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ARTICLE

Bioenergetics and Population Dynamics of Flannelmouth Sucker and Bluehead Sucker in Grand Canyon as Evidenced by Tag Recapture Observations

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Abstract

Flannelmouth suckers *Catostomus latipinnus* and bluehead suckers *C. discolobus* in the Grand Canyon of the Colorado River are among the few native species to persist after river conditions changed with the completion of Glen Canyon Dam in 1963. To evaluate the effectiveness of adaptive management manipulations to the system for recovering native species, it is necessary to estimate basic demographic and population dynamic parameters for the species of interest, such as growth, mortality, and recruitment. With this in mind, we present a two-stage analysis in which we first estimated growth and individual ages using a field-based bioenergetics model and then input the age estimates into age-structured mark-recapture (ASMR) models to estimate mortality and recruitment. The analysis was based on 18,500 flannelmouth suckers and 13,975 bluehead suckers that had been tagged with passive integrated transponder tags in the main-stem Colorado River in Grand Canyon and its tributaries since 1989. The bioenergetics estimates of growth suggest that the growth of flannelmouth suckers is faster and that of bluehead suckers slower than in the tributaries reported in other studies. The results from the bioenergetics model provide necessary parameters for input into future ecosystem models. The ASMR models that include the effects of age-specific gear vulnerability indicate that annual natural mortality rates are about 0.2 for flannelmouth suckers and 0.4 for bluehead suckers, which is in agreement with independent estimates from growth parameters and longevity. The estimates of age-1 sucker recruitment and adult abundance correspond well with independent electrofishing catch rate data. The estimated recruitment and abundance estimates provide insights into the efficacy of adaptive management actions targeted to benefit native fishes over the past two decades.

The Grand Canyon of the Colorado River is widely recognized as one of the seven natural wonders of the world and is considered a national treasure of the United States. Once conditions in the Grand Canyon reach of the Colorado River downstream from Glen Canyon Dam (NRC 1987) were recognized as being degraded, the Glen Canyon Dam Adaptive Management Program (GCDAMP), formed in 1996, has attempted to use adaptive management for river restoration. Glen Canyon Dam changed the Colorado River in Grand Canyon from a highly sea-

sonal, turbid, warmwater environment into a diurnally varying, often clear, coldwater environment (Topping et al. 2003). These physical changes in the Colorado River resulted in a dramatic restructuring of the aquatic biota (Gloss et al. 2005). Only a few native fish species have persisted in the face of this change, and a key objective of the GCDAMP has been to identify flow management regimes and other management measures (like control of nonnative fishes) that would allow persistence and recovery of the remaining native fishes (Gloss and Coggins 2005).

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One of the key outcomes of discussions with GCDAMP stakeholders is a desire to use more integrative analyses of past research and monitoring data that would be useful to screen management policy options. A particular desire is the construction of ecosystem models that can predict the effects of various system manipulations under alternative assumptions of how biotic and abiotic factors influence key resources. The goal of these simulations is to explore the interactive (and often opposing) effects of various stakeholder activities and desires with the hope of finding an agreement on how to regulate different activities in the system as management of the system proceeds (Walters and Martell 2004). These simulations also expose uncertainties in the system, which help guide decisions about investment in research efforts and future experimental manipulations of the system to address knowledge gaps (Walters 1986). However, before ecosystem models such as Ecopath with Ecosim (Christensen and Walters 2004) can be run, parameters on single-species abundance, feeding, growth, and recruitment are needed. For several species in the Colorado River, including the flannelmouth sucker *Catostomus latipinnus* and bluehead sucker *C. discolobus*, current estimates and trends in abundance are missing or need to be updated before ecosystem simulations can proceed.

Intensive monitoring of native fish species, with particular emphasis on the endangered humpback chub *Gila cypha*, along with the flannelmouth sucker and bluehead sucker, has occurred since 1989 in support of the adaptive management process. Information on abundance trend and size composition has been collected along the main-stem Colorado River (COR) and in major tributaries, particularly the Little Colorado River (LCR), by means of a variety of netting and electrofishing protocols. As of 1991, the sampling protocol called for passive integrated transponder (PIT) tagging of all native fish individuals exceeding 150 mm body length, and this PIT-tagging database now provides a rich source of information on growth, survival, and total abundance trends.

In this paper, we provide an assessment of growth, mortality, and abundance trends of flannelmouth and bluehead suckers in Grand Canyon, based mainly on the PIT-tagging database. We represent growth by using a relatively simple bioenergetics model (Walters and Essington 2010) that accounts for seasonal growth variation associated with seasonal temperature changes and allows the back-calculation of apparent food intake rates for use in ecosystem trophic models. The bioenergetics model is also used to estimate ages at tagging for all recaptured suckers, and these ages are applied to the capture–recapture data used in an age-structured mark–recapture model (ASMR; Coggins et al. 2006). Mortality and abundance are estimated by using a combination of longevity information and the ASMR. We evaluate this method for estimating long-term trends in abundance and recruitment against other, more traditional, population estimates.

The purposes of this study are threefold. First, we present bioenergetics parameter estimates for two species for which

bioenergetics examinations have not previously been undertaken. We also estimate parameters that can be used in ecosystem models as part of a future study. Second, we use estimates of abundance and recruitment from the ASMR model to qualitatively evaluate flannelmouth and bluehead sucker population responses to past manipulations to the system that have taken place as part of the GCDAMP. Finally, we present a novel approach to the estimation of growth and recruitment for endangered species that requires minimally invasive sampling. We close by discussing sampling issues that have arisen over time in the Grand Canyon monitoring program that may introduce bias into parameter estimates and suggest ways to mitigate this in the future.

METHODS

Data used in the analyses described below were extracted from databases maintained by the U.S. Geological Survey, Grand Canyon Monitoring and Research Center. These databases contain information on fish sampling effort, sizes of fish captured, and PIT tag codes from 1989 to 2008. Size and tagging records that were obviously in error, e.g. recapture sizes much smaller than tagging sizes, were omitted from the analysis; these represented approximately 1% of the records. A total of 18,500 flannelmouth suckers and 13,975 bluehead suckers have been tagged since 1989, and there have been 4,082 live recaptures of flannelmouth suckers and 703 bluehead suckers that occurred at least one calendar year after tagging.

PIT tagging and recapture.—Flannelmouth and bluehead suckers mainly spawn in tributary streams to the Colorado River, and juvenile rearing occurs almost entirely in the main stem and the Little Colorado River (LCR; Valdez and Ryel 1995). Though there is a concentration of juveniles in the main stem just below the LCR, flannelmouth sucker juveniles from all tributaries are thought to disperse widely downstream. Fewer bluehead sucker juveniles appear to show such long distance dispersal. Older (spawning) fish have been tagged in most tributaries, but sampling and tagging effort has been concentrated in the main-stem Colorado River near the LCR and in the LCR where the main target species of the tagging program (humpback chub) is concentrated (Figure 1; Table 1). An intensive tagging effort that was specific for flannelmouth suckers spawning in the Paria River (Figure 1B) was done in some years. About half of the juvenile fish (150–400 mm) tagged were in the LCR, and most of the remainder were tagged in the main-stem Colorado River near the confluence with the LCR (Figures 1b and 2). Relatively few suckers were caught in the 1992–1994 period compared with the period after 2000 (Figure 2) despite intensive monthly sampling, particularly in the LCR during the 1992–1994 period. Also, sampling effort was very low during the 1995–1999 period, making interpretation of long-term mark–recapture and trend data particularly difficult.

A consistent tagging procedure has been followed since 1991. All fish caught greater than 150 mm were PIT-tagged

TABLE 1. Proportions of fish tagged in various locations that were recaptured in the same and other locations. Sample sizes are shown in Figure 1. Abbreviations are as follows: COR<100 = the main-stem Colorado River upstream from river mile (RM) 100 (rkm 161); COR>100 = the main stem downstream from RM 100; HAV = the Havasu River; KAN = Kanab Creek; LCR = the Little Colorado River; Par = the Paria River; and SHI = Shinamu Creek.

Tag location	Recapture location						
	COR <100	COR >100	HAV	KAN	LCR	PAR	SHI
Flannemouth suckers							
COR<100	0.73	0.01	0.00	0.00	0.25	0.01	0.00
COR>100	0.18	0.42	0.06	0.05	0.25	0.04	0.00
HAV	0.19	0.20	0.30	0.07	0.21	0.04	0.00
KAN	0.21	0.15	0.07	0.24	0.28	0.02	0.01
LCR	0.25	0.01	0.00	0.00	0.72	0.01	0.00
PAR	0.35	0.02	0.00	0.00	0.10	0.52	0.00
SHI	0.29	0.06	0.06	0.06	0.29	0.00	0.24
Bluehead suckers							
COR<100	0.41	0.00	0.00	0.00	0.59	0.00	0.00
COR>100	0.08	0.08	0.08	0.00	0.75	0.00	0.00
HAV	0.00	0.14	0.86	0.00	0.00	0.00	0.00
KAN	0.00	0.00	0.00	1.00	0.00	0.00	0.00
LCR	0.09	0.00	0.00	0.00	0.91	0.00	0.00
PAR	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SHI	0.00	0.00	0.00	0.00	0.00	0.00	0.00

immediately after capture and without anesthesia. Tags were inserted by needle into the abdominal cavity near the anus. Fish were released immediately after tagging. There has been no evidence of significant tag loss or tag-induced mortality (Ward et al. 2008). All fish caught greater than 150 mm were scanned for both 134 kHz tags used early in the program and 125 kHz tags used after 2000.

Bioenergetics and growth analysis.—A total of 6,965 recapture observations have been made on flannemouth suckers; of these 3,912 were recaptured at least 0.5 years later, a length of time that is long enough for measurable growth to have occurred. Records for which length at tagging and recapture differed by more than 200 mm were identified as a likely measurement error and thus removed (12 records). Preliminary analysis of this usable subset of the recaptures showed essentially a linear decrease in growth rate (as measured simply by change in length divided by time from tagging to recapture) as body length increased; there was little indication of differences in growth between fish captured in the cold Colorado River main stem and those tagged in the warmer LCR (Figure 3). From the Fabens (1965) growth model that was used for all sucker recaptures from the Colorado River and Little Colorado River combined, von Bertalanffy growth parameters were estimated to be $K = 0.27$ and $L_{\infty} = 540$ mm. This is similar to the growth pattern measured for flannemouth suckers in other larger tributaries of the Colorado River (Sweet et al. 2009; summarized in Figure 4).

Far fewer (704) usable recapture observations for growth analysis have been made on bluehead suckers and over a much

narrower range of sizes than for flannemouth suckers; these data do not show a clear pattern of variation in growth rate with body length at tagging (Figure 3). The growth rate versus length regression indicates K to be unreasonably low (0.13) and L_{∞} (370) to be apparently too high. Bluehead suckers in the Grand Canyon apparently do not reach sizes as large as those reported by Sweet et al. (2009) for this species in other Colorado River tributaries.

Small fish tagged in the LCR show slightly higher average growth than that for fish first tagged in the main stem (Figure 3). But in view of evidence of high mixing rates between the LCR and main stem (Table 1), we elected to treat all fish as having come from the same population for both growth and population dynamics analyses. To predict temperature effects on growth, we considered available water temperature data in the LCR and COR (Voichick and Wright 2007) and used an average seasonal temperature pattern measured for 1992–2005 in the LCR, which essentially treats all the fish as having experienced an LCR-like temperature regime as they grew.

In addition to the growth information from tagging, there are estimates of monthly mean length at age for 0–2-year-old flannemouth and bluehead suckers from modal progression analysis of monthly samples taken mainly during the 1991–1994 period (Robinson and Childs 2001). We checked the Robinson–Childs estimates against modal size data collected since 2000, and recent growth appears to be similar to what those investigators found, though recent sampling has not been frequent enough to permit precise modal progression analysis.

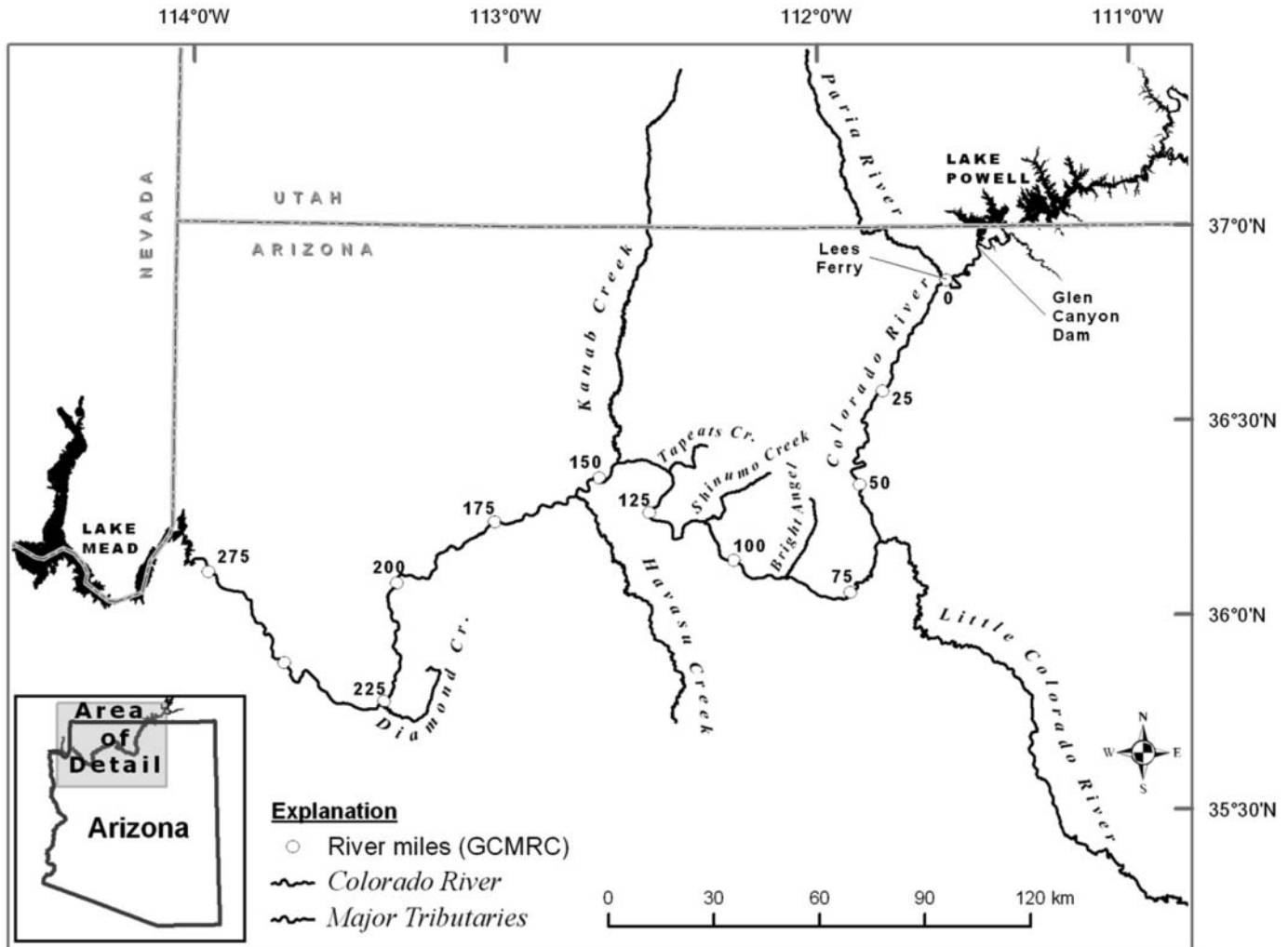


FIGURE 1. The Colorado River in the Grand Canyon, Arizona, with river miles (RM) downstream from Lees Ferry (RM 0) and major tributaries indicated.

We fit the tag-recapture length and juvenile growth data to a general bioenergetics model of the form (Walters and Essington 2010)

$$dW/dt = HW^d Q_c^{(T-10)/10} - mW^n Q_m^{(T-10)/10}, \quad (1)$$

where W is body weight, T is water temperature ($^{\circ}\text{C}$), H and m are body-size scaling parameters for food consumption and metabolism, respectively, d and n are body-size allometry parameters for consumption and metabolism, respectively, and Q_c and Q_m are Q_{10} parameters for the effect of temperature on consumption and metabolism, respectively (note that Q_{10} represents the factor by which a physiological rate increases for a 10°C rise in temperature). We elected not to use a more complex model for temperature effects on feeding rate because temperatures where fish have been sampled have rarely exceeded 20°C , so suppression of feeding rate at higher temperatures is unlikely to have occurred for these warmwater species (Valdez and Ryel 1995). Numerical integration of equation (1) over time from hatching

at age $a = 0$ to any age gives a predicted mean body weight at age, $W(a)$, which we convert to predicted mean length at age, $L(a)$, using a length-weight relationship of the form $W = cL^3$, i.e. $L(a) = [W(a)/c]^{1/3}$, where c is assumed to be 5.997×10^{-6} (Valdez and Ryel 1995).

The length-at-age model $L(a)$ was then fitted to the data by varying the H , m , d , and Q_c parameters (we assumed $Q_m = 2$ and $n = 1.0$ following the analysis of Essington et al. 2001) by maximizing a log-likelihood function with two components. The first component is a simple sum of squared deviations of $L(a)$ from the Robinson-Childs mean lengths at age for $a = 0-2$ years. The second is a sum over all recaptured fish of complex log-likelihood terms for each individual fish (i). The log-likelihood term for each fish is derived by assuming (1) independent, normally distributed measurement errors at both marking and recapture, and (2) a persistent, normally distributed deviation, D_i , for each fish from $L(a)$ so that $L_i(a) = L(a)D_i$. Under these assumptions, the log-likelihood term for each fish is then evaluated at conditional—based on the parameters

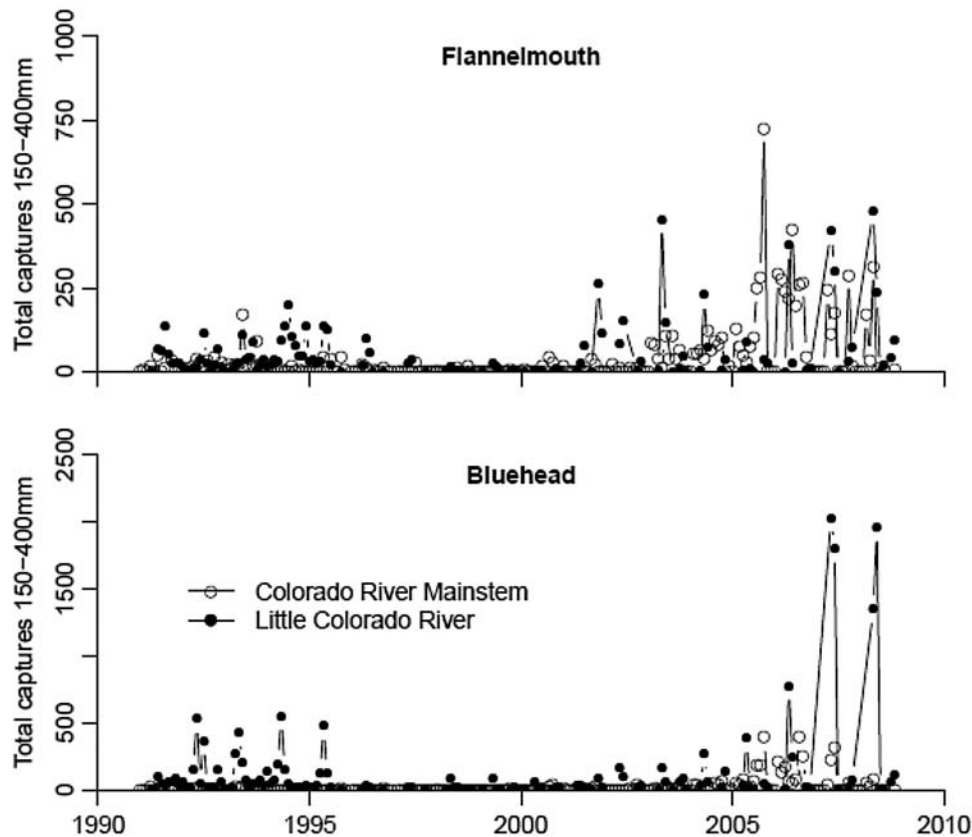


FIGURE 2. Numbers of juvenile flannelmouth and bluehead suckers (150–400 mm) captured in the Little Colorado River versus the main-stem Colorado River. All untagged fish among these captures were tagged at the time of capture. Low captures in the 1995–1999 period were due largely to reduced sampling effort, while high captures after 2000 probably reflect abundance increases, since sampling effort has been relatively stable since 2000.

determining $L(a)$ —maximum likelihood estimates of the age a_i of the fish at time of tagging. In statistical terms, the growth deviation, D_i , and ages at tagging, a_i , are treated as “nuisance parameters” to be estimated for each fish; for details of this calculation, see Walters and Essington (2010). A bonus of the complex likelihood approach is that we obtain an estimate of the age distribution of fish at tagging and can do diagnostic plots of lengths at estimated tagging ages, a_i , as though they were direct observations of length at age. Unfortunately, too few otoliths have been collected from Grand Canyon suckers to provide independent validation of the estimated age–length relationship for fish older than 2 years.

The bioenergetics model fitting can be used to explain that part of the observed variation in growth rates from tagging (Figure 3) could be due to seasonality in feeding and metabolic rates. In fact, the general model (equation 1) reduces to the von Bertalanffy model when $d = 2/3$, $m = 1$, $w = cL^3$, and the Q_{10} values are set to 1.0.

Food consumption rates were estimated by noting that the first term of equation (1), $HW^d Q_c^{(T-10)/10}$, represents food intake rate multiplied by the product of assimilation efficiency, the proportion of intake not lost to specific dynamic action, and the proportion of food intake not used for active metabolism

associated with food capture. This overall product or efficiency averages around 0.5 in bioenergetics studies, so we estimated food intake rate (q) as simply $q = 2HW^d Q_c^{(T-10)/10}$. Integrating this instantaneous intake rate q over time then gives estimates of annual and lifetime consumption rates, and integrating the product of it times relative biomass of fish alive at age (i.e., survivorship to age \times weight at age) gives estimates of consumption rate per biomass (Q/B) needed for food web modeling.

ASMR tag-recapture analysis.—The ASMR (Coggins et al. 2006) model is based on reconstructing N_{at} , the total number of animals alive at age a in year t ($a = 2 \dots A$, $t = 1 \dots T$) as the sum of marked M_{at} and unmarked U_{at} individuals ($N_{at} = M_{at} + U_{at}$), where M_{at} and U_{at} are predicted from number of animals marked and survival rates S . Note that unlike the bioenergetics model, which runs on a short time step to explain intra- and interannual variation in growth, the ASMR model runs on an annual time scale and is based on the cumulative number of unmarked and recaptured fish caught each year. The reconstructed numbers are compared with observed numbers of recaptures (m_{at}) and unmarked fish caught (u_{at}) by using a likelihood function to estimate capture probabilities (P_{at}), survival rates (S_a), and unmarked numbers alive in the last study year (U_{aT}). For this study, we treated fish of ages greater than or equal to A as

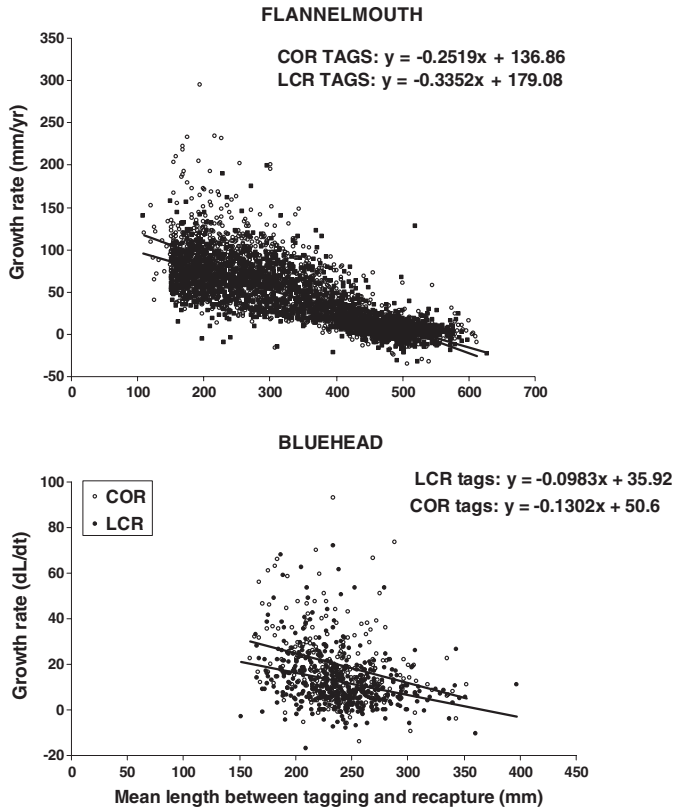


FIGURE 3. Growth rates of PIT-tagged flannelmouth and bluehead suckers from the Little Colorado River and Colorado River in the Grand Canyon. Rate for each fish is determined as its change in size from tagging to recapture, divided by the time between tagging and recapture. Slope of the fitted linear trend is an estimator of the von Bertalanffy metabolic parameter K . Fish first tagged in the Little Colorado River are plotted as LCR, while fish first tagged in the Colorado River main stem or other tributaries are plotted as COR.

a “plus group” of individuals whose age cannot be reliably distinguished. Preliminary analysis using time- and age-structured mortality showed dramatic reductions in model parsimony, so we estimated a single, time-independent survival rate S . Various discrete assumptions on the maximum age, A , along with constraints on age- and time-dependence in capture probabilities, P_{at} , create a range of alternative models for estimation of S .

Predicted numbers of marked and unmarked fish alive are predicted for any survival rate estimate S from forward and backward time equations. The forward equations for the marked population are

$$M_{a+1,t+1} = S(M_{at} + u_{at}) \text{ for } a = 2 \dots A - 1 \quad (2a)$$

and

$$M_{A,t+1} = S(M_{A-1,t} + M_{A,t} + u_{A-1,t} + u_{A,t}) \text{ for } a = A \quad (2b)$$

These equations simply state that to obtain the number of marked fish alive at year $t + 1$, one would take the number of marked fish alive at year t , add newly marked (previously

unmarked) fish, and apply the survival rate S to the resulting total number. The backward (virtual population analysis) equations for the unmarked population are

$$U_{a,t} = U_{a+1,t+1}/S + u_{at} \text{ for } a=2 \text{ to } A - 2, t = 1 \dots T - 1, \quad (3a)$$

$$U^*_t = U_{A,t+1}/S + u_{At} + u_{A-1,t} \text{ for } t = 1 \dots T - 1, \quad (3b)$$

$$U_{A-1,t} = U^*_t [u_{A-1,t}/(u_{A-1,t} + u_{A,t})] \text{ for } t = 1 \dots T - 1, \quad (3c)$$

and

$$U_{A,t} = U^*_t [u_{At}/(u_{A-1,t} + u_{A,t})] \text{ for } t = 1 \dots T - 1. \quad (3d)$$

In this formulation, U^*_t is the back-calculated total number of unmarked fish aged $A-1$ and older, and equations (3c) and (3d) partition this total between age-classes $A-1$ and A in proportion to the number of unmarked fish of each class caught in year t . To perform the back-calculations in equations (3a-d), it is necessary to specify terminal abundances U_{at} for all a in the last year T ; these terminal abundances are treated (along with S) as unknown parameters to be estimated by fitting the model to the m_{at} , u_{at} data. Also, while the newly marked animals, u_{at} , appear as arbitrary, known removals or additions in equations (2a, b) and (3a-d), the predicted state dynamics do not depend on the number of recaptures m_{at} ; the recapture data are assumed to carry information only about survival and capture probabilities. In addition, equations (3c) and (3d) fail when A is set so large that the proportions of age- $A-1$ and age- A fish in the u sample do not provide a reliable estimate of the proportion of age- $A-1$ fish in U^*_t ; in the flannelmouth sucker case, this limited us to A less than 11 years and in the bluehead sucker case to A less than 8 years.

Application of equations (2a, b) and (3a-d) requires an assignment of age to each tagged fish at first capture (m_{at} , u_{at} data), regardless whether that fish was subsequently recaptured. We used estimated ages from the bioenergetics model fitting to construct age-from-length relationships and applied these ages to all tagged fish. We initially tried simple relationships, like inverse growth curves, but these gave unsatisfactory age estimates especially for smaller fish (e.g., assigned no fish to age 1, when in fact modal progression data indicated substantial numbers of smaller fish are age 1 in at least the fall samples). To obtain good back-calculations of ages for fish that were recaptured and aged from the bioenergetics model, the best approach we could find was to group the recapture ages into bins by 5-mm length increments and calendar month, then assign each fish the mean age for its length-month bin at tagging. About one-half of the length-month bins had no recaptured fish age observations, and for fish tagged in these bins we assigned an age equal to the average of ages for all fish tagged in the age bin, independent of calendar month of tagging. As noted by Coggins et al. (2006),

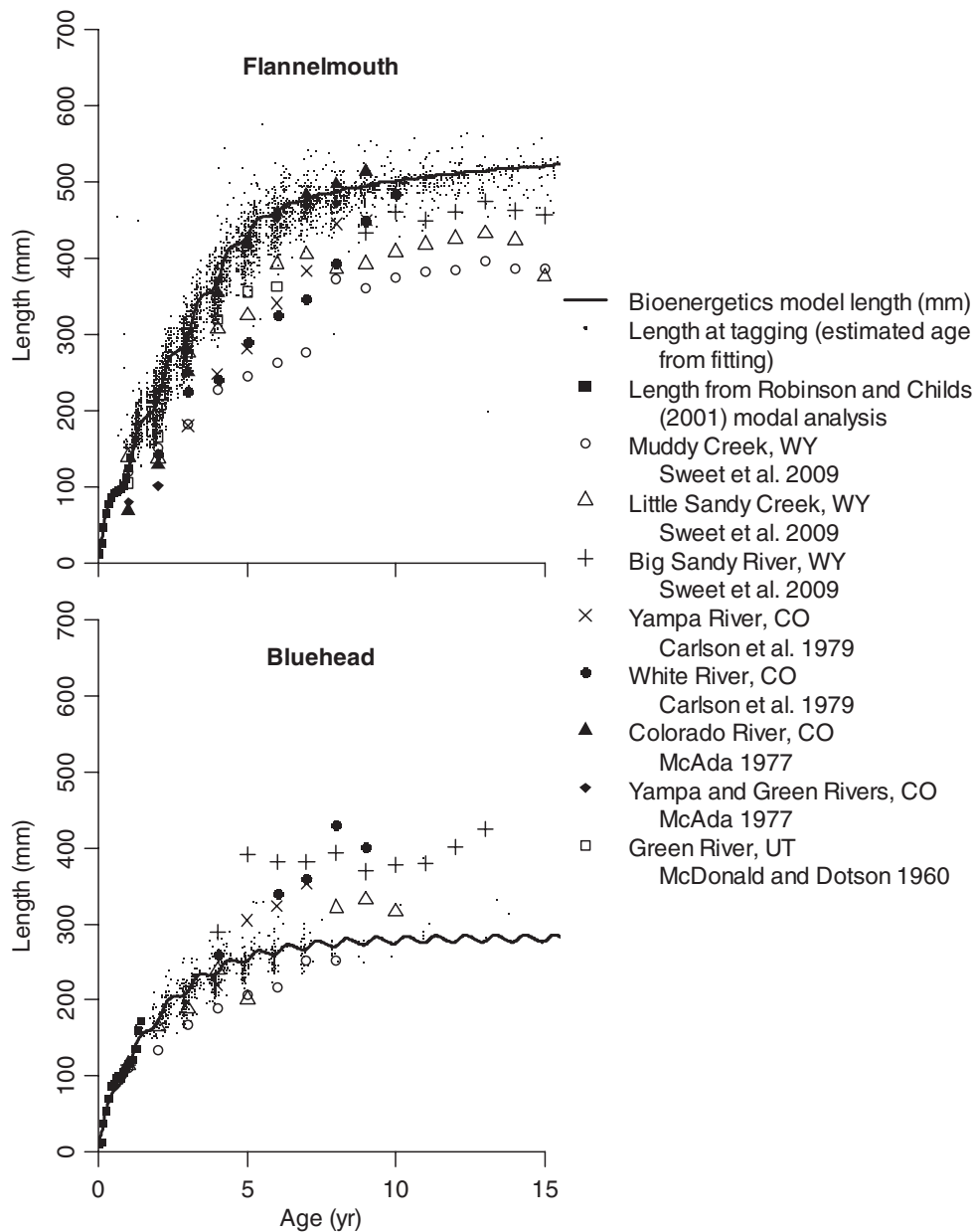


FIGURE 4. Size at age of flannelmouth and bluehead suckers estimated from modal progression analysis and bioenergetics model fitting, and summarized for other areas in the Colorado River basin by Sweet et al. (2009). The fine points, or dots, show lengths at maximum likelihood estimates of age at tagging for tagged fish included in the bioenergetics model fitting. Note that there was a truncation of the x -axis for flannelmouth suckers to enhance the visualization of intra-annual growth patterns.

errors in age assignment from length can cause a distributional spread of the data (and thus the fish) over cohorts regardless of what method is used for the age assignment. We reiterate that there are no substantial samples of known age at length for Grand Canyon suckers based on hard parts like otoliths, otherwise we would have used that information to validate and improve the age assignment.

For fitting the data, we assumed that the m_{at} and u_{at} were sampled from independent Poisson distributions with expected

(mean) catches \hat{m}_{at} and \hat{u}_{at} , which implied an additive log-likelihood term for each observation equal to just $-\hat{m}_{at} + m_{at}\log_e(\hat{m}_{at})$ or $-\hat{u}_{at} + u_{at}\log_e(\hat{u}_{at})$ when additive terms in the log-likelihood expression that depend only on the data are ignored. The expected catches were predicted to be $\hat{m}_{at} = P_{at}M_{at}$ and $\hat{u}_{at} = P_{at}U_{at}$. The problem then is how to estimate the capture probabilities P_{at} . These capture probabilities are likely to have varied in complex ways over the history of sampling, owing to size-age-related shifts in fish distributions relative to

concentrations of sampling effort and to changes in sampling effort with the various differentially size-selective gears used. We conducted estimation trials with three alternative assumptions about the P_{at} .

1. No age dependence past age 1: $P_{at} = P_t$ for a greater than 1; $P_{1t} = v_t P_t$, P_t evaluated at its conditional maximum likelihood estimate [(total catch in year t)/(total calculated abundance in year t)], v_t estimated by the fitting procedure.
2. Separable age–time dependence: $P_{at} = v_a P_t$, with conditional maximum likelihood estimate $P_t = [(total\ catch\ in\ year\ t)/(total\ vulnerable\ abundance\ in\ year\ t)]$, and age-specific vulnerable proportions v_a estimated by the fitting procedure with $v_{A-1} = v_A = 1.0$.
3. Full age and time dependence: conditional maximum likelihood estimates $P_{at} = (m_{at} + u_{at})/(M_{at} + U_{at})$ for all a and t .

Alternative assumptions about maximum discernable age A along with these capture probability assumptions define a set of alternative ASMR models, which we refer to in the results as ASMR $n.A$: ASMR1.4 represents $A = 4$, assumption (1) above, ASMR2.10 represents $A = 10$, assumption (2) above, and so forth. We tested $A = 4, 10$, and 25; the $A = 10$ and 25 models gave essentially the same results, so only the $A = 4$ and 10 trend results for flannelmouth suckers and $A = 4$ and 7 for bluehead suckers are presented below.

For each maximum age (A) and capture probability model, we used Solver in Microsoft Excel to maximize the log-likelihood function by varying S, N_{at} , for $a = 1 \dots A$, and for the separable capture probability assumption, v_a for $a = 1 \dots A - 2$. The P_t for no age dependence and P_{at} for full age and time dependence are also unknown parameters, but were evaluated only at their conditional maximum likelihood values given the other parameter estimates. Uncertainty in the natural mortality estimates $M = -\log_e(S)$ and relative credibility of the alternative capture probability models were assessed with a quasiliikelihood measure of information loss (QAIC; Burnham and Anderson 2002), which was obtained by multiplying the log-likelihood function in the Akaike information criterion (AIC) calculation by a correction factor $c = 10$. Burnham and Anderson (2002) suggest $c = 1-4$ in calculations of the QAIC information measure for overdispersed data; we used a larger value to reflect not only overdispersion but also nonindependence in the size–age composition sampling. The larger c values also give likelihood profiles with a spread similar to what we find in M estimates across Monte-Carlo simulation trials with an individual-based model (IBM) that was developed to evaluate bias in ASMR estimates (Coggins and Walters 2009). The IBM simulates variability in the ASMR M estimates due to binomial sampling variation in the capture–recapture process and to errors in assigning age at tagging from length.

All of the capture probability assumptions in the previous paragraph have probably been violated owing to at least two factors. First, recapture probabilities are likely to have been

higher than first capture probabilities for fish of all ages and years owing to the residence of marked fish in areas like the LCR where sampling (and hence recapture) effort has been high. In other words, there could be a large main-stem resident subpopulation with persistently low capture probabilities, which would lead overall to underestimation of total population size. Second, the differentially high recapture probabilities for fish marked in intensively sampled areas could decline over time, owing to the dispersal of marked fish from those areas into less intensively sampled main-stem areas. This would lead to low apparent survival rates. We tried to minimize the second problem by using only recaptures made in at least the next calendar year after tagging. To deal with the second problem we would require a spatial movement model, which from our experience with other populations would very likely fail.

We used two alternative assessment methods for comparison with the ASMR results. First, we calculated a simple mark–recapture estimate of age-1 recruits and age-4+ adults for each year using the formula $N_t = M_t + u_t/P_t$, where N_t is total abundance in the age-class, M_t is total marked fish in the age-class predicted to be at risk to recapture in year t , u_t is total catch of unmarked fish in the age-class in the year t , and P_t is the overall capture probability estimated from marked fish in the age-class only, $P_t = m_t/M_t$. For this method, we calculated M_t by using equations (2a) and (2b) with a survival rate $S = 0.82$. Again, all fish ages are assigned based on either maximum likelihood estimates for recaptured fish generated from the bioenergetics model, or from back-calculation based on length. Second, total abundance estimates for 2000–2009 for the Colorado River main stem were made by Scott Rogers (Arizona Game and Fish, personal communication) by expanding electrofishing catch-per-unit-effort (cpue) data by using a catchability coefficient estimated from local depletion experiments along the river. The S. Rogers estimates involve a detailed stratification of cpue data by 12 river reaches from Glen Canyon Dam to river mile (RM) 225 (river kilometer [rkm] 362), division of each reach-specific cpue by estimated catchability $q = 0.02$ to give total abundance, and partitioning of the total abundance estimate by 25-mm length categories by using sampled length frequency proportions. We used S. Rogers' sampled length frequency proportions for each year (totaled over all reaches) to estimate proportions of his total abundance estimate that were most likely age 1 (175–250 mm for flannelmouth sucker, less than 150 mm for bluehead sucker) and age 4+ (350 mm and larger flannelmouth sucker, 300 mm and larger bluehead sucker).

RESULTS

The simple bioenergetics model (equation 1) appears to describe flannelmouth and bluehead sucker growth in the Grand Canyon quite well (Figure 4). Maximum likelihood estimates of its parameters (Table 2) imply a growth pattern quite close to that predicted by the von Bertalanffy model when corrected for seasonal temperature effects, with the d parameter close to the

TABLE 2. Bioenergetics model parameter estimates for flannelmouth (FMS) and bluehead (BHS) suckers in the Grand Canyon. The growth pattern predicted by equation (1) with these parameter values is shown in Figure 4.

Parameter	FMS	BHS
W_0 (body weight at hatching in May [g]; assumed)	0.0133	0.0073
H (anabolic rate per body weight at 10°C to the power of $-d$)	1.918	3.130
d (power parameter for variation in the anabolic rate with body weight; assumed $2/3$ for BHS)	0.649	0.667
m (catabolic rate per unit body weight at 10°C)	0.162	0.778
n (catabolic rate per body weight; assumed value)	1	1
Q_c (Q_{10} parameter for food consumption versus temperature)	4.656	3.130
Q_m (Q_{10} parameter for metabolism versus temperature; assumed value)	2.0	2.0

value of $2/3$ assumed in derivation of the von Bertalanffy model (Essington et al. 2001) and metabolic parameter m that implies a von Bertalanffy K of around 0.27 for flannelmouth suckers and 0.48 for bluehead suckers. Estimated food consumption rates (Figure 5) vary in a reasonable pattern with season and age, and the high estimate of Q_c relative to Q_m probably arises from strong seasonal variation in food availability as well as from the effects of temperature on digestion rates. For flannelmouth suckers, assuming a stable natural population with an annual natural mortality rate of $M = 0.2$, the food consumption rate estimates imply an annual food consumption rate per biomass (Q/B in trophic mass balance models) of 0.96 for the age-1 + population and a quite reasonable production : consumption ratio (or ecological efficiency, P/Q) of around 0.2. For bluehead suckers, assuming $M = 0.4$, food consumption estimates imply an annual Q/B of 1.81 and P/Q of around 0.22.

Estimated ages at tagging for 3,912 individual flannelmouth suckers and 704 bluehead suckers (Figure 6) from the bioener-

getics model imply somewhat higher maximum ages for flannelmouth suckers, but similar maximum ages for bluehead suckers, than have been reported in other studies (Sweet et al. 2009). The distribution of estimated ages at tagging (Figure 6) implies about the same number of older fish (same apparent mortality rate when ages are plotted as a catch curve) as would be expected from a stable population with natural mortality rate M of around 0.2 for flannelmouth suckers and 0.53 for bluehead suckers. This is roughly the same M as would be expected from the growth parameter estimates and maximum longevity reported in other studies (Table 3). However, about 3% of the flannelmouth suckers were assigned estimated ages greater than

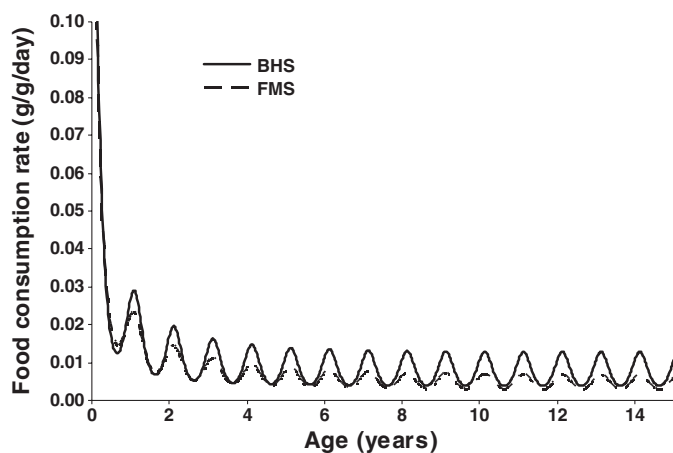


FIGURE 5. Estimated food consumption rates from the bioenergetics model, expressed as daily proportion of mean body weight at age. These estimates are predicted rates from the bioenergetics equation with parameter values estimated from growth increment data; these parameter values predict the body growth patterns shown in Fig. 4. Age 0 corresponds to the assumed May 1 hatching date, and sinusoidal seasonal pattern is caused by estimated temperature effects (Q_{10} parameters, Table 2) in the bioenergetics model. FMS = flannelmouth sucker, BHS = bluehead sucker.

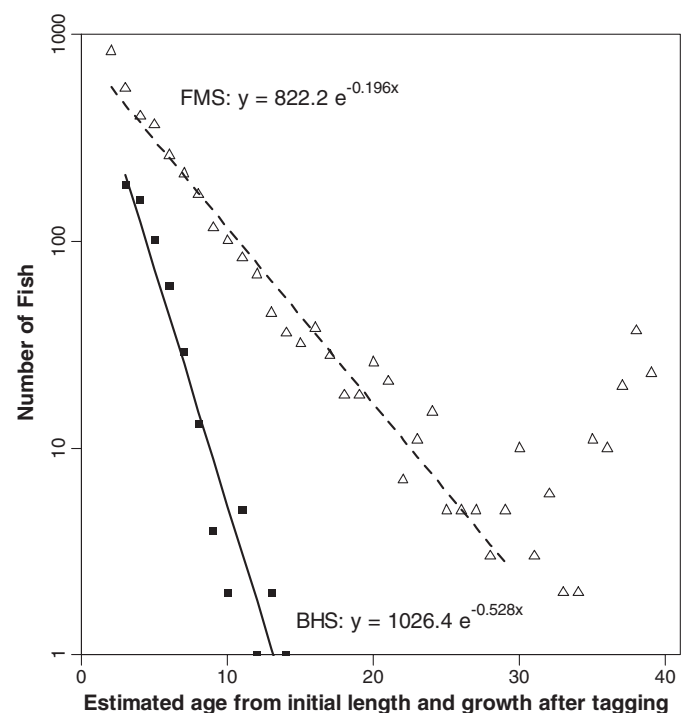


FIGURE 6. Age distributions of flannelmouth suckers (FMS) and bluehead suckers (BHS) at maximum likelihood estimates of ages at first capture from bioenergetics model fitting to growth data from PIT-tagging. The age exponent of the fitted exponential regression is an estimator of the natural mortality rate M .

TABLE 3. Alternative estimates of the flannelmouth (FMS) and bluehead (BHS) sucker natural mortality rate (M). A range is given for the Pauly (1980) prediction owing to uncertainty about mean temperature experienced by fish; fish resident in the main-stem Colorado River experienced an annual mean temperature of 11°C, while those resident in the Little Colorado River experienced a mean temperature of 17°C. The maximum observed ages of 25 years for flannelmouth suckers and 11 years for bluehead suckers were assumed for the Hewitt and Hoenig (2005) estimate and based on the maximum ages reported in Mueller and Wydowski (2004) and Sweet et al. (2009).

Method of estimation	FMS	BHS
Maximum observed age (Hewitt and Hoenig 2005)	0.17	0.37
Pauly (1983) prediction from growth and temperature	0.20–0.25	0.39–0.47
Catch curve from apparent ages at first capture (Figure 5)	0.20	0.52
Ratio of age-3 to age-4 and older fish at first capture	0.26	0.45
Jolly–Seber model (recapture data, vulnerability equal for all ages)	0.35	0.65
Jolly–Seber model (recapture data, vulnerability variable with age)	0.22	0.29
ASMR 1.10/7 (vulnerability equal over ages after age 1)	0.20	0.56
ASMR 2.10/7 (vulnerability estimated by age, increasing with age)	0.22	0.63
ASMR 3.10/7 (complex age–time vulnerability pattern)	0.16	0.62
ASMR 1.4 (age-4 + fish pooled, vulnerability equal over age > 1)	0.16	0.38
ASMR 2.4 (age-4 + fish pooled, vulnerability estimated by age)	0.15	0.40
ASMR 3.4 (age-4 + fish pooled, complex vulnerability pattern)	0.16	0.40

30 years, mostly in a cluster around 35–38 years; these fish were all large (>500 mm) individuals with observed growth increments clustered around 0.0 mm and tagged during both the 1991–1991 and post-2000 periods of more intensive sampling. If these old fish been seen only in the earlier period, we would suspect them to be a residual population from before construction of Glen Canyon Dam; but since some were also seen at the same apparent ages after 2000, it is more likely that they simply reflect inaccuracy in the age assignment approach when applied to larger, slow-growing fish.

The various ASMR versions all resulted in similar trends in age-1 sucker recruitment and abundance (Figure 7), but with substantially different absolute abundances depending on capture probability assumptions. Recruitments were low during the 1990s and then increased dramatically after 2000. The largest recruitment estimates that were consistent across ASMR versions coincided with brood years 2003 and 2004, when there was a sudden increase in main-stem water temperatures (Figure 8) because warmer water from the Lake Powell thermocline was drawn into Glen Canyon Dam penstocks during a period of very low reservoir levels. Adult abundance was apparently stable or decreasing slowly during the 1990s, but since 2005 it has increased dramatically as expected from the recruitment increases.

Comparisons of QAIC favored the ASMR2.A vulnerability assumption for $A = 4$ and 10, and ASMR1.4 was slightly favored over ASMR2.4 for $A = 4$. These results indicate that it is not sufficient to include differential vulnerability of only age-1 fish (ASMR1.A), and that attempts to estimate the full age–time pattern of change in vulnerabilities (ASMR3.A) can lead to overparameterized models even for $A = 4$.

Estimates of overall capture probabilities (total recaptures / total marked fish at risk to recapture, total new captures / total

unmarked fish at risk to capture) indicate that capture probabilities were highest in the early 1990s when there was monthly sampling in the LCR, and again after 2000 when there was more intensive and regular sampling effort in the main-stem Colorado River (Figure 9). As expected from the relative numbers of small fish captured in the LCR versus the main-stem COR (Figure 2), the ASMR model results indicated that capture probabilities for small (age 1) fish were actually higher after 2000 than during the early 1990s when there was relatively little sampling effort in the main stem (where most juvenile rearing probably occurs, at least for flannelmouth suckers). A comparison of capture probabilities for marked versus unmarked fish indicated there was a differentially high probability of recapturing fish once they had been marked, particularly those marked in the early 1990s, which would be expected from the concentration of sampling in the LCR.

The various ASMR formulations resulted in substantially different estimates of the natural mortality rate M (Table 3), with likelihood profiles that are narrow and do not always overlap (Figure 10). Independent methods for estimating M (the equation of Pauly 1980 based on growth parameters, and the equation of Hewitt and Hoenig 2005 based on maximum observed age of around 25 years) suggest that M is relatively low for flannelmouth sucker, in the range 0.2–0.25, and is around 0.4 for bluehead sucker. Simple Jolly–Seber analysis of the recapture data indicates the apparent M is much higher, around 0.35 for flannelmouth sucker and 0.6 for bluehead sucker, when capture probabilities are assumed to be independent of age, but M is considerably lower with values of 0.22 and 0.4, respectively, when vulnerabilities at age are estimated for fish of ages 2–10, in which case the vulnerability estimates decline considerably with age for ages 2–5.

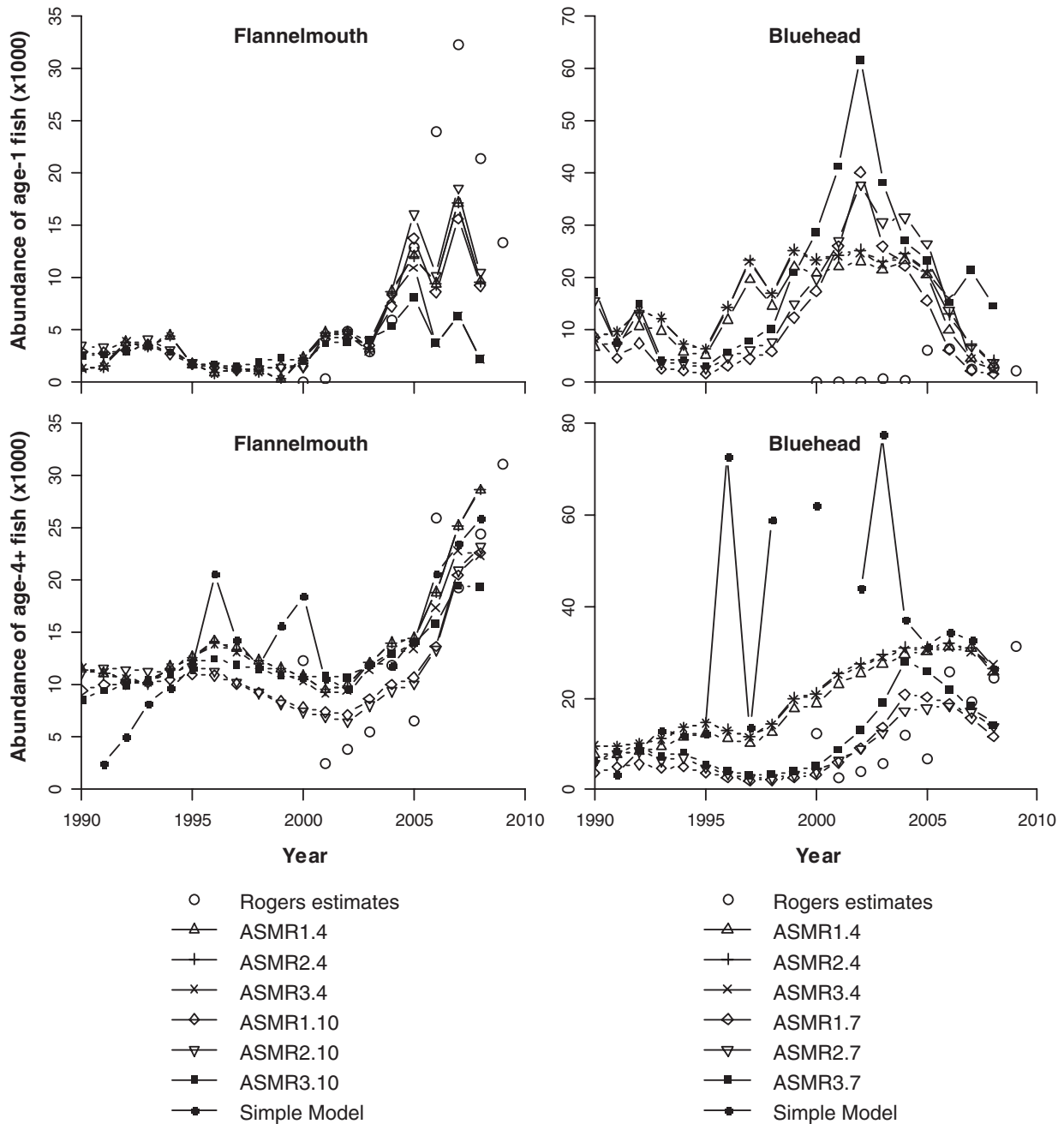


FIGURE 7. Estimated age-1 recruitments and adult (age 4+) population sizes from the age-structured mark-recapture (ASMR) models. ASMR1.4 refers to fish 4 years old and older treated as a plus group and assumption 1 about capture probability (no variation in capture probability with age; see text). ASMR2.10 refers to fish 10 years old and older treated as a plus group and assumption 2 about capture probability (separate capture probability for every age and year; see text). For bluehead sucker, ASMRx.7 refers to fish 7 years old and older being treated as a plus group.

DISCUSSION

Flannelmouth and bluehead suckers in the Grand Canyon appear to have a relatively stable and predictable growth pattern, similar to that seen in the Colorado River (COR) main stem and large tributaries upstream (McAda and Wydowski 1985; Sweet et al. 2009). The bioenergetics model parameter estimates are quite reasonable and indicate a strongly seasonal

growth pattern despite a high proportion of the sampled fish being resident at relatively low and stable water temperatures in the COR main stem. The parameter estimates indicate overall production-consumption (*P/Q*) efficiencies of around 0.2 for both flannelmouth and bluehead suckers. These findings will be useful for future attempts at ecosystem modeling of this system to help drive decision making. Estimates of ages at length and

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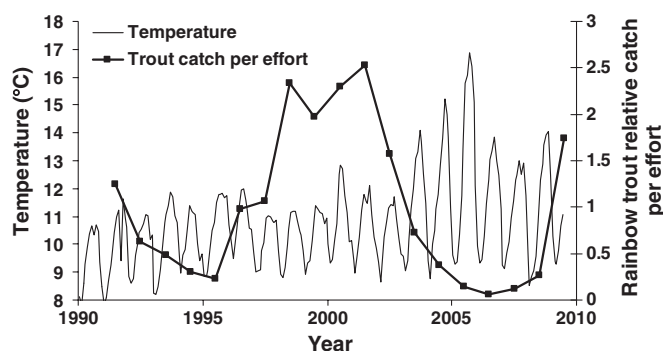


FIGURE 8. Colorado River water temperatures and trends in rainbow trout relative abundance near the Little Colorado River confluence. Temperatures are from model of Wright et al. (2009). Relative trout abundances are means of electrofishing catch rates from springtime night electrofishing along the river shores; numbers and sizes of electrofishing sites varied from year to year, but there were at least five sites covering at least 100 m each year.

age composition at tagging from the bioenergetics model fitting also appear quite reasonable.

It was surprising to see little difference in growth rates of fish tagged in the Little Colorado River versus those in fish in the main stem. Growth rates of fish in the LCR were expected to be higher owing to higher water temperatures, greater nutrient inputs, and lower discharge than in the COR. Length-increment data for age-0 fish collected monthly in the main stem during the early 1990s hint at lower growth rates for at least age-0 fish rearing in the main stem, and both our bioenergetics model and the Robinson and Childs (2001) growth assessment predicted such a difference. But Trammell et al. (2002) noted that it is impossible to assess growth rates of age-0 flannelmouth suckers in the main stem from size composition sampling because of continued dispersal into the main stem over the first summer of growth of new, late-hatching juveniles from the LCR. Despite relatively consistent growth patterns for fish large enough to PIT-tag (>150 mm), we cannot rule out the possibility that fish reaching this size consist of a mixture of older juveniles that had reared for some time in the main stem and of younger, faster-growing fish from the LCR.

Considering the large number of PIT-tagged fish included in the ASMR estimation, it was disappointing not to find robust and precise estimates of population trend and survival rate. Changes in the spatial distribution and intensity of tagging effort, combined with age-related changes in sucker distributions, have evidently led to a complex age-time pattern of capture probabilities, making it impossible to clearly separate the effects of survival rate and vulnerability on disappearance rates of tagged fish over time. Spatial concentration of marking and recapture effort (in the LCR and adjacent main stem) has evidently caused recapture probabilities to be considerably larger than first-capture probabilities. A similar pattern of PIT-tag recapture probabilities that result in underestimates of flannelmouth sucker abundance was found in the Lower Colorado River by Mueller and Wydowski (2004), where the mark-recapture estimates could

be checked against independent estimates from visual surveys. The only reassurance we have that the estimates of absolute abundance are not wildly incorrect is that they are roughly similar to the estimates that S. Rogers (Arizona Game and Fish, personal communication) constructed from electrofishing catch rate and catchability estimates. But even the comparison with the estimates of S. Rogers is suspect, owing to difficulties in partitioning his overall estimates between age-1 and adult fish by using sampled length frequency data.

In fact, three lines of evidence suggest that bluehead sucker recruitment first increased dramatically in 2002 rather than over several earlier years as estimated with the ASMR model. First, a large mode of age-0 or age-1 bluehead suckers (40–80 mm) first appeared in the spring (April–May) length frequency sample in 2002 for the LCR, concurrent with a dramatic increase in hoop-net CPUEs for fish less than 150 mm, compared with 2001; CPUEs of juvenile bluehead suckers then declined after 2002 in a pattern similar to the ASMR estimates (R. VanHaverbeke, U.S. Fish and Wildlife Service, Flagstaff, personal communication). Second, length frequency samples for both the LCR and the main stem showed a large mode of fish with modal sizes around 150–200 mm appearing in 2005–2006, when they were expected for the 2002 cohorts, but with wide variation in length so that the length-to-age function for ASMR assigned a high proportion of these fish to older ages. Third, sampling effort has been relatively stable over the 2000–2009 period (and this is reflected in relatively stable capture probability estimates for flannelmouth suckers), but the bluehead sucker ASMR estimates show capture probability estimates for 2000–2002 that are dramatically lower owing to the virtual population analysis equations of ASMR that led to large numbers of fish calculated to have been present over 2000–2003; most likely, such older fish (and earlier high recruitments) were not in fact present in the system in 2000–2003.

We have encountered similar problems with complex age-time capture probabilities and aging errors from length data in assessments of humpback chub abundance in the Grand Canyon (Coggins et al. 2006; Coggins and Walters 2009); although, these are somewhat less severe since humpback chub are concentrated in and near the LCR and capture probabilities for them have generally been much higher. In both cases, errors in estimation of age from length have probably caused spurious smoothing of the estimated abundance and recruitment trends. This smoothing effect of aging errors has also made it appear as if the sharp increases in recruitment beginning with the 2003 spawning year had actually begun sooner; although, the electrofishing catch rate data of S. Rogers do support the possibility that modest recruitment increases for flannelmouth suckers began as early as 2000.

The recruitment estimates from the ASMR model suggest a possible 2-year cycle in flannelmouth sucker recruitment in recent years, and stronger cohorts were evident from spawning in odd years. Interestingly, monthly length frequency data collected during 1991–1995 also suggest more abundant

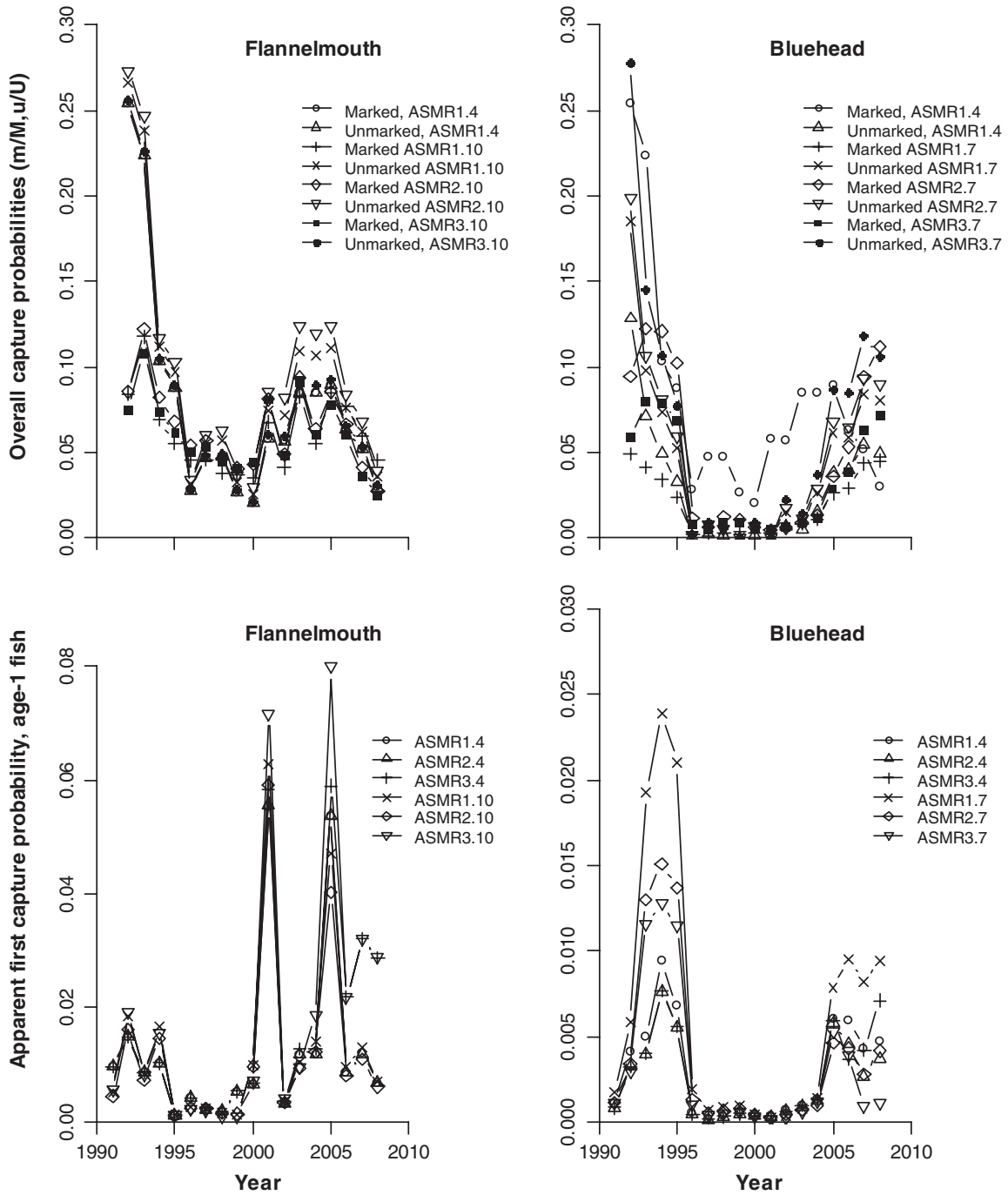


FIGURE 9. Estimates of capture probabilities over time from age-structured mark-recapture (ASMR). Top panels: overall capture probabilities for marked versus unmarked fish, estimated as total numbers caught or recaptured divided by ASMR-calculated total numbers at risk to capture. Bottom panels: capture probabilities for age-1 fish, estimated as number of (unmarked) age-1 captures (u_{2t}) divided by ASMR-back-calculated number of unmarked age-1 fish at risk to capture (U_{2t}).

age-0 flannelmouth suckers in odd years (1991, 1993, and 1995) during that period. Humpback chub show a strikingly similar pattern, again with much higher relative abundance of age-0 fish in odd years. A possible explanation for such cycles is intercohort cannibalism and predation by age-1 humpback chub juveniles on age-0 chub and flannelmouth sucker fry, as sug-

gested for other species by Walters and Martell (2004, p. 142). However, no such pattern is evident in the bluehead sucker data or in flannelmouth sucker catch rates in the lower 1,200 m of the Little Colorado River.

An abundance trend data set that has been collected since 1987 in the lower 1,200 m of the LCR provides evidence that

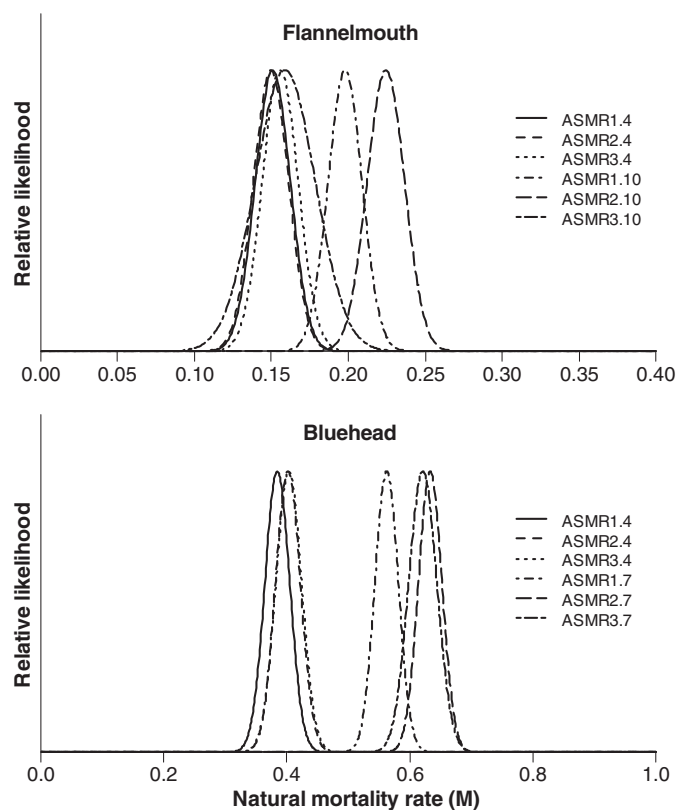


FIGURE 10. Likelihood profiles for natural mortality rate M for the various age-structured mark-recapture (ASMR) formulations.

juvenile survival of both flannelmouth and bluehead suckers from age 1 to adult may have increased substantially since 2000. In each spring, the Arizona Game and Fish Department has set hoop nets for 2 weeks to a month in the lower LCR for most years (except 2000–2001). The CPUEs of larger (>100 mm) fish in these samples suggest somewhat less dramatic increases have occurred after 2000 than is indicated by the ASMR and main-stem electrofishing data (Figure 11), but more importantly they indicate that for at least a few years during the 1990s very high juvenile (<100 mm) densities occurred (bluehead suckers in 1989 and 1996; flannelmouth suckers in 1996–1997), and these were not followed by substantial increases in the abundance of older fish. In particular, there is no evidence in the ASMR back-calculations of recruitment that 1996 was a strong cohort for either species, yet apparently similar or weaker cohorts after 2000 were followed by increases in the abundance of older fish.

Despite high uncertainty about absolute population size, the trend estimates do allow us to draw some conclusions about the efficacy of a few experimental treatments that have been part of the Grand Canyon adaptive management program. Three main treatments have been applied since 1990: (1) a reduction in diurnal flow fluctuations starting in 1991, the modified low fluctuating flows (“MLFF”) policy; (2) a low summer steady flow (“LSSF”) experiment in summer 2000; and (3) “mechanical removal” by using electrofishing of nonnative fish predators

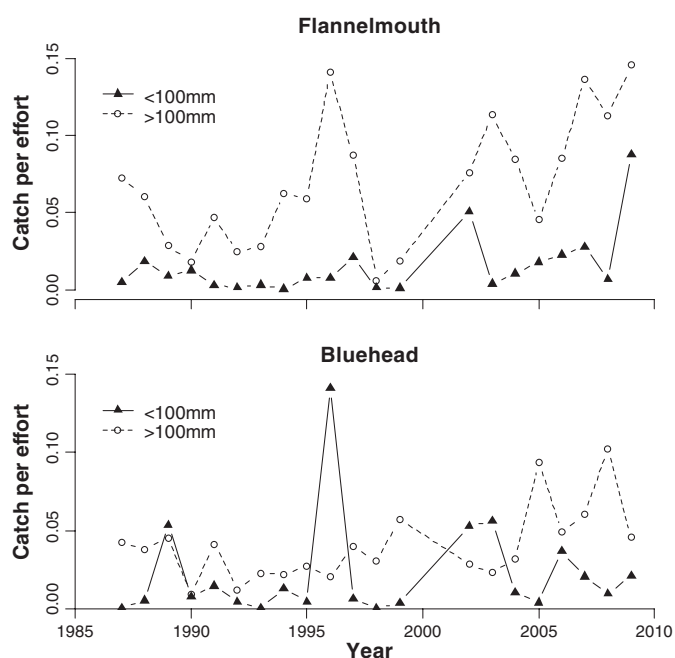


FIGURE 11. Trends in spring hoop-net catch per effort for age-1 (<100 mm) and older flannelmouth and bluehead suckers in the lower 1,200 m of the Little Colorado River. Data are from Grand Canyon Monitoring and Research Center (GCMRC) databases, summarized by W. Persons, GCMRC (personal communication). Each data point represents a mean of 127–479 (average, 292) net-nights of fishing over mid-April to mid-May.

(mainly rainbow trout *Oncorhynchus mykiss*) from the main stem near the LCR from 2003 onward. A particularly controversial issue is the relative importance of diurnal flow variation versus cold water as negative influences on native fish recruitment. Some stakeholders call for complete elimination of such variation (so-called “SASF” or seasonally adjusted steady flow policy) while others argue that restoration of warmer waters (through policies like putting a temperature control device on Glen Canyon Dam) combined with control of nonnative predators could be just as effective without the high costs associated with lost power production during peak demand periods. The sucker abundance trends support the latter argument, i.e. substantial increases in native fish recruitment can apparently be achieved without resorting to the relatively expensive SASF policy. There was apparently no beneficial effect of MLFF, as evidenced by low recruitments and declining overall sucker abundance from 1990 to 2000. There was no substantial persistent effect of the LSSF experiment; CPUE sampling during and after the steady flow period showed very high abundances of juvenile suckers in the main stem during the steady flow, but then showed an immediate decline when the experiment ended (Trammell et al. 2002). There was a very large flannelmouth sucker recruitment response beginning in 2003 when warming coincided with initiation of the mechanical removal program, but a large increase in bluehead sucker recruitment occurred a year earlier apparently owing to conditions in the LCR that were

unrelated to main-stem water management. Cooling of the river again in 2006 did not apparently cause immediate recruitment failure, at least as evidenced by continued high catches of juvenile flannelmouth suckers (i.e., ASMR estimates for the 2006 spawning year are not reliable); this indicates that there has probably also been a substantial benefit from the mechanical removal program.

The CPUE data and ASMR results both indicate that upward trends in flannelmouth sucker recruitment started before the major temperature and predator removal treatments of 2003, which is coincident with declines in rainbow trout abundance that also started before 2003. This is evidence of the effect of rainbow trout on flannelmouth sucker recruitment independent of a temperature effect. Further support for this effect comes from intensive rainbow and brown trout diet composition sampling conducted during the mechanical removal (Yard et al. 2011), which showed enough juvenile suckers in trout stomachs to account for as much as 50% annual mortality rates of these juveniles when data were combined with trout abundance estimates and bioenergetics estimates of trout food consumption rates.

The electrofishing cpue data provided by S. Rogers (Arizona Game and Fish, personal communication) indicate that the most dramatic increases in juvenile flannelmouth sucker abundance occurred well downstream from the LCR where mechanical removal efforts were concentrated, i.e., below RM 100 (rkm 161) (the LCR is at RM 61.5 [rkm 99]). However, tributary-spawning populations below the LCR are relatively small, and it is quite possible that the increase in downstream juvenile abundances largely represents LCR-origin juveniles that now enjoy much improved survival (due to the mechanical removal of rainbow trout) in the early part of their downstream dispersal. There is a similar downstream trend in bluehead sucker juvenile abundance in the electrofishing data, but the overall main-stem abundance estimates are much lower than those estimated by ASMR for the combined LCR and main-stem population.

Problems with the ASMR analysis reveal a clear need in the Grand Canyon and in other systems with tagging programs for temporal and spatial consistency in sampling effort and for spreading that effort to make capture probability for all fish as nearly equal as possible. A consistent sampling regime would also lead to better cpue trend indices, which are critical for cross-validation and troubleshooting methods based on mark-recapture data. Unfortunately, the sampling program appears to be moving in the opposite direction, and there has been a reduction in main-stem sampling effort since 2006 and a current discussion about cutting the LCR mark-recapture effort.

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