation of this closure assumption (Pollock et al. 1990). For example, if unmarked animals immigrate into the sampling area, then the Lincoln–Petersen population estimate is not biased for the second sample. If both marked and unmarked animals emigrate between the samples, then the Lincoln–Petersen estimate is unbiased by emigration for the first sample. If only untagged animals emigrate between samples, then population size estimates would be negatively biased. However, it is unlikely that tagging effects only occurred in the early 2000s, and any bias caused by tagging probably occurred across all closed-population estimators in the 1990s and 2000s. As such, these estimates still serve as a relative indicator of an apparently large decline in the humpback chub population.

Using open-population models (Jolly–Seber and ASMR), the estimated LCR humpback chub population of adult fish (i.e., TL >200 mm, age 4 and older) is currently between 2,400 and 4,400 individuals (Figure 5). No other open-population size estimates have been published for this endangered species. The TSM open-population trend estimates provide an alternative to the age-dependent Jolly–Seber and ASMR model annual population estimates. Population growth estimates using TSM methods are robust to heterogeneity in capture probability under the assumption that the heterogeneity of the population does not change over time (e.g., capture rates for smaller fish are always lower than those for larger fish; Williams et al. 2002). Estimates of population growth also do not depend on geographic closure of the sample area as long as the measured population change of the sampled area matches that of the population as a whole (Schwarz 2001; Hines and Nichols 2002). All biologically reasonable TSM models, including constrained models that allow survival and capture probability to remain time dependent and population change to be time independent (Franklin 2001), indicate annual declines in population size of up to 14%. If the trends in annual estimated population size from open-, closed-, or TSM population models are examined, all approaches agree that the abundance of the LCR humpback chub population has declined significantly since at least the early 1990s.

Model Performance and Potential Assessment Errors

Abundance trends from the Jolly–age and ASMR models are similar, though the absolute abundance estimates differ between the two approaches, particularly in the early years of the study. These differences arise because the ASMR model predicts the number of fish available for capture by using the existing age structure of the population at the beginning of the study while the Jolly–age approach only uses information gained from recapture of tagged fish. Thus, as the tagged-fish population increases in the middle to late years of the study, the estimates from the two approaches converge (Figure 4).

The modeling approach for the age-structured Jolly–Seber and ASMR methods assumes that the initial age is correctly assigned based on size at first capture. Errors in initial age assignment could lead to a negative bias in population point estimates and to the "smearing" of estimated recruitment among cohorts in the ASMR model (Coggins et al. 2006). However, the population trend estimates from the TSM models are not age dependent, so that incorrect age assignment does not bias the population trend estimates from these methods.

The most critical assumption in the open-population models is that mortality rates of fish have been stable over time. Without this assumption, cumulative survivors of fish tagged in previous years cannot be safely used in calculating capture probabilities (and population estimates) for any one year. If, for example, there had been a high mortality rate of all fish in any one year, we would have seen a subsequent drop in the recapture rates of tagged fish from all previous years. But because sampling has changed over time (so that capture probabilities cannot be assumed to have been stable), we would attribute that drop in recapture rates to changes in capture probability rather than to the change in survival and we would therefore overestimate the number of surviving fish. We do not see trends in calculated monthly capture probabilities that would indicate such an error. However, the limited sampling effort in the late 1990s and the associated low catch rates make it difficult to evaluate the mortality and contribution of these year-classes to the overall population (new recruits to the population in the late 1990s were unlikely to be collected given the low sampling effort).

Is it possible that the adult population was in fact stable from the early 1990s to the early 2000s and that the analyses indicating large declines over this period have been misleading? All of the tagging-based estimates, using both open- and closed-population estimates, indicate such a decline, as does the trammel net catch rate index for the LCR inflow reach. Only the hoop net catch rate index of larger (TL >200 mm) fish does not show a decline over the key decade of intensive monitoring (the 1990s). However, the hoop net index suggests a decline from the beginning of data collection (i.e., the late 1980s) to the present.

For the tagging-based methods, there is no assumption that sampling methodology was consistent over time (i.e., capture probabilities are not assumed to have been stable). For the newer tagging estimates to be biased downward by 50% or more, these estimates would have to involve a doubling in recapture probability for marked fish relative to the probability of capturing an unmarked fish. In capture–recapture studies, such bias is typically due to restricting sampling to a reduced portion of the area occupied by the population (Seber 1982). There has been no such systematic reduction in area sampled within the LCR or the LCR inflow reach. There has been a restriction in the seasonal time coverage of sampling (from monthly sampling in the early 1990s to spring and fall events in the 2000s) that could have the same effect as a spatial restriction of sampling. This seasonality could cause downward bias in closed-population estimates based on monthly aggregated data, but it is difficult to see how it would affect the tagging methods based on annually aggregated data (annual ASMR, Jolly–Seber) where there is ample time (1 year) for marked and unmarked fish to mix before recaptures are used in estimation.

Another possible cause of differentially high capture probabilities for marked fish is the use of baited hoop nets in the LCR in 2001–2002. If that practice caused marked fish to be more likely to reenter nets than unmarked fish were to enter them in the first place, then capture probabilities were overestimated for both the closed- and open-population estimation methods. This would have caused underestimates of the numbers of unmarked fish at the end of 2002, and in the ASMR methods this would in turn have caused the back-calculated (virtual population) numbers of unmarked fish to be too low for at least the 1998–2001 time period. However, when we artificially inflated the 2002 unmarked numbers by a factor of two, we found that the back-calculated overall population trend from ASMR methods still indicated a decline of at least 40% over the last decade, even though the calculated 2001 population size was increased by only 500–800 adult fish. When we simply excluded the likelihood terms for catches of unmarked fish during the baiting period from the calculation of maximum likelihood estimates, there was no noticeable effect on the parameter estimates. When we attempted to directly estimate the relative capture probability for marked versus unmarked fish during the baiting period, we obtained estimates of 0.96–0.98 for all the ASMR (annual, monthly, and with or without movement) formulations, suggesting that there is no differential capture probability between marked and unmarked fish. These statistical checks do not prove that there was no strong differential baiting effect, but they do indicate that it is not parsimonious to assume such an effect.

Finally, the effects of random sampling variation on the ASMR estimates can be evaluated by comparing estimates of recruitment or adult population trends

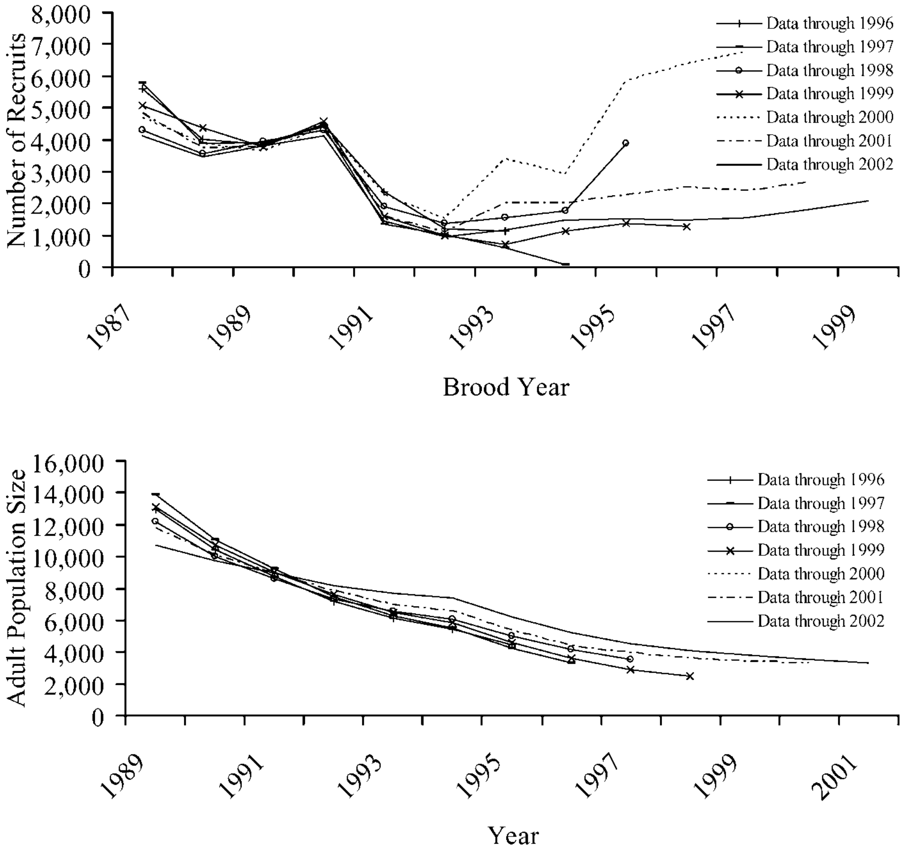

FIGURE 6.—Retrospective analysis of age-2 humpback chub recruitment by brood year (top panel) and adult (age-4 and older) humpback chub abundance (bottom panel) using the first of the three annual age-structured, open-population capture–recapture models (ASMR 1). The trend lines reflect analyses using annually truncated data sets beginning in 1989 and ending as specified in the legend.

based on different total numbers of years of sample data. This retrospective analysis (Figure 6) indicates that the recruitment estimates for the early years (brood years 1987–1992) of the sampling program are quite stable (i.e., are not altered by including more years of data), but that the estimates for the later sampling years are more variable. Additionally, the adult abundance estimates display more variability in both trend and magnitude and generally suggest lower initial abundance (1989) and higher terminal abundance (2001) when more years of data are considered. This trend in adult abundance is a result of changes in sampling intensity over time that essentially cause the model to trade off higher mortality estimates with lower capture probability during the years of low sampling intensity (1996–1999). As the analysis is supplied with more recapture data during the 2000–2002 time period, mortality estimates fall and the trend in adult abundance becomes less severe. Although the retrospective analysis does not suggest any severe structural problem in model formulation, as there is a general convergence in recruitment and abundance estimates during the early years of data collection, it does further reinforce the need to minimize the variability in sampling effort over time to minimize assessment errors resulting from parameter confounding.

All of the evidence suggests that the LCR humpback chub population suffered a major decline in adult abundance between the late 1980s and the present. All of the evidence also points to major declines in recruitment sometime in the 1980s. Though it is difficult to believe that the adult population size remained stable over the 1990s despite these recruitment declines, changes in sampling intensity between the early 1990s and early 2000s make it impossible to categorically deny that the adult population size has been stable since 1990. Efforts to improve monitoring since 2000 (e.g., baited hoop nets) have contributed to uncertainty in each of the assessments, as have reductions in overall sampling effort since 1995.

Management Implications

U.S. Fish and Wildlife Service recovery goals for humpback chub state that down-listing can proceed if the following developments occur over a 5-year period (USFWS 2002):

1. The trend in adult (age-4 and older) point estimates for each of the populations does not decline significantly;
2. Mean estimated recruitment of age-3 naturally produced fish equals or exceeds mean annual adult mortality;
3. Two genetically and demographically viable, self-sustaining core populations are maintained such that the point estimate for each core population exceeds 2,100 adults; and
4. Certain site-specific management tasks to minimize or remove the threats to the population are performed.

The results of the present assessment suggest that items 1–2 are not being met for the LCR population of humpback chub. Although our analysis suggests that there are currently more than 2,100 adults (item 3), at the present rate of population decline the abundance will fall below the minimum levels listed within 10–15 years.

In addition to the concerns they raise relative to ESA listing status, humpback chub are a central concern in the design of adaptive, experimental water management plans for the Colorado River in Grand Canyon. Planned and ongoing experimental treatments range from mechanical removal of nonnative fishes to warming of the Colorado River through temperature control devices on Glen Canyon Dam. Timely estimates of the responses in recruitment and abundance to these treatments are critical to the experimental program. None of the methods we have used to date give quick results, as all ongoing experiments require several years of monitoring. Our analyses of the historical data indicate that no existing monitoring method can provide reliable estimates of such responses for at least 3 years after the response has begun. It takes 2–3 years until the larger number of humpback chub recruits caused by an experimental treatment have reached the ages at which PIT tagging can begin to give estimates of abundance, and it may take several more years until a reliable estimate of the population trend caused by this recruitment change becomes evident. Earlier response indications may be obtained from index hoop netting in the lower LCR, but we do not consider such indices reliable enough to use as a guide for experimental treatment planning. There is a critical need to develop new abundance indexing and tagging methods that allow detection of abundance changes earlier in the life cycle.

Acknowledgments

This assessment of the Little Colorado River population of humpback chub is based on an assimilation of data collected between 1987 and present. Many individuals belonging to governmental, academic, and private institutions contributed to this database. We acknowledge all the individuals who have been involved in sampling humpback chub in the Grand Canyon. In particular, Arizona State University, Arizona Game and Fish Department, U.S. Fish and Wildlife Service, the Navajo Nation, and BioWest conducted field sampling that contributed importantly to the database and thus to current understanding of humpback chub. Permits allowing humpback chub research have been provided through time by Grand Canyon National Park, Arizona Game and Fish Department, U.S. Fish and Wildlife Service, and the Navajo Nation. We also thank J. Kitchell, C. Grimes, S. Lindley, D. Otis, J. Rice, C. Schwarz, M. Alldredge, S. Martell, and K. Pollock for providing an earlier review and much discussion on the ASMR method and humpback chub stock assessment in the Grand Canyon.

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Appendix Follows

Appendix: Likelihood Function for Tag Recaptures Including Movement

For each tagged fish *i*, we have a recapture history of the form $Y_t = \{0, k, 0, 0, \ldots, k, 0, \ldots\}$, where for each possible sampling date an observation of $y_t = 0$ denotes no recapture and an observation of $y_t = k$ denotes at least one recapture in location *k* (in this case either the Little Colorado River or the Little Colorado River inflow reach). We calculate the likelihood $P(Y_t)$ of each history using the recursive method reviewed in DeValpine and Hastings (2002), where $P(Y_t)$ is represented by the equation

$$P(Y_t) = P(Y_{t-1})P(y_t|Y_{t-1}). \tag{A.1}$$

To use this representation, we note that the probability $P(y_t|Y_{t-1})$ can be written as

$$P(y_t|Y_{t-1}) = \sum_s P(s_t|Y_{t-1})P(y_t|s_t, Y_{t-1}), \tag{A.2}$$

where s_t represents possible fish states (dead, alive in location 1, alive in location 2, etc.) and $P(y_t|s_t, Y_{t-1})$ is the probability of the observation y_t given that the fish is in state s_t (i.e., the capture probability for fish in state s_t at time *t* if $y_t > 0$, 1 minus this capture probability if $y_t = 0$). Representing $P(y_t|Y_{t-1})$ in terms of states s_t expresses the problem of calculating it as two simpler problems, namely, calculating location state probabilities $P(s_t|Y_{t-1})$ over time and the capture probabilities.

The location state probabilities are updated over time using Bayes' theorem. We first calculate the "posterior" probabilities as

$$P(s_t|Y_t) = p(y_t|s_t)P(s_t|Y_{t-1})/P(y_t), \tag{A.3}$$

where the total probability of the y_t data is given by $P(y_t) = \Sigma_s\, p(y_t|s_t)P(s_t|Y_{t-1})$ and $p(y_t|s_t)P(s_t|Y_{t-1})$ is simply 1 or 0 (0 if the fish is either dead or not recaptured in location s_t, 1 if the fish is recaptured in location s_t). Calculation of $P(s_t|Y_t)$ is nontrivial only for the case $y_t = 0$. We then calculate $P(s_{t+1}|Y_t)$ (which is $P(s_t|Y_{t-1})$ for the next time step) as follows:

$$P(s_{t+1}|Y_t) = S\sum_s P(s_t|Y_t)M(s, s'), \tag{A.4}$$

where *S* is a (possibly age- and time-varying) survival rate to be estimated from the data and $M(s, s')$ is a movement probability matrix representing the probability of a live fish's moving from location state *s* at time *t* to state s' at time $t + 1$ (the elements are set to 0 for s = dead; $M(s, s)$ is the probability of a fish's staying in location *s*).

In calculating the likelihood function, the capture probabilities $P(k_t|s_t, Y_{t-1})$ are set to their conditional maximum likelihood estimates given by

$$P(k_t|s_t, Y_{t-1}) = n_{kt}/\sum_i P_i(s_t|Y_{t-1}), \tag{A.5}$$

where n_{kt} is the number of fish captured at location *k* at time *t*, and the sum over fish *i* of the probabilities of being alive and at location *k* represents the expected number of fish at risk of capture in location *k* at time *t*.

Seasonal and age dependencies are incorporated in the estimation by (1) assigning each fish *i* an apparent age at first capture based on length, then varying *S* for subsequent recapture times using apparent age and the Lorenzen survival function (Lorenzen 2000); (2) calculating the capture probabilities in equation (A.5) separately by apparent fish ages up to age 10; and (3) using a different movement rate matrix $M_m(s, s')$, $m = 1, \ldots, 8$, for at least the first eight calendar months of each year (we believe that there is relatively little movement in late summer and fall; Valdez and Ryel 1995). These assumptions require estimating at least $2 \times 8 + 1$ leading parameters (assuming capture probabilities to be given by equation A.5), 16 parameters for movements to and from the LCR and 1 parameter for the asymptotic mortality rate, M_{adult}. In some estimation trials we have multiplied the $M(s, s')$ movement rates by a logistic age factor representing lower probabilities of movement out of the LCR for younger fish, thereby adding two parameters.