

Abundance Trends and Status of the Little Colorado River Population of Humpback Chub: An Update Considering 1989–2006 Data



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By Lewis G. Coggins, Jr.
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Cover photograph: Adult humpback chub (*Gila cypha*). Photograph courtesy of the Arizona Game and Fish Department.

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Abundance Trends and Status of the Little Colorado River Population of Humpback Chub: An Update Considering 1989–2006 Data

By Lewis G. Coggins, Jr.

Executive Summary

In 1967, the humpback chub (*Gila cypha*) (HBC) was added to the federal list of endangered species and is today protected under the Endangered Species Act of 1973. Only six populations of humpback chub are currently known to exist, five in the Colorado River Basin above Lees Ferry, Arizona, and one in Grand Canyon, Arizona. The majority of Grand Canyon humpback chub are found in the Little Colorado River (LCR)—the largest tributary to the Colorado River in Grand Canyon—and the Colorado River near its confluence with the Little Colorado River. Monitoring and research of the Grand Canyon humpback chub population is overseen by the U.S. Geological Survey's (USGS) Grand Canyon Monitoring and Research Center (GCMRC) under the auspices of the Glen Canyon Dam Adaptive Management Program (GCDAMP), a Federal initiative to protect and improve resources downstream of Glen Canyon Dam.

This report provides updated information on the status and trends of the LCR population in light of new information and refined assessment methodology. An earlier assessment of the LCR population (Coggins and others, 2006a) used data collected during 1989–2002; the assessment provided here includes that data and additional data collected through 2006. Catch-rate indices, closed population mark-recapture model abundance estimates, results from the original age-structured mark recapture (ASMR) model (Coggins and others, 2006b), and a newly refined ASMR model are presented. This report also seeks to (1) formally evaluate alternative stock assessment models using Pearson residual analyses and information theoretic procedures, (2) use mark-recapture data to estimate the relationship between HBC age and length, (3) translate uncertainty in the assignment of individual fish age to resulting estimates of recruitment and abundance from the ASMR model, and (4) evaluate past and present stock assessments considering the available data sources and analyses, recognizing the limitations inherent in both.

A major task of this study was to improve the overall methodology used to conduct HBC stock assessment by addressing concerns identified in an independent review conducted in 2003 (Kitchell and others, 2003). The review

report identified that the current technique of assigning age to individual fish based on length was a potential source of bias in ASMR estimates of abundance and recruitment, and called for a more complete examination of this potential error source. Additionally, the review suggested that further work to develop procedures to better arbitrate among alternative assessment models (e.g., ASMR 1–3) would be beneficial.

To address the first of the concerns identified by the independent review, this study uses mark-recapture data to develop a temperature-dependent growth model to characterize the relationship between HBC age and length. This model attempts to account for temperature differences resulting from both ontogenetic habitat shifts between the Little Colorado and the mainstem Colorado Rivers as well as seasonal variation in water temperature within the LCR. The resulting growth model is then used to characterize the error in assigning age to individual fish based on length. Results presented in this study suggest that ageing error does not result in large bias in either abundance or recruitment estimates from the ASMR model. However, incorporating ageing error into the assessment does result in less precise estimates, particularly for recruitment.

To address the second concern brought forward in the review report related to model selection procedures, this study arbitrated among the competing models by both examining model fit using Pearson residual analyses and considering information theoretic measures. Although adult abundance estimates and trend varied little among all models considered, these procedures identified ASMR 3 as the model whose underlying assumptions were most consistent with the data. Because ASMR 3 is also the most complex model, with a structure that allows for complex patterns in capture probability across ages and through time, further examination of model results suggest a decline in sampling efficacy for middle-aged fish since approximately 2001. Although the cause of this shift in sampling efficacy is still unknown, it is possible that changes in the timing of LCR sampling events or subtle changes in sampling gear may be, at least, partly responsible for this finding.

Monitoring data and assessment model results reported herein continue to support the hypothesis that the adult (age-4+) component of the LCR population experienced

approximately a 40%–50% decline between 1989 and 2001. More recently, the population appears to have increased, reaching between 5,300 and 6,800 individuals in 2006. This increase in adult fish abundance since 2001 appears to be a result of increased recruitment beginning in the mid- to late-1990s and continuing through at least 2002.

Inclusion of ageing error in the assessment procedures has resulted in less precise estimates of adult abundance and recruitment. These results suggest that experimental management actions that result in large changes in recruitment are much more likely to be detected than actions resulting in small changes in recruitment. Therefore, if ASMR results continue to be used as the primary measure of HBC recruitment variation, experimental management actions designed to induce large changes in HBC recruitment should be preferred to those likely to induce only small changes. Adherence to this recommendation will help guard against failing to recognize beneficial management policies simply because the magnitude of the response was not sufficient to be detected by the current stock assessment program.

Introduction

The humpback chub is a focal resource of the Glen Canyon Dam Adaptive Management Program, a federally authorized initiative to protect and mitigate adverse impacts to resources downstream of Glen Canyon Dam. The focus on HBC is primarily a result of its unique ecological role as one of the few remaining endemic aquatic species within Grand Canyon and its endangered listing status under the Endangered Species Act of 1973 (Gloss and Coggins, 2005). The purpose of this report is to provide updated information on the status and trends of the Little Colorado River population of HBC in light of new information and refined assessment methodology. Such information constitutes the cornerstone of the HBC monitoring program within the GCDAMP and is also potentially useful to evaluate the recovery goals for this species as specified by the U.S. Fish and Wildlife Service (USFWS; U.S. Fish and Wildlife Service, 2002). The U.S. Geological Survey's Grand Canyon Monitoring and Research Center has responsibility for the scientific monitoring and research efforts for the GCDAMP, including the preparation of reports such as this one.

The unique life-history attributes of HBC and the large variety of sampling and monitoring programs ongoing since the 1980s (Coggins and others, 2006a) prompted the development of a new type of age-structured open population capture-recapture model called the age-structured mark recapture model (Coggins and others, 2006b). This model was subsequently used in combination with other capture-recapture and index-based assessments to provide a comprehensive assessment of the LCR population of HBC (Coggins and others, 2006a). The ASMR approach has been subjected to a series of independent peer evaluations, both as part of the GCDAMP

(Kitchell and others, 2003; Otis and Wickham, U.S. Geological Survey, written commun., 2006) and peer-review processes required to publish journal articles and USGS products. These reviews all provide support for the ASMR as an appropriate modeling approach to evaluate trends in HBC population size and recruitment patterns. The ASMR model has undergone continuous refinement since the publication of the last assessment to improve the model's ability to provide insight into HBC population dynamics and responses to management actions. Presented herein are improvements to the model that include the development of a formal model comparison approach using Pearson residuals and information theory to evaluate model fit. Comparison of the three main formulations of ASMR, detailed below and in Coggins and others (2006b), allows more precise examination of model fit and shows how incorrect structural assumptions may bias model output.

A central problem in conducting HBC stock assessment is the assignment of age to individual fish. Though this problem is ubiquitous in fish assessment programs (Coggins and Quinn, 1998; Sampson and Yin, 1998), it is particularly difficult when working with endangered fish and when determination of age is only possible by killing the fish. In the case of humpback chub, an endangered species, determining the age of an individual requires killing the animal. To avoid this problem, individual fish ages must be assigned based on fish lengths and assuming some relationship between these two metrics. In past HBC assessments (Coggins and others, 2006a), it was assumed that the age-length relationship was adequately described (U.S. Fish and Wildlife Service, 2002); however, this age-length relationship is based on an extremely small sample size ($n \approx 57$) and is therefore suspect. Additionally, when assigning individual age based on this relationship, it was originally assumed that fish could be aged without error, clearly not a valid assumption. To alleviate these shortcomings, a new method is presented here for estimating the relationship between fish age and length using capture-recapture data. The uncertainty in the relationship between fish age and length is used to evaluate how uncertainty in the determination of age translates to uncertainty in abundance and recruitment estimates from ASMR using Monte Carlo simulations. These analyses offer insight into the HBC assessment and other monitoring programs for aquatic and terrestrial species where capture-recapture methodologies serve as the core of the assessment approach and precise trends in recruitment and mortality are difficult to quantify because of uncertainty in assigning age.

Retrospective analyses were employed to evaluate the performance of past model predictions of trends in adult HBC abundance and recruitment. These retrospective analyses consider only a subset of the available data and are structured to demonstrate how information collected annually is used to "update" estimates from previous years. Mortality and capture probability are potentially confounded in open population models (Williams and others, 2001). As an example, if an animal is not captured in a sample year is it because the animal died, or is it simply because the animal was not captured?

Though it is possible to estimate capture probability using only marked animals known to be alive because of subsequent recaptures, as in the Jolly-Seber model (Jolly, 1965; Seber, 1965), this method limits the sample size available to estimate capture probability and does not help with parameter confounding in the terminal year. In ASMR, the virtual population analysis structure allows the use of both marked and unmarked animals in the calculation of capture probability, but confounding between mortality and capture probability is not explicitly minimized via model structure. Retrospective analyses illustrate how perceptions of key population parameters, such as mortality rate, have been modified as more information becomes available, particularly following publication of Coggins and others (2006a and 2006b). These analyses are also useful in understanding how large changes in sampling intensity and protocols (e.g., minimal sampling in the LCR during 1996–99) may bias or otherwise distort understanding of HBC population dynamics based on capture-recapture analyses.

The primary objective of this report is to provide an updated stock assessment for the LCR population of HBC using data collected during 1989–2006. This assessment includes catch-rate indices, closed population mark-recapture model abundance estimates, the original ASMR model (Coggins and others, 2006b), and a newly refined ASMR model (detailed below). Coggins and others (2006a) used data collected during 1989–2002, and this report includes that data and additional data collected through 2006. Supporting objectives include (1) formally evaluating alternative stock assessment models using Pearson residual statistics and information theoretic metrics (Burnham and Anderson, 2002), (2) using mark-recapture data to estimate the relationship between HBC age and length, (3) translating uncertainty in the assignment of individual fish age to resulting estimates of recruitment and abundance from the ASMR model, and (4) evaluating past and present stock assessments considering the available data sources and analyses, recognizing the limitations inherent in both.

The ongoing monitoring program for HBC in Grand Canyon has varied in intensity over the years, but the primary sample locations, techniques, and personnel have remained remarkably consistent (Coggins and others, 2006a). Insight into the performance of the model is provided by conducting the annual stock assessment and continuously evaluating the performance of the assessment with retrospective analyses, independent peer evaluations, and tests of the model with simulated data. This comprehensive examination may prove useful to other adaptive management programs that seek to develop a robust monitoring component. In particular, the model may provide insight into (1) the limitations of monitoring alone in assigning cause and effect in association with prescriptive management actions, (2) the pathologies associated with large changes in monitoring protocols, and (3) a realistic assessment of the considerable uncertainty in results for a rare, elusive, long-lived organism, even after many years of intensive monitoring.

Methods

The methods employed for this analysis are presented in three separate sections. Section 1 describes methods used to update the 2002 HBC assessment metrics as presented in Coggins and others (2006a) and to refine the ASMR models. Additionally, section 1 describes the criteria used to assess model fit for each of the ASMR models. Section 2 outlines the methods used to estimate the relationship between HBC age and length based on mark-recapture information. Finally, section 3 describes the Monte Carlo simulations conducted to capture the uncertainty in the abundance and recruitment estimates that result from uncertainty in age assignment.

Section 1—2006 Humpback Chub Assessment Update with Refinements

Monitoring efforts for the humpback chub began in 1987 when a standardized hoop-net sampling program was implemented in the lower reaches of the Little Colorado River. During the subsequent 19 years, four sampling periods can be generally defined that correspond to different levels of sampling effort and protocol (Coggins and others 2006a). The initial sampling period (1987–91) consisted mainly of limited hoop netting in the lower 1,200 m of the LCR. Sampling period 2 (1991–95) involved an intensive sampling effort in both the LCR and the mainstem Colorado River as part of an environmental impact statement on the operation of Glen Canyon Dam (U.S. Department of the Interior, 1995). The third sampling period (1996–2000) also included both the Colorado River and the LCR but with severely reduced intensities compared to period 2. The final sampling period (2000–06) involved a higher sampling intensity relative to period 3 but decreased relative to period 2. During each of these sampling periods, HBC have been collected using multiple types of gear, including hoop nets and trammel nets in the LCR, and this same gear plus pulsed-DC electrofishing in the mainstem Colorado River (Valdez and Ryel, 1995; Douglas and Marsh, 1996; Gorman and Stone, 1999; Coggins and others, 2006a).

Index-Based Metrics

Although index-based metrics (e.g., catch rate) can be unreliable in tracking trends in population size (MacKenzie and others, 2006), these indices are frequently examined and are potentially useful for comparison with previous assessment efforts. With this caveat in mind and following Coggins and others (2006a), two long-term catch-rate time series were updated with data from 2003 through 2006, including (1) hoop-net catch rate of HBC in the lower 1,200 m of the LCR and (2) trammel-net catch rate of HBC in the LCR inflow reach of the Colorado River (defined as approximately 9 km upstream and 11 km downstream of the confluence; Valdez

and Ryel, 1995). Details about these sampling programs are provided by Coggins and others (2006a).

Tagging-Based Metrics

The heart of tagging-based assessment is the large number of uniquely tagged sub-adult [150–199-mm total length (TL)] and adult (≥ 200 -mm TL) fish that have been captured, measured, and implanted with passive integrated transponder (PIT) tags. Since 1989, more than 19,000 HBC have been captured, tagged, and released with unique identifiers. These data are maintained in a central database housed at the USGS Grand Canyon Monitoring and Research Center.

Mark-recapture methods to assess population abundance and vital rates have been widely used in fisheries and wildlife studies for more than 50 years, and numerous reviews have been conducted highlighting the general approaches (e.g., Seber, 1982; Williams and others, 2001). Traditional methods (e.g., Jolly-Seber-type methods) generally rely on recaptures of tagged individuals to estimate abundance, recruitment, and survival. Basically, the approach is to create a known population of marked, or tagged, fish that are repeatedly sampled to obtain time series estimates of mark rate (i.e., the proportion of the overall population that is marked) and the number of marked fish alive in the population. These metrics are subsequently used to estimate capture probability, abundance, recruitment, and survival.

The ASMR model differs from the traditional approach, because, in general, it contains more structural assumptions through the specification of a population accounting structure that governs transition of both marked and unmarked animals through ages and time. Age-structured stock assessment theory (Edwards and Megrey, 1989) is used to annually predict the numbers of marked and unmarked fish available for capture in a standard fisheries virtual population analysis framework (Quinn and Deriso, 1999). The total number of marked fish depends on the number of fish recently marked as well as the number of previously marked fish decremented by mortality rate. The number of unmarked fish depends on the recruitment over time, the number of fish marked from a given brood-year cohort, and the mortality rate. These annual predictions of the abundance of marked and unmarked fish are further segregated by age such that age-specific survival and capture probability may be modeled. Parameters are estimated by comparing predicted and observed age- and time-specific captures of marked and unmarked fish in a Poisson likelihood framework.

The ASMR model has three different parameterizations (ASMR 1–3) that vary in how the terminal abundance is estimated and how age- and time-specific capture probability is modeled. Both ASMR 1 and ASMR 2 assume that age- and time-specific capture probability can be modeled as the product of an annual overall capture probability multiplied by age-specific vulnerability. This is similar to the common parameterization of fishing mortality in assessment models under the “separability assumption” (Megrey, 1989) and diminishes the size of the parameter set since it is not necessary to separately

estimate each age- and time-specific capture probability. These models further assume that vulnerability is asymptotic with age. As such, vulnerability is assumed to be unity for fish age-6 and older and estimated only for the younger fish. Finally, annual age-specific vulnerabilities are assumed to be equal among each sampling period, as described above. Implicit in this assumption is that within a sampling period, annual age-specific capture probabilities differ only as a scalar value related to the annual overall capture probability.

The primary difference between ASMR 1 and ASMR 2 is how the terminal abundances are calculated. ASMR 1 estimates an overall terminal-year capture probability and calculates age-specific terminal abundances (both marked and unmarked) as the ratio of age-specific catch (both marked and unmarked fish) and age-specific capture probability (i.e., product of the terminal-year capture probability and sampling period 4 age-specific vulnerability). In contrast, ASMR 2 treats age-specific terminal abundances up to age-13 as individual parameters. Terminal abundances for subsequent ages are estimated by applying age-specific survivorship to the age-13 abundance. This difference in formulations decreases the parameter count for ASMR 1 relative to ASMR 2 at the expense of assuming that the vulnerability schedule in the terminal year is identical to the rest of period 4.

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

In addition to the ASMR assessments, the time series of the annual spring abundance estimates in the LCR are updated. Abundance of HBC in the LCR greater than or equal to 150 mm TL was estimated during the early 1990s and 2001–06, using closed population models. These models included the CAPTURE suite of models (Otis and others, 1978) and Chapman-modified, Lincoln-Petersen, length-stratified models (Seber, 1982). The recent estimators use data collected annually during two sampling occasions in the spring. Full details of the sampling and estimation methods are provided by Douglas and Marsh (1996) and Coggins and others (2006a).

Coggins and others (2006b) recommended exploring the use of individual capture histories within the ASMR framework to reduce confounding between capture probability and mortality. Though the updated ASMR models presented in this report do not yet incorporate individual capture histories, they do model recaptured fish by annual-tagging cohort with the intent of reducing parameter confounding by increasing the number of observations available for parameter estimation. In the non-tag cohort, or pooled, version of ASMR described above and by Coggins and others (2006b), age- and time-specific predictions of recaptured fish are not separated by year of tagging. As an example, assume that ASMR 3 predicts that 50 marked age-6 HBC should be captured in 2002. These 50 fish could be comprised of fish tagged as age-5 in 2001, age-4 in

2000, age-3 in 1999, or age-2 in 1998. However, as the model is currently formulated, all age-6 fish recaptured in 2002 are pooled for a single observation. Assuming that the age- and time-specific captures of marked and unmarked fish are Poisson distributed, the log-likelihood, ignoring terms involving only the data, is computed as:

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

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

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

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

Evaluating Model Fit

Following Baillargeon and Rivest (2007), standardized Pearson residuals of observed and predicted age composition for both unmarked and marked fish were used to evaluate model fit among the three different ASMR models. The standardized Pearson residual is the difference between the observed and predicted values scaled by an estimate of the standard deviation as:

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

where n_t is the number of observations (e.g., the number of marked fish recaptured each year) and $o_{a,t}$ and $p_{a,t}$ are the proportions of fish in each year and age class observed and

predicted, respectively. The individual Pearson residuals for each combination of age and time were plotted to look for consistent bias for individual brood-year cohorts. In addition, quantile-quantile (Q-Q) plots were used to compare the distribution of the Pearson residuals to a theoretical normal distribution. The intercept of the theoretical curve is approximately the standard deviation of the distribution of Pearson residuals, where a small value of the intercept indicates a narrow distribution of the residuals. Deviations from the theoretical curve indicate a non-normal distribution of the Pearson residuals and imply that the model error is not well distributed (e.g., tending to more often either over- or under-predict age proportions) and possibly inducing bias in parameter estimates.

In addition to examination of model fit using Pearson residuals, information theory was also used to aid in model evaluation. The use of this approach is increasingly common in ecological studies to arbitrate among competing models and is primarily concerned with estimating the Kullback-Leibler (K-L) distance between the model and the “truth” as a measure of model support (Burnham and Andersen, 2002). The Akaike information criterion (AIC; Akaike, 1973) is the standard estimator for the relative K-L distance and is computed as a function of model likelihood and number of model parameters. Following review of the ASMR method in 2003 (Kitchell and others, 2003), it was pointed out that although ASMR uses a quasi-likelihood structure of estimating equations and true likelihood, estimates of relative K-L distance using AIC, though not strictly appropriate, would be useful for model arbitration (C. Schwartz, Simon Fraser University, written commun., 2003). Therefore, in addition to the evaluation based on Pearson residuals, an AIC evaluation was conducted.

Section 2—Estimating the Humpback Chub Growth Function Using Mark-Recapture Data

Capture-recapture data have long been used by biologists in an attempt to characterize growth rates of fish. The basic technique for estimating growth model parameters from capture-recapture data is to predict the amount of growth in the elapsed time between capture and recapture. Assuming the standard von Bertalanffy growth curve (Bertalanffy, 1938) predictions of length at time t and at time $t+\Delta t$, Fabens (1965) developed the most basic model where the predicted growth increment is given as:

$$\Delta L = L(t + \Delta t) - L(t) = (L_\infty - L(t))(1 - e^{-k\Delta t}), \quad (4)$$

where L_∞ and k are the asymptotic length and the rate at which length approaches L_∞ , respectively (Quinn and Deriso, 1999). Parameter estimates are found by minimizing the difference between predicted and observed growth increments.

Though this technique has been widely applied, numerous authors have pointed out that resulting parameter estimates will be biased if individual fish exhibit growth variability (e.g.,

Sainsbury, 1980; Kirkwood and Somers, 1984; Francis, 1988). Typically, k will be negatively biased and L_∞ will be positively biased using this technique. This, in turn, has prompted others to develop models to account and adjust for these biases (e.g., James, 1991; Wang and others, 1995; Laslett and others, 2002). Von Bertalanffy growth functions were estimated with these most recent methods. In general, however, poor results were obtained primarily because of the inability of the models to predict growth increments exhibited by small fish and large fish simultaneously (U.S. Geological Survey, unpub. data, 2007). These results suggest a “kink” in the growth curve, as would be found if fish grew along one curve when small and then switched to another when larger.

Because water temperature is a dominant driver of metabolic rate, and hence the von Bertalanffy k parameter (Paloheimo and Dickie, 1966; Essington and others, 2001), the “kink” hypothesis is consistent with a fish that is demonstrating an ontogenetic shift among habitats that have different water temperatures, as is the case with the LCR and mainstem Colorado River. The current reproductive ecology paradigm for the LCR population of HBC is that most successful recruitment occurs when fish are spawned and reared within the LCR (Valdez and Ryel, 1995; Gorman and Stone, 1999). However, as fish approach some critical size, it is thought that they begin to engage in a potadromous migration between the Colorado River and the LCR (Gorman and Stone, 1999). This ontogenetic shift in primary occupancy between two thermal habitats, and therefore two basal metabolic rates, could induce a pattern of shifting growth rate.

To account for this apparent pattern of shifting growth rate, methods proposed by Walters and Essington (University of British Columbia, University of Washington, respectively; written commun.; 2007) (hereafter Walters and Essington, written commun., 2007) to fit growth increment data to a general growth model (Paloheimo and Dickie, 1965) were used to describe the rate of change in weight as:

$$\frac{dW}{dt} = HW^d - mW^n, \tag{5}$$

where the first term describes anabolic (i.e., mass-acquisition) processes and is governed by a term representing the mass-normalized rate at which the animal acquires mass (H), the mass of the animal (W), and a parameter (d) describing the scaling of the anabolic process with mass. The second term represents catabolic (i.e., mass loss through basal metabolism, activity, and gonad production) processes where m is the mass-normalized rate at which the animal loses mass and n is the scaling factor of catabolic processes with mass. Assuming a constant relationship between length and weight over time as:

$$W = aL^b, \tag{6}$$

where L is length and a and b are constant, simple algebra provides an analogous relationship for the rate of change in length as:

$$\frac{dL}{dt} = \alpha L^\delta - \kappa L^\eta. \tag{7}$$

Constants in this relationship are related to those in equations (5) and (6) as:

$$\alpha = \frac{a^{d-1}H}{b}, \tag{8}$$

$$\kappa = \frac{a^{n-1}m}{b}, \tag{9}$$

$$\delta = bd - b + 1, \text{ and} \tag{10}$$

$$\eta = bn - b + 1. \tag{11}$$

Essington and others (2001) review these relationships and describe the derivation of the standard von Bertalanffy growth function as the integral of equation (7) when $n = 1$, $b = 3$, and $d = 2/3$. This is the situation where catabolism scales linearly with mass, the length–weight relationship is isometric, anabolism scales as $2/3$ mass, and results in the standard von Bertalanffy growth model:

$$L(t) = L_\infty \left(1 - e^{-k(t-t_0)}\right), \tag{12}$$

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

Walters and Essington (written commun., 2007) then define a protocol to estimate the parameters of equation (5). To restate this definition, first assume that measurement errors in the length of fish are normal with variance σ_m^2 , and that all fish follow a standard von Bertalanffy growth curve (equation 12) with shared k and individual L_∞ . The predicted length of fish at time of recapture can be found by rearranging the Fabens equation (4) as:

$$L(t + \Delta t) = L(t) + (L_\infty - L(t))(1 - e^{-k\Delta t}). \tag{13}$$

Assuming that individual L_∞ is normally distributed with variance σ_L^2 , the variance of each $L(t + \Delta t)$ given $L(t)$, mean L_∞ , σ_L^2 , and σ_m^2 will be:

$$\sigma_{L(t+\Delta t)}^2 = \sigma_m^2 \left(1 + e^{-2k\Delta t_i}\right) + \sigma_L^2 \left(1 - e^{-k\Delta t_i}\right)^2. \tag{14}$$

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

$$D_i = L(t + \Delta t)_i - L(t)_i - (L_\infty - L(t)_i)(1 - e^{-k\Delta t}) \quad (15)$$

Walters and Essington (written commun., 2007) note that it is then possible to estimate the parameter vector $\theta = \{L_\infty, k, \sigma_L^2, \sigma_m^2\}$ by maximizing the log-likelihood function:

$$\ln L(\theta|L(t), L(t + \Delta t)) = -\frac{s}{2} \sum_i \frac{D_i}{\sigma_{L(t+\Delta t)}^2} - \frac{1}{2} \sum_i \sigma_{L(t+\Delta t)}^2, \quad (16)$$

where s is the number of growth increments. This is essentially an inverse-variance weighting strategy. However, they further note that the variance components of the measurement error and L_∞ are typically not separately estimable, such that, in practice, it is usually necessary to specify one of them a priori.

Though this procedure is applicable assuming fish growth is described by equation (12), if fish growth is described by equation (7), there is no analytical solution of $\sigma_{L(t+\Delta t)}^2$, as in equation (14). However, Walters and Essington (written commun., 2007) note that if one first estimates θ , and in particular k , using equations (14–16), and assuming that the individual variances computed using equation (14) are adequate, then deviations from the general model (equation 7) can be used in the log-likelihood. These deviations are computed as:

$$D_i = L(t + \Delta t)_i - \int_{t=t_i}^{t=t_i+\Delta t} (\alpha L^\delta - \kappa L^\eta) dt \quad (17)$$

After specifying the parameters a and b from equation (6), estimation proceeds as above with the parameter vector $\theta = \{H, d, m, n, \sigma_L^2, \sigma_m^2\}$.

The above procedure was implemented using both Excel Solver tool (Lasdon and Allan, 2002) and AD Model Builder (ADMB; Fournier, 2000) to obtain estimates of θ . The parameter set was reduced by specifying $\sigma_m^2 = 31.8 \text{ mm}^2$, based on an analysis of the observed error between consecutive measurements of identical fish within 10 days. The a and b parameters for equation (6) were specified as 0.01 and 3, respectively. To calculate the conditional variance of each $L(t + \Delta t)$, k was specified as 0.145, based on previous analyses. Additionally, penalty terms were included in the log-likelihood equation (16) to constrain d and n so that they did not deviate too far from the theoretical values, assuming standard von Bertalanffy growth of 2/3 and 1, respectively. Alternative weight values on these penalty terms were evaluated to find an appropriate tradeoff between minimum weights and decreased log-likelihood.

Because all the information contained in the mark-recapture data are for fish larger than 150 mm TL, extrapolating results to the growth rate of smaller fish could be problematic. Though this is not necessarily a concern related to assignment of age to fish greater than or equal to 150 mm TL, as required by ASMR, an accurate growth curve across all sizes would be desirable. Fortunately, Robinson and Childs (2001) conducted rigorous monthly sampling of juvenile HBC in the LCR during 1991–94. They used these data to estimate average monthly length from age-0 months to age-32 months. These estimates were used in an additional log-likelihood term to constrain the predicted lengths from the general model to be similar to those reported by Robinson and Childs (2001). Using these auxiliary data and assuming normal deviations allowed the incorporation of information on the growth rate of fish before they are large enough to be implanted with PIT tags. With these constraints in place, the full log-likelihood was:

$$\ln L(\theta|L(t), L(t + \Delta t)) = -\frac{s}{2} \sum_i \frac{D_i}{\sigma_{L(t+\Delta t)}^2} - \frac{1}{2} \sum_i \sigma_{L(t+\Delta t)}^2 - \frac{1}{2\lambda} \left(d - \frac{2}{3}\right)^2 - \frac{1}{2\lambda} (n-1)^2 - \frac{mos}{2} \sum_{i=1}^{mos} \ln(L(i) - \ell(i))^2, \quad (18)$$

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

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

Walters and Essington (written commun., 2007) present a method to allow temperature dependence in α and κ in

equation (7). This is accomplished by defining temperature-dependent multipliers of α and κ as:

$$f_c(T) = Q_c \frac{(T-10)^{\delta}}{10^{\delta}} \quad \text{and} \quad (19)$$

$$f_m(T) = Q_m \frac{(T-10)^{\eta}}{10^{\eta}}, \quad (20)$$

where $f_c(T)$ is the temperature-dependent multiplier of α , and $f_m(T)$ is the temperature-dependent multiplier of κ . The consumption and metabolism coefficients (Q_c and Q_m) of a Q10 relationship allow these multipliers ($f_c(T)$ and $f_m(T)$) to increase or decrease with temperature (T). One can think of these constants as the amount that the anabolic or catabolic processes will change with an increase in temperature from 10°C to 20°C. Inclusion of these temperature-dependent multipliers into equation (7) yields:

$$\frac{dL}{dt} = \alpha L^{\delta} f_c(T) - \kappa L^{\eta} f_m(T). \quad (21)$$

Equation (21) accounts for growth rate differences as a function of temperature but does not account for movement between the two thermal habitats. Thus, a logistic function was used to model the probability of occupancy in either the LCR or the mainstem Colorado River as a function of fish length. The probability of LCR occupancy is assumed to be:

$$PLCR = 1 - \frac{0.8}{1 + e^{-\frac{(L-L_i)}{20}}}, \quad (22)$$

where L is fish total length and L_i is the fish total length where the probability of year-round residence in the LCR is 0.6. The behavior of this model is such that the probability of year-round LCR residency approaches unity at lengths much less than L_i and decreases to 0.2 at lengths much larger than L_i . The number 20 in the denominator of the exponent governs the rate at which the probability changes from near unity to near 0.2. The asymptote at 0.2 requires at least some LCR residency for even the largest fish and is consistent with the observation that adult HBC use the LCR for spawning (Gorman and Stone, 1999).

A weighted temperature function experienced by fish of a particular length can then be defined as:

$$T(t) = (PLCR)T_{LCR}(t) + (1 - PLCR)T_{MS}(t), \quad (23)$$

where $T_{LCR}(t)$ is the time-dependent water temperature in the LCR and $T_{MS}(t)$ is the time-dependent water temperature in the mainstem Colorado River. This overall temperature experi-

enced by a fish of a given length is then used in equation (21) to predict growth rate considering time-dependent changes in water temperature and size-dependent changes in LCR versus mainstem Colorado River occupancy.

To model the time-dependent water temperature in the LCR, data reported by Voichick and Wright (2007) were used to predict average monthly water temperature. A sine curve was fit to these data as:

$$T_{LCR}(t) = T_{ave} + (T_{max} - T_{ave}) \sin(2\pi(t + t_{peak})), \quad (24)$$

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

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

The parameter vector $\theta = \{H, d, m, n, Q_c, L_i\}$ was estimated by maximizing the log-likelihood equation (18). With this more complex model, predicted recapture lengths were found by integrating the temperature-dependent growth model (equation 21) with respect to time. These predictions were then used in the second term of equation (17) to compute the deviations between observed and predicted growth. Walters and Essington (written commun., 2007) recommend constraining $1.8 < Q_m < 2.4$ following guidance from a meta-analysis by Clark and Johnson (1999). Therefore, Q_m was specified as 2. The weighting term for the log-likelihood penalties were specified equal to those found to be optimum for the previous analysis. To further reduce the parameter set, σ_L^2 was specified as 2,000 to correspond with a coefficient of variation of about 10%, as is typically observed in fish populations (S. Martell and C. Walters, University of British Columbia, oral commun., 2006). The relative fit to the data for the temperature-independent growth model (TIGM) and the temperature-dependent growth mode (TDGM) were evaluated using AIC techniques (Burnham and Andersen, 2002).

Section 3—Incorporation of Ageing Error in ASMR Assessments

As mentioned above, Coggins and others (2006a) assigned age to individual fish strictly as an inverse von

Bertalanffy function. This procedure ignores variability in the age of fish of a particular length and tacitly assumes that age assignments can be made much more precisely than is true. To account for uncertainty in the assignment of age using length, the probability of age for fish having length within a particular length interval $P(a|l)$ was estimated following methods reported by Taylor and others (2005). First, the probability of an age- a fish having length within length bin l is specified as:

$$P(l|a) = \frac{1}{\sigma_a \sqrt{2\pi}} \int_{l-d}^{l+d} \exp\left[-\frac{(l-l_a)^2}{2\sigma_a^2}\right] dl, \quad (25)$$

where length bin l has mid-point length l , minimum length $l-d$, and maximum length $l+d$. These probabilities can be thought of as a matrix with rows corresponding to length bins and columns as ages. As is obvious from equation (25), entries within a particular column (age) can be thought of as resulting from the integral over each length bin of a normal probability density with mean l_a and variance σ_a^2 . The mean length-at-age is computed from the temperature-dependent growth model and procedures described previously. The variance in length-at-age is $\sigma_a^2 = l_a cv_l$, according to the assumption that coefficient of variation in length (cv_l) at age is constant ($cv_l = 0.10$).

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

$$p(a|l) = \frac{P(l|a)}{\sum_{i=1}^A P(l|i)}. \quad (26)$$

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

$$N_{l,a} = N_a P(l|a), \quad (27)$$

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

$$N_a = R e^{-\sum_{i=1}^{a-1} M_i}. \quad (28)$$

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

$$P_{l,a} = \frac{N_{l,a}}{N_T}, \quad (29)$$

where

$$N_T = \sum_l \sum_a N_{l,a}.$$

The probability of age given length is then calculated as:

$$P(a|l) = \frac{P_{l,a}}{\sum_{i=1}^A P_{l,i}}. \quad (30)$$

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

$$M_a = \frac{M_\infty L_\infty}{l_a}, \quad (31)$$

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

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

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

number of categories equal to the number of ages. Assigned age for a single fish having length in bin l is therefore a multinomial random variable with probabilities $P(a|l)$ with a single draw. The multinomial random number generator within program R (R Development Core Team, 2006) was used to randomly assign age to tagged fish. Age-at-recapture was calculated as the sum of age-at-tagging and time-at-large. For each resulting dataset of captures- and recaptures-at-age, adult (age-4+) abundance and recruitment was estimated using ASMR 3. Additionally, ADMB was used to compute the 95% profile confidence interval for adult abundance and recruitment. This procedure was repeated to generate and analyze 1,000 datasets (i.e., Monte Carlo trials).

Results

2006 Humpback Chub Assessment Update with Refinements

Index-Based Assessments

Between 1987–99 and 2002–present, the Arizona Game and Fish Department sampled HBC using hoop nets in the lower 1,200-m section of the LCR. Examination of this catch-rate index suggests that abundance of both subadult (150–199-mm TL) and adult (≥ 200 -mm TL) HBC declined between 1987 and 1992 and remained relatively constant through much of the 1990s (fig. 1a). Since 2003, this index suggests a slight upward trend in the abundance of subadult fish. Note that several data points in the index are shifted slightly relative to those reported by Coggins and others (2006a). This adjustment resulted from additional standardization of the data used to construct this index (David Ward, Arizona Game and Fish Department, oral commun., 2007). The index of adult abundance in the LCR inflow reach of the Colorado River indicates a similar trend in adult fish (≥ 200 mm, fig. 1b). In general, this index shows a stable to declining trend in relative abundance through the 1990s with a slight indication of increased abundance in most recent years. All monthly trammel-net samples from the LCR inflow reach for 1990–2006 are presented in figure 1b. However, only samples from 1990–93, 2001, and 2005–06 (i.e., dark circles in figure 1b) represent robust sampling coverage throughout the entire reach. Annual sample sizes in 1994–2000 and 2002–03 (i.e., hollow circles in figure 1b) were between 2% and 50% of the 1990–93 average sample size, and in some years effort was focused near the LCR confluence where HBC density may have been highest. Thus, the 1990–93, 2001, and 2005–06 data are likely to best depict the overall trend of relative abundance within this reach. Simple linear regression analyses provide

estimated slopes that are not significantly different from zero ($p = 0.16$ for all data and $p = 0.26$ for the preferred data; fig. 1b).

Tagging-Based Assessments

As described above, the data required for the ASMR models are numbers of fish marked and recaptured each year and for each age. For the results contained in this section, all ages were assigned based on the standard von Bertalanffy growth curve as described in Coggins and others (2006b). With that in mind, examination of the age distribution of fish marked and recaptured since 1989 provides insight into the trends in sampling effort and also provides important information related to HBC survival (fig. 2). The top panel of figure 2 shows the numbers of newly tagged fish by age and year. The total number of fish marked annually is influenced by both trends in sampling effort and numbers of unmarked fish alive. The most consistent period of sampling has been 2001–present; approximately 1,100 fish have been tagged annually. Because a large fraction of the population was tagged in sampling periods 1 and 2, the majority of fish tagged in recent years are young fish and the number of new fish tagged each year declined with fish age. The bottom panel of figure 2 represents the numbers of fish of each age recaptured each year. The same patterns related to sampling effort are evident, but there are some very interesting patterns that result from the high sampling effort in the early to mid-1990s (fig. 2). For example, in 1995 a total of 1,244 HBC were collected and 902 of these fish had been marked in previous years. This pattern is evident for several years of data, indicating that the high sampling effort in the early 1990s resulted in marking upwards of 70% of the HBC population. The sampling program since 2000 (period 4) has been plagued by the low sampling effort in the mid- to late-1990s. For example, figure 2 shows that because few age-3 to age-5 fish were tagged during period 3, there were few age-8 to age-10 fish recaptured in the early 2000s. This contributes to the “spoon” shapes in the lower panel of figure 2, where there were relatively large numbers of fish younger than age-10 recaptured in period 4, lower catches of age-10 to age-15 fish, and relatively stable numbers of older than age-15 fish.

Another finding is the extreme longevity of HBC. This is most evident by examining the number of HBC of each age marked in each year and recaptured in subsequent years (fig. 3). Figure 3a shows the number of HBC of each age marked in 1989–92 and recaptured in subsequent years. This figure shows that a remarkable number of old fish (>age-15), first tagged in the early 1990s, continued to be recaptured into 2006. This slow decay pattern of tagged fish demonstrates the low mortality rate suffered by older HBC.

Closed Population Models

The time series of abundance estimates for HBC greater than or equal to 150 mm TL in the LCR during spring indicate

a decline in abundance from the early 1990s to the present (fig. 4). However, as is apparent in the data, these estimators are very imprecise with corresponding poor ability to detect significant trends. Additionally, preliminary analyses of data collected in this program suggest that the 2007 estimate may be up to twice as large as the 2006 estimate (R. Van Haverbeke, U.S. Fish and Wildlife Service, oral commun., 2007).

ASMR without Tag-Cohort Specific Data

Overall, the three ASMR formulations generally agree that adult (age-4+) HBC abundance has gradually increased since about 2001 (fig. 5). Among these three models, the 2006 adult abundance estimate is 6,690 (95% credible interval (CI) 6,403–6,994), 6,768 (95% CI 6,397–7,131), and 6,648 (95% CI 6,222–7,102) for models ASMR 1, 2, and 3, respectively. These results suggest that this population has increased 35%–40% from an estimated low abundance of approximately 4,800–5,000 during 2000–01. Estimated recruitment (age-2) among models is also in agreement (fig. 6). Following low recruitment for brood years during the early 1990s, all the models suggest that recruitment increased through the latter part of the 1990s. The biggest discrepancy among the three models is that ASMR 1 suggests a decline in recruitment following the 2000 brood year, while the other two models suggest stability. The structural assumptions of model ASMR 3 (see Coggins and others, 2006b) do not permit a reliable recruitment estimate for brood year 2003. An additional difference in the model results is in the estimation of instantaneous adult mortality (M_{∞}), where adult mortality ranges from 0.119 (ASMR 1) to 0.133 (ASMR 3).

Model Evaluation and Selection

With these results in hand, the question becomes which model is best? Stated another way, which model produces results most consistent with or best supported by the data? In this case, the discrepancies among model results related to adult abundance are not large; as a result, selecting the best model is probably not critical from a management or conservation perspective. However, the models do reflect rather different hypotheses about recruitment trends. Model ASMR 1 supports the hypothesis that recruitment has declined following the 2000 brood year, while the other two models suggest relative stability. Therefore, selecting the model (hypothesis) that is the most consistent with the data is desirable.

Model fit to the data was assessed by plotting the Pearson residuals of the observed and predicted numbers of fish marked and recaptured for each year and age (figs. 7–9). The patterns in Pearson residuals for both ASMR 1 (fig. 7) and ASMR 2 (fig. 8) demonstrate systematic lack of fit for particular sets of cohorts. This is best seen in the recapture residuals where it is apparent that there are more fish observed than predicted for about eight pre-1990 cohorts, particularly for observations after 2000. Additionally, there are fewer recaptures associated with the 1992 cohort than are predicted. These

systematic trends are likely imposing bias in the model results for ASMR 1 and ASMR 2. In contrast, there is much less systematic lack of fit in the residual patterns for ASMR 3 (fig. 9). Additionally, among the three models the Pearson residual standard deviation is smallest for ASMR 3.

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

Although it is comforting to find agreement between these two evaluations, one should ask: why is the more complicated structure of ASMR 3 needed to adequately fit the data? Since the fundamental difference between ASMR 1 and 2 and ASMR 3 is the amount of flexibility in age- and time-specific capture probabilities, the pattern in ASMR 3 estimated capture probabilities is of interest (fig. 10). The discrepancy in capture probabilities between sampling period 2 (i.e., 1991–95; heavy gray lines) and sampling period 4 (i.e., 2000–06; heavy black lines) suggests a major shift in the gear selectivity. Sampling since 2000 appears to be much less effective at capturing fish between ages 9–20 years old than was sampling during the second period. Since structural assumptions in ASMR 1 and ASMR 2 require that vulnerability is asymptotically related to age, it is not surprising that these models are not able to account for this unexpected pattern, and thus display poor model fit.

ASMR with Tag-Cohort Specific Data

In addition to repeating the analyses by Coggins and others (2006a) above, the ASMR models were also fit to the tag-cohort specific data using the log-likelihood in equation (2). The trends in adult abundance and recruitment are quite similar to those found using the simpler log-likelihood (figs. 11 and 12). In general, adult abundance estimates are slightly higher at the beginning of the time-series and slightly lower at the end. Adult abundance estimates for 2006 are 6,057 (95% CI 5,797–6,308), 6,138 (95% CI 5,842–6,458), and 5,893 (95% CI 5,554–6,242) for the ASMR 1, 2, and 3 models, respectively. Adult mortality (M_{∞}) estimates from the models fit to the stratified data indicate slightly higher adult mortality (0.128, 0.137, and 0.148 for ASMR 1–3, respectively) than when fit to the pooled data. This finding is consistent with the more rapid decay observed in the time-series of adult abundance. Another difference is a slight increase in the precision of the estimates using the stratified data (fig. 13). This observation provides marginal confirmation of the assertion that it

might be possible to extract additional information considering the stratified, rather than pooled, data.

Model Evaluation and Selection

Examination of Pearson residuals for the tag-cohort specific models suggests similar patterns in model misspecification for ASMR 1 and ASMR 2 (figs. 14 and 15). However, there appears to be even less residual pattern for ASMR 3 (fig. 16), suggesting slightly better agreement with the data than the pooled data model fit. This, again, suggests that segregation of the data is permitting greater extraction of information. Model evaluation using AIC methods strongly indicates that ASMR 3 is preferable (table 2), which is generally in agreement with the residual evaluation. Finally, a very similar pattern in estimated capture probability from ASMR 3 emerges, suggesting a similar mechanism to explain the poor performance of models ASMR1 and 2 (fig. 17).

Assessment Update Summary

The adult portion of the LCR HBC population appears to have increased in recent years as a result of increased recruitment, particularly associated with brood years 1999 and later. In addition, model evaluation procedures indicate that the results from model ASMR 3 are most consistent with the available data. Using data stratified by tagging cohort added additional information to the assessment, as indicated by the slightly higher precision of adult abundance estimates. However, adult abundance estimates, as reported, are extremely precise. This level of precision is questionable, since the assessment doesn't incorporate uncertainty in the assignment of age.

Estimating the Humpback Chub Growth Function Using Mark-Recapture Data

Both the temperature-independent (TIGM) and temperature-dependent (TDGM) growth models described in the methods section were fit to 14,971 observed growth intervals extracted from the HBC mark-recapture database. All fish were larger than 150 mm TL and the time interval between capture and recapture exceeded 30 days. Though greater than 60% of the fish were at large for 1 year or less, a small fraction of the observations were for much longer time intervals (fig. 18). The longest time interval in the dataset was 5,538 days (about 15 years).

The measurement error contained in the dataset was estimated by computing the observed difference in measured lengths of fish captured and recaptured within 10 days. This resulted in a measurement error variance of 31.8 mm² across all sizes of fish, implying that most TL measurements were within 11 mm of the true TL. This amount of measurement error is fairly high but not unexpected, considering the difficulty in measuring live fish. However, this error rate contributes substantially to the variability of observed growth rate.

The TIGM was fit with prior variance weighting terms on the d and n parameters $\lambda = \{0.00001, 0.0001, 0.001, 0.01, 0.1, 0.5, 1, 10, 100, 1,000, \text{ and } 10,000\}$ to explore the effect of constraining these parameters to values near standard von Bertalanffy values. The log-likelihood is nearly identical for all values of $\lambda = 0.01$ and greater, but reducing below $\lambda = 0.01$ caused large changes in the log-likelihood (fig. 19). Therefore, $\lambda = 0.01$ was specified as the optimal weighting value for both the TIGM and TDGM.

To estimate the parameters of the TDGM it was necessary to first fit the time-dependent LCR water temperature model. Fortunately, the sine curve function with parameters $t_{peak} = -0.011$, $T_{ave} = 17.9$, and $T_{max} = 23.2$ fit the observed average monthly temperatures very well (fig. 20).

The estimated parameters, log-likelihood, and AIC statistics for the TIGM and TDGM are presented in table 3. The parameter values for the TIGM suggest an extremely low value for the catabolic constant (m) and a catabolic scaling parameter value (n) greater than unity. This is a rather unlikely situation from a biological perspective and indicates that this model may not be well supported by the data. In contrast, the estimated scaling parameters for the TDGM are not much different than what would be expected under the standard von Bertalanffy model, where the anabolic scaling parameter (d) should be close to 2/3 and the catabolic scaling parameter (n) should be close to unity. Results from AIC indicate strong support for the TDGM over the TIGM. However, the parameter correlation matrices for each of these models show very high correlation, indicating that all of the parameters are not separately estimable (table 4). In situations such as this, where the model is not full rank, it has been suggested that the K-L distance is undefined (Viallefont and others, 1998; Bozdogan, 2000).

An alternative way to arbitrate among these two models is simply to examine the model fit to the data. The observed growth rate as a function TL at the start of the interval is extremely variable, particularly at smaller sizes (fig. 21). It is also apparent that all three lines (the fit of the TIGM and the fit of the TDGM corresponding to LCR water temperatures during summer and winter) differ from the strict linear relationship implied by a standard von Bertalanffy model. The temperature-independent model is somewhat of a compromise between the temperature-dependent summer fit and the temperature-dependent winter fit. It is also clear that observed summer growth is generally greater than observed winter growth, suggesting that growth rate is oscillating with temperature (fig. 22).

Each of the models was used to predict length as a function of age. In addition to the two models fit above, length-at-age was also predicted using the growth function reported in the USFWS recovery goals document (U.S. Fish and Wildlife Service, 2002) and using the TDGM for a constant temperature of 10°C (fig. 23). This last curve is equivalent to a fish experiencing a constant 10°C temperature and is a prediction of length-at-age for a fish spending its entire life in the mainstem Colorado River. Examination of these curves show

that the USFWS growth curve tends to predict somewhat smaller sizes at young ages and larger sizes at older ages than is implied by the mark-recapture data. The TIGM and TDGM predict very similar length-at-age with the exception of 10–25-year-old fish. Two features are apparent in the TDGM: (1) temperature-dependent periodic change in growth rate at ages younger than about age-5, and (2) an apparent “bend” in relationship at approximately age-4. This age corresponds to the length-at-transition (L_t) where HBC are rapidly shifting from primarily LCR occupancy to primarily mainstem Colorado River occupancy. A L_t length of 236 mm TL is most strongly supported by the data and the TDGM (table 3).

Finally, it is informative to use the TDGM to predict monthly growth increments as a function of TL. These predictions, based solely on field data, can then be compared to laboratory observations of the same or similar species. Growth rate predictions from the LCR population are much higher than a population experiencing constant 10°C temperature (fig. 24). This latter growth rate is presented as a prediction of monthly growth rates that would be observed in the mainstem Colorado River.

Incorporation of Ageing Error in ASMR Assessments

The TDGM and the procedures identified in the methods sections were used to construct seasonal $P(a|l)$ matrices. The resulting probability distributions were subsequently plotted as surfaces to allow examination of the uncertainty in predicting age given length (fig. 25). The most obvious feature of these probability surfaces is the increasing uncertainty in age assignment with increasing length. For instance and considering the April–June $P(a|l)$ surface (fig. 27, top left panel), one can see that a 150-mm-TL fish is age-2 with highest probability, but there is some chance that it could be any age between age-1 and age-4. In contrast, a 300 mm fish is approximately age-7 with highest probability, but could be as young as age-4 or as old as age-18. It is such uncertainty that this assessment was intended to incorporate.

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

Estimated adult abundance (age-4+) ranged from 9,322 (95% CI 8,867–9,799) in 1989 to 6,017 (95% CI 5,369–6,747) in 2006 (fig. 26). The coefficient of variation for these

estimates ranges from approximately 1%–7%, in contrast to 0.5%–3% if uncertainty in assignment of age is ignored (figs. 13 and 27). The trend in recruitment considering the new growth function and ageing error contains much greater uncertainty than when ageing error is ignored (figs. 12 and 28). Although the point estimates from the two models are in agreement that recruitment has been increasing since the mid-1990s, the uncertainty in the recruitment estimates from the latter assessment makes statements about differences among years tenuous.

Discussion

2006 Humpback Chub Assessment Update with Refinements

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

The LCR hoop-net abundance index suggests a modest increase in the abundance of juvenile fish and stability in the abundance of adult fish. The LCR inflow reach trammel-net abundance index indicates stability with a slight indication of increased abundance in 2005 and 2006. Although confidence in the mark-recapture-based open population model results might be higher if the catch-rate metrics indicated similar trends, it is not surprising that the catch-rate metrics are not able to detect a 25% increase in abundance. The basic, and frequently violated, assumption that must be made when evaluating a catch-rate time series is that capture probability must remain constant for the metric to be well correlated with abundance (MacKenzie and Kendall, 2002). There is good reason to suspect that this assumption is violated for the index data series presented in this update because of the influence of abiotic factors on catchability (Arreguin-Sanchez, 1996). As an example, a likely significant driver of catchability in the LCR is turbidity (Dennis Stone, U.S. Fish and Wildlife Service, oral commun., 2007; U.S. Fish and Wildlife Service, unpub. data, 2007), and turbidity varies greatly in the mainstem Colorado River and the LCR as a function of tributary freshets and dam operations.

A more significant concern is the lack of correlation between ASMR 3 results and the closed population model

mark-recapture estimates in the LCR. However, given the low precision in the LCR estimates and the possible influence of migration magnitude and timing on the results of this program, it is, again, not too surprising that these assessments are not strongly correlated with the ASMR 3 results. The low precision of these estimates may not permit detection of a 25% increase in adult abundance. Additionally, preliminary analyses of data collected during 2007 suggests that the abundance estimate for 2007 may be twice as large as the 2006 estimate (R. Van Haverbeke, U.S. Fish and Wildlife Service, oral commun., 2007). Though this result would provide support for the ASMR 3 results, it would also call into question the ability of the LCR program to provide a consistent metric of overall population size. One would have to reconcile whether that level of change was related to a very large age class entering the sampled population, a larger than normal fraction of the population entering the LCR during the sampling period, or some other factor.

Though the GCDAMP is fortunate to have such a large mark-recapture database for these high-profile endangered animals, significant changes in sampling protocol over time continue to cause ambiguity. As identified by Melis and others (2006), retrospective analyses of the data suggest a continual updating of the adult mortality rate estimates as additional information has been collected since 2000. Following addition of the 2006 data, this updating is again apparent (fig. 29). It appears that adult mortality rate estimates may be stabilizing as more data are collected, but it is difficult to be certain. The likely cause of this updating is the sampling program essentially having to “catch-up” following the low sampling effort during period 3. When focused analyses of this dataset began with open population models in 2000 (U.S. Geological Survey, unpub. data, 2000), there had been so little sampling in the mid- to late-1990s that the models interpreted the lack of old fish captures as a relatively high adult mortality rate. As additional data were collected through a more rigorous sampling program during 2000–06, mortality rate and capture probability estimates were adjusted. The hope is that if the GCMRC continues with a fairly uniform sampling program over time, adult mortality rate will stabilize and only abundance estimates in the last few years of the dataset will be subject to significant updating.

An additional finding, identified by Martell (2006) and in this assessment, is the major change in gear selectivity between sampling period 2 and sampling period 4. Though it is presently unknown what may have caused this change, several possibilities have been suggested. First, it is possible that elimination of the extensive trammel-netting effort during sampling period 4 may have reduced the capture probability of middle-aged fish. If this is true, fitting the ASMR 3 model only to data collected in the LCR should indicate similar patterns in capture probability during both sampling periods. However, when this fit was conducted, the patterns were essentially unchanged from those predicted from the entire dataset (U.S. Geological Survey, unpub. data, 2007). This is not too surprising, since fish captured in the LCR inflow

reach of the Colorado River represent only about 11% of the entire HBC mark-recapture database. Second, it is possible that reducing the use of large hoop nets in the LCR during sampling period 4 reduced the catch rate of larger fish. Though this is possible, the ASMR 3 results indicate a reduction in capture probability of mid-sized fish, rather than in the largest individuals. Finally, it is possible that sampling in the LCR only 4 months of the year during period 4, as opposed to 10–12 months of the year during period 2, may be the cause. This is certainly possible, particularly if there is some differential migration timing for the middle-aged fish relative the oldest individuals.

One obvious result of all this confusion is that large changes in sampling protocol should be carefully considered in light of how those changes may affect the ability to infer population change. This is particularly true for populations that are in low abundance and exhibit low capture probability. A careful simulation of considered changes may help to expose potential problems or, at the very least, help to clarify thinking related to proposed changes in sampling protocol. Finally, those considering implementing a mark-recapture-based monitoring program should plan to expend considerable sampling effort using similar protocols for the duration of the monitoring program. The results herein support the recommendations of Williams and others (2001) that the objectives of the monitoring program, with regard to issues such as precision of measured quantities, should not only be clearly identified, but that the measured quantities should be directly linked to the management objectives.

Estimating the Humpback Chub Growth Function Using Mark-Recapture Data

Understanding the relationship between fish age and fish length is necessary to address a host of fundamental issues across a broad spectrum of fisheries management. Though this relationship is typically estimated using paired observations of individual fish age and length (Quinn and Deriso, 1999), this often requires sacrificing the animal to obtain the age information. The TIGM and TDGM seek to obtain this information through non-lethal sampling and using information that is frequently collected in routine mark-recapture studies. Particularly for endangered species such as the HBC, a non-lethal method to obtain information on growth rate is mandatory.

In the postdam Colorado River, temperature is thought to be a limiting factor affecting native fish spawning, rearing, growth, and survival (Kaeding and Zimmerman, 1983; Valdez and Ryel, 1995; Gorman and Stone, 1999). As a result, much effort has been expended attempting to better understand how temperature affects basic functions such as growth (Clarkson and Childs, 2000; Robinson and Childs, 2001; Petersen and Paukert, 2005), swimming ability (Ward and others, 2002), and predation risk (Ward and Bonar, 2003). However, because of the sensitivity of HBC at larval and juvenile stages, much of the emphasis on understanding the effects of temperature

on growth has been focused on these smaller individuals. The analyses described in this report address the effect of temperature on growth rate of HBC and attempt to estimate the length at which fish transition from primarily LCR occupancy to primarily mainstem occupancy. The general implication from the findings reported herein is that growth rate will increase substantially with a temperature increase from 10°C to 20°C, as is indicated by the values of $Q_c = 4.6$ and $Q_m = 2.0$. These coefficients suggest that anabolic processes will more than double relative to catabolic processes across this temperature range.

As an additional evaluation of the results of the analysis, monthly growth rates from the TDGM were compared to laboratory observations of juvenile HBC growth. Clarkson and Childs (2000) conducted laboratory experiments to evaluate the growth rate of larval HBC at 10°C, 14°C, and 20°C. They report monthly growth rates of 1 mm/month, 13 mm/month, and 17 mm/month for these temperatures, respectively. Considering the estimated monthly growth rates from the TDGM in figure 24, the TDGM tends to overestimate the growth rates reported by Clarkson and Childs (2000) at 10°C and underestimate the growth rate at 20°C. However, the results reported herein are in overall agreement with the laboratory study.

The TDGM and related age-length function should be of considerable use to researchers studying HBC throughout the Colorado River Basin. Additionally, this case history should also be useful to anyone wishing to recover temperature-dependent bioenergetic parameters for fish using capture-recapture data, or to estimate the relationship and associated uncertainty between fish age and length using non-lethal techniques. This technique shows considerable promise in extracting useful information on fish growth from field data, rather than from laboratory studies, where such information is typically obtained.

Incorporation of Ageing Error in ASMR Assessments

A major criticism of the ASMR technique, as previously applied, is that it does not explicitly account for uncertainty in the assignment of age to individual fish (Kitchell and others, 2003). As a result, abundance, recruitment, and mortality estimates may contain excessive bias. Additionally, estimates of precision are likely overstated by not incorporating this important source of uncertainty. The analyses presented in this report attempt to address these concerns by constructing a more rigorous model to predict length as a function of age and to incorporate uncertainty from age assignments into estimates of abundance and recruitment. Coggins and others (2006b) conducted sensitivity analyses on the effect of random ageing error and found little systematic bias in reconstructed recruitment trends. However, the current analysis is a more rigorous treatment of the problem and has two major implications.

First, model results of estimated adult abundance are still very precise even when uncertainty in the assignment of age is explicitly accounted for in the assessment. Following reviews

by Kitchell and others (2003) and Otis and Wickham (U.S. Geological Survey, written commun., 2006), this assessment lends additional credibility to results from ASMR, indicating that it provides a rigorous measure of the state of the adult portion of the LCR HBC population. It is recommended that this assessment be considered “best available science” for use in contemplating management decisions both within the Glen Canyon Dam Adaptive Management Program and the U.S. Fish and Wildlife Service.

Second, this analysis points out the difficulty that open population models generally have in the precise estimation of recruitment (Williams and others, 2001; Pine and others, 2003). Because many of the most critical management questions for HBC center around how best to improve recruitment, particularly considering improved rearing conditions in the mainstem Colorado River, it will be difficult for ASMR to detect statistically significant changes in recruitment, unless those changes are quite large. As a result, experimental adaptive management actions designed to increase recruitment should consider first and foremost how to achieve large changes in recruitment. Small-scale experimental treatments of short duration, or so-called “mini-experiments,” should be summarily discounted recognizing that the monitoring program is unlikely to detect small recruitment change even if it occurs. Additionally, multiyear experiments should be strongly favored in order to help offset not only unexpected and uncontrollable effects, but the low precision in recruitment estimates.

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Figures

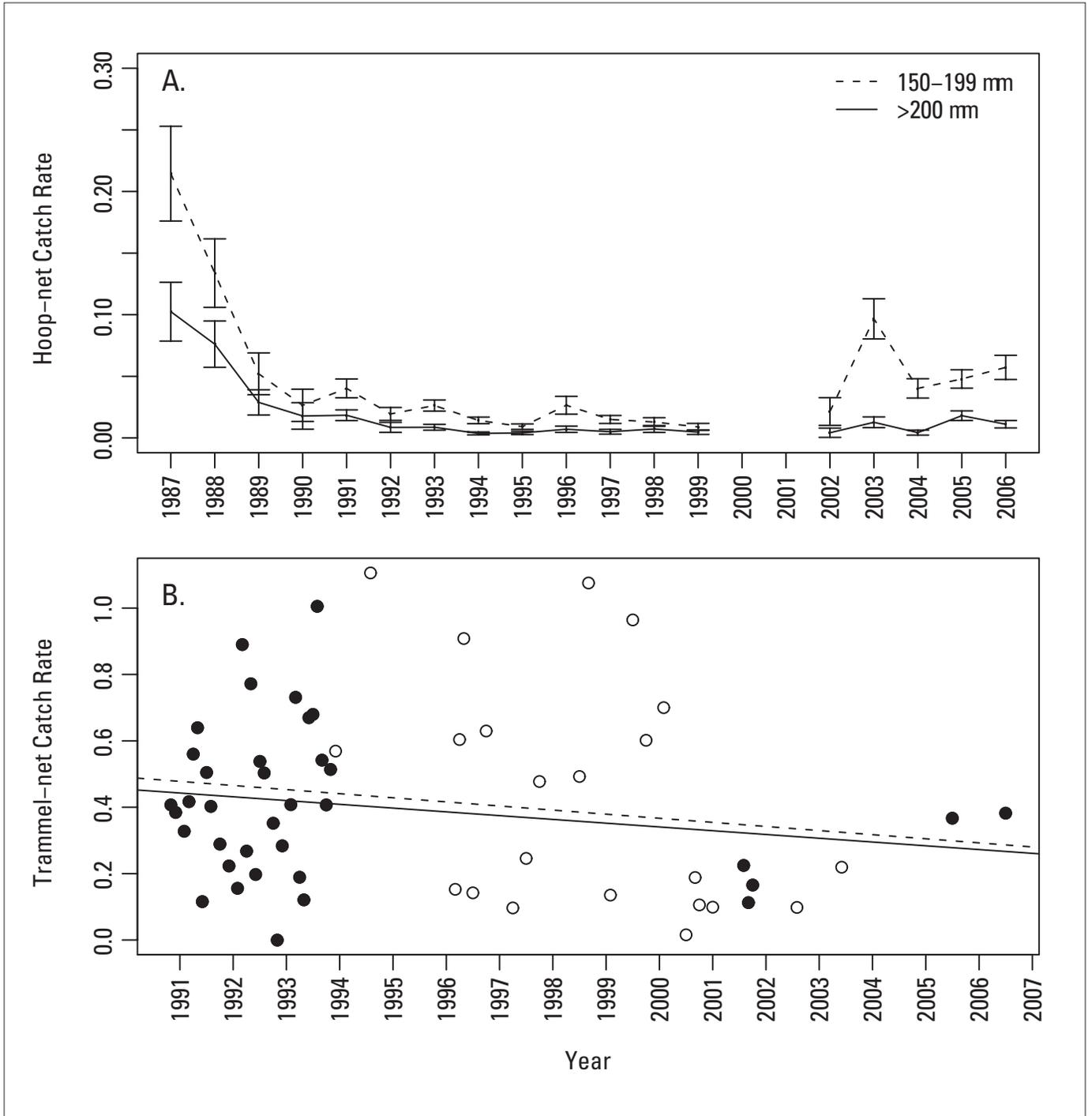


Figure 1. Relative abundance indices of sub-adult (150–199 mm total length (TL)) and adult (>200 mm TL) humpback chub based on hoop-net catch rate (fish/hour) in the lower 1,200-m section of the Little Colorado River (A) and trammel-net catch rate (fish/hour/100m) of adult (>200 mm TL) humpback chub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

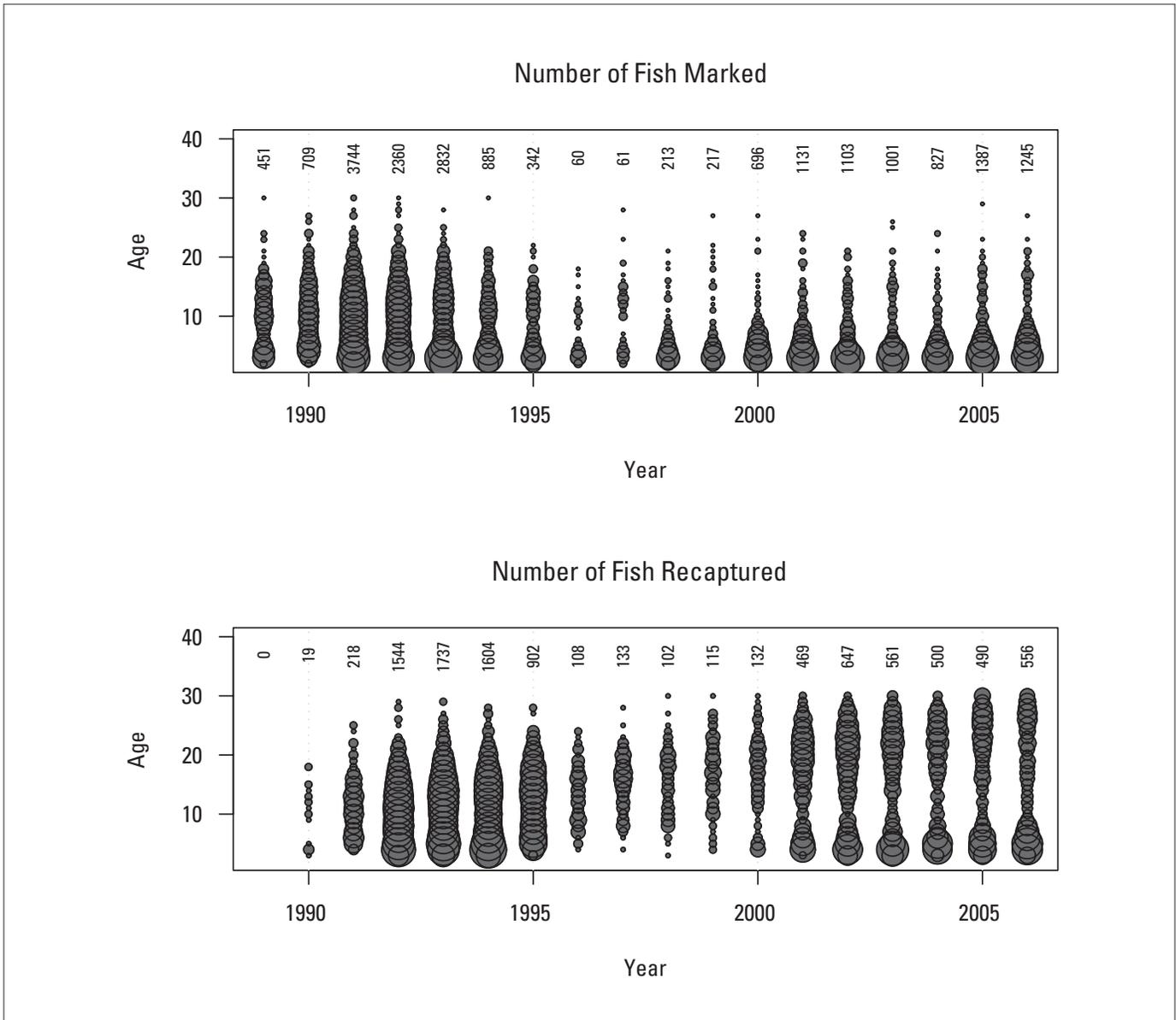


Figure 2. Numbers of humpback chub marked and recaptured by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages is indicated by relative size of bubbles within each column.

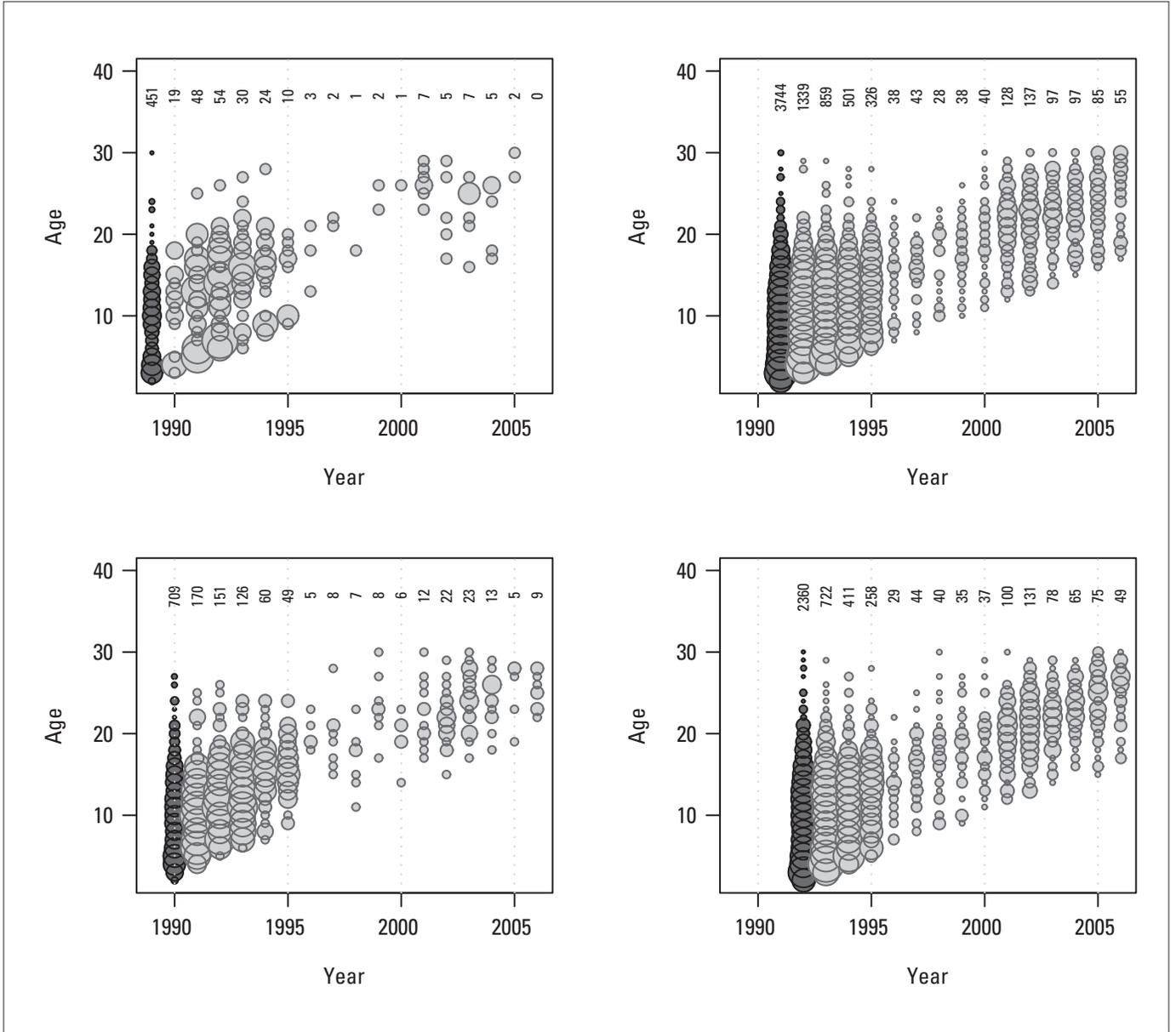


Figure 3a. Numbers of humpback chub marked by age in years 1989–92 (dark circles) and subsequently recaptured (light circles) by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages is indicated by the relative size of the bubbles within each column.

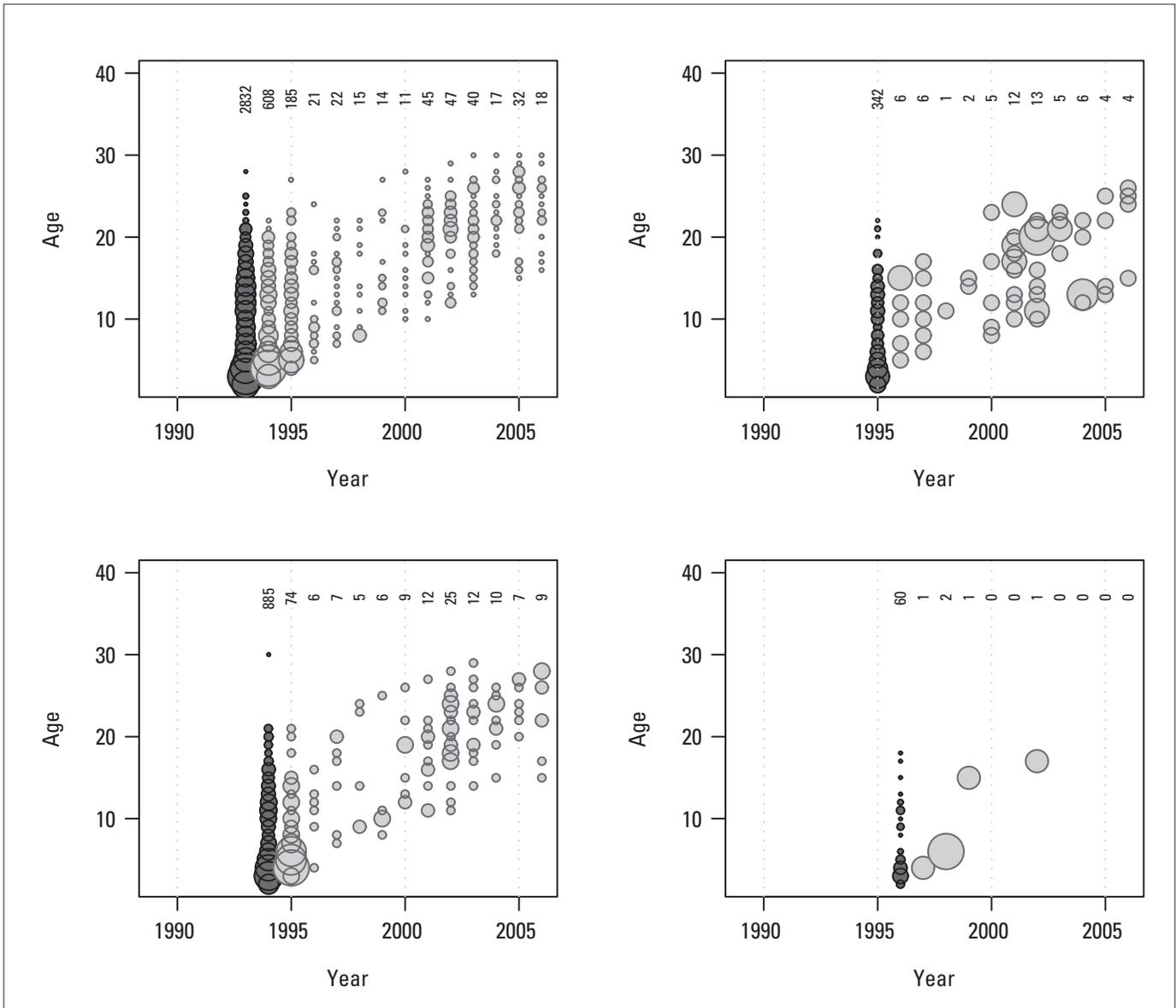


Figure 3b. Numbers of humpback chub marked by age in years 1993–96 (dark circles) and subsequently recaptured (light circles) by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages is indicated by the relative size of the bubbles within each column.

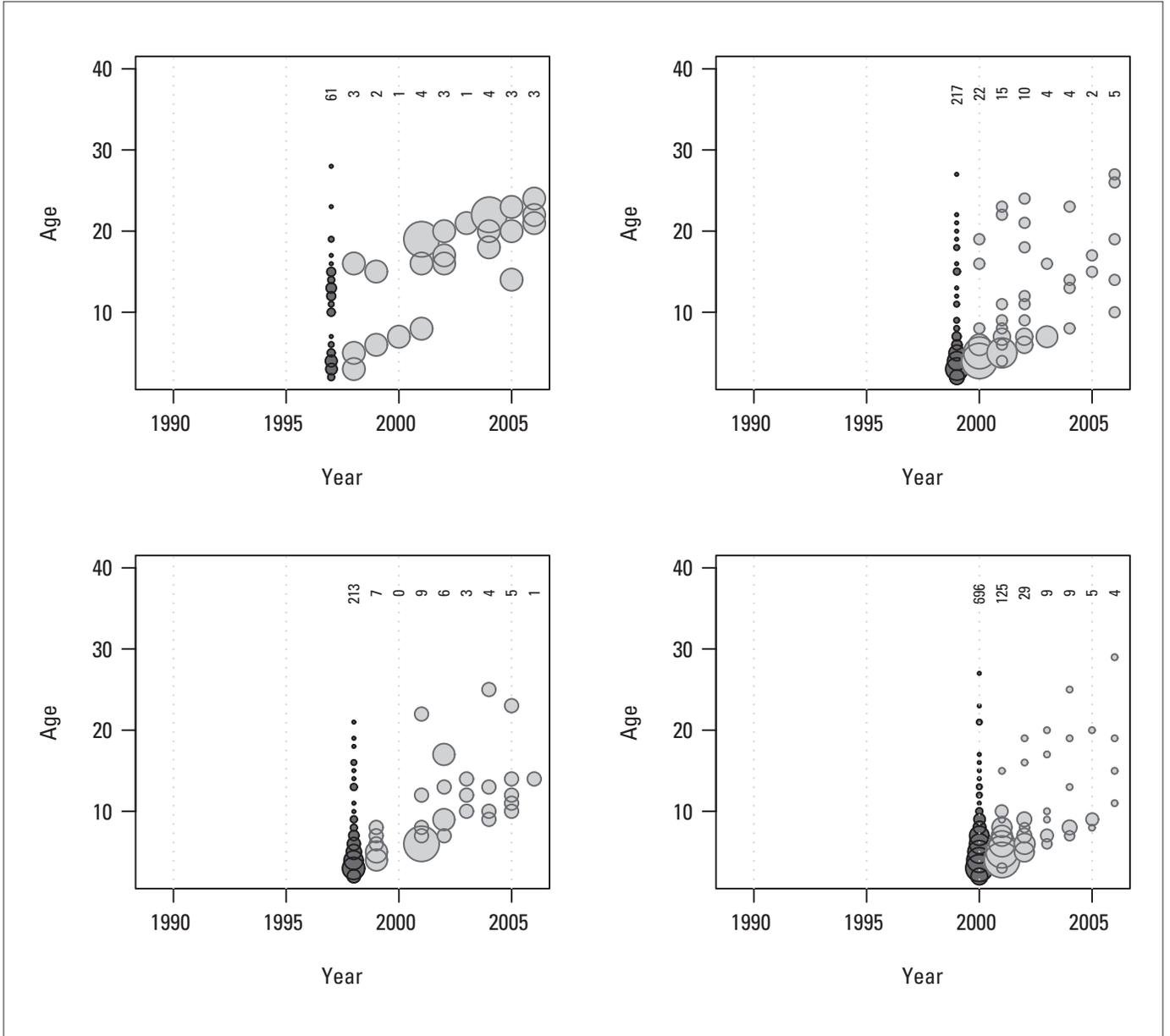


Figure 3c. Numbers of humpback chub marked by age in years 1997–2000 (dark circles) and subsequently recaptured (light circles) by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages is indicated by the relative size of the bubbles within each column.

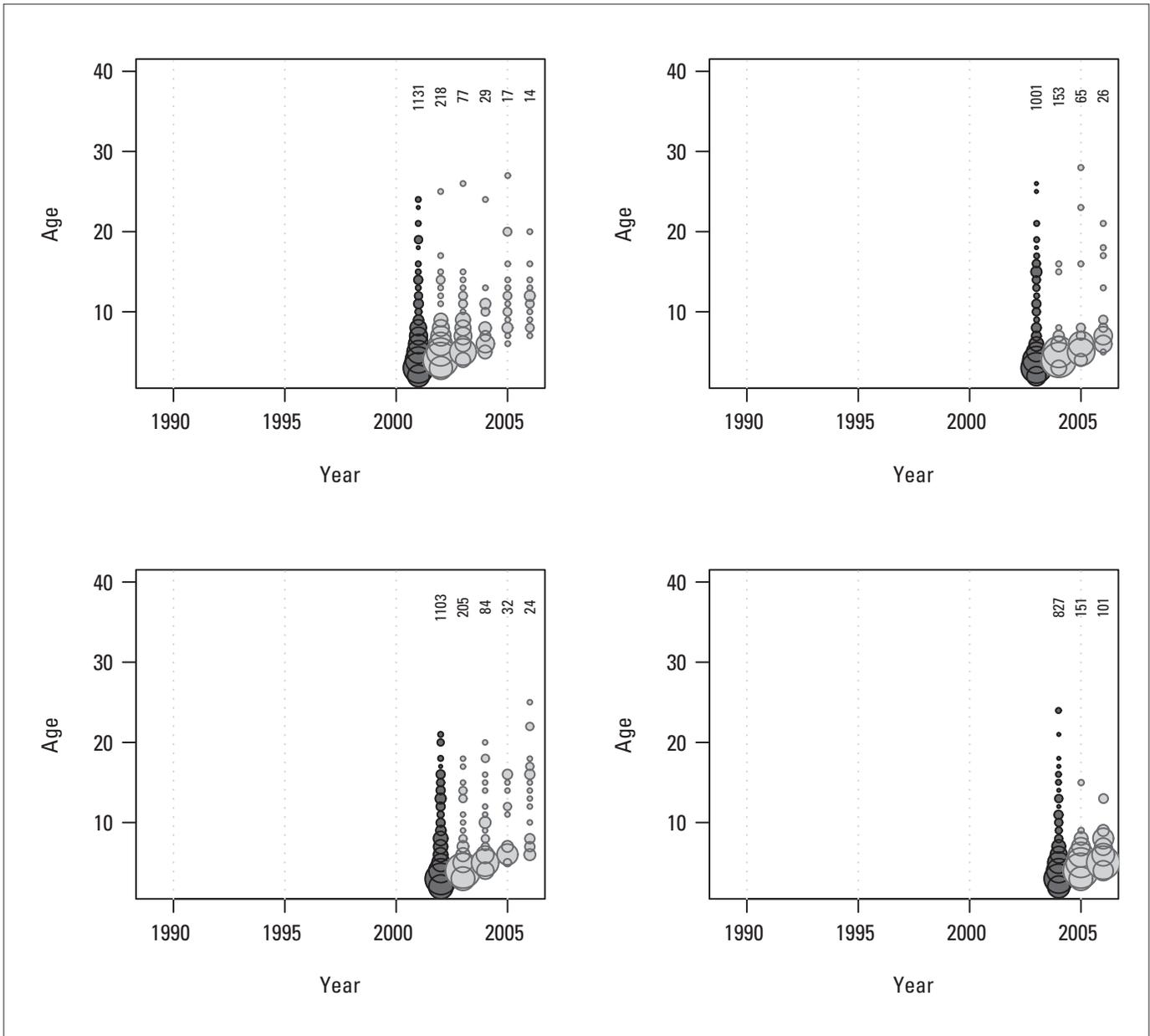


Figure 3d. Numbers of humpback chub marked by age in years 2001–04 (dark circles) and subsequently recaptured (light circles) by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages is indicated by the relative size of the bubbles within each column.

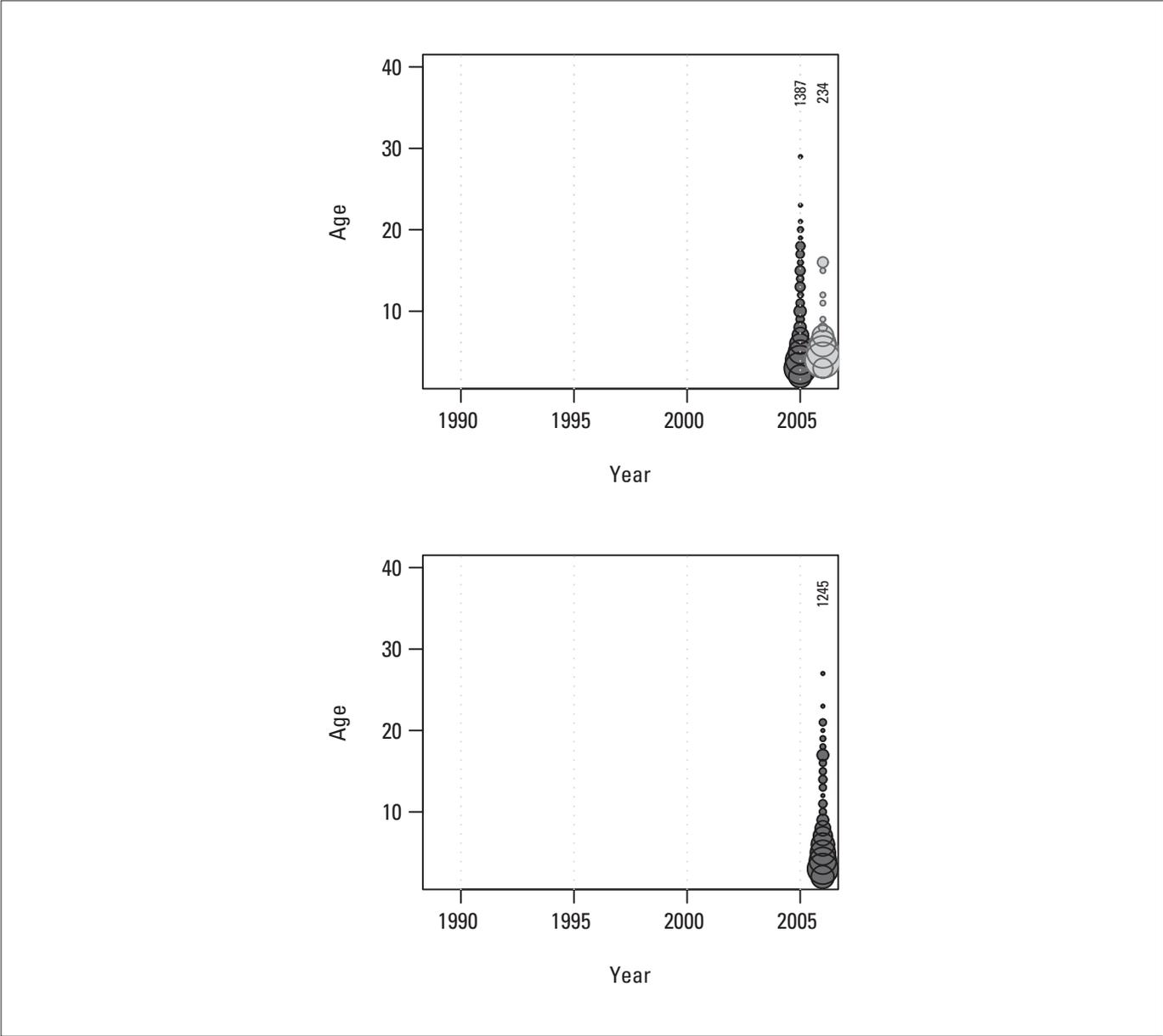


Figure 3e. Numbers of humpback chub marked by age in years 2005–06 (dark circles) and subsequently recaptured (light circles) by age and year. The annual sample size is indicated by the number at the top of each bubble column and the distribution among ages is indicated by the relative size of the bubbles within each column.

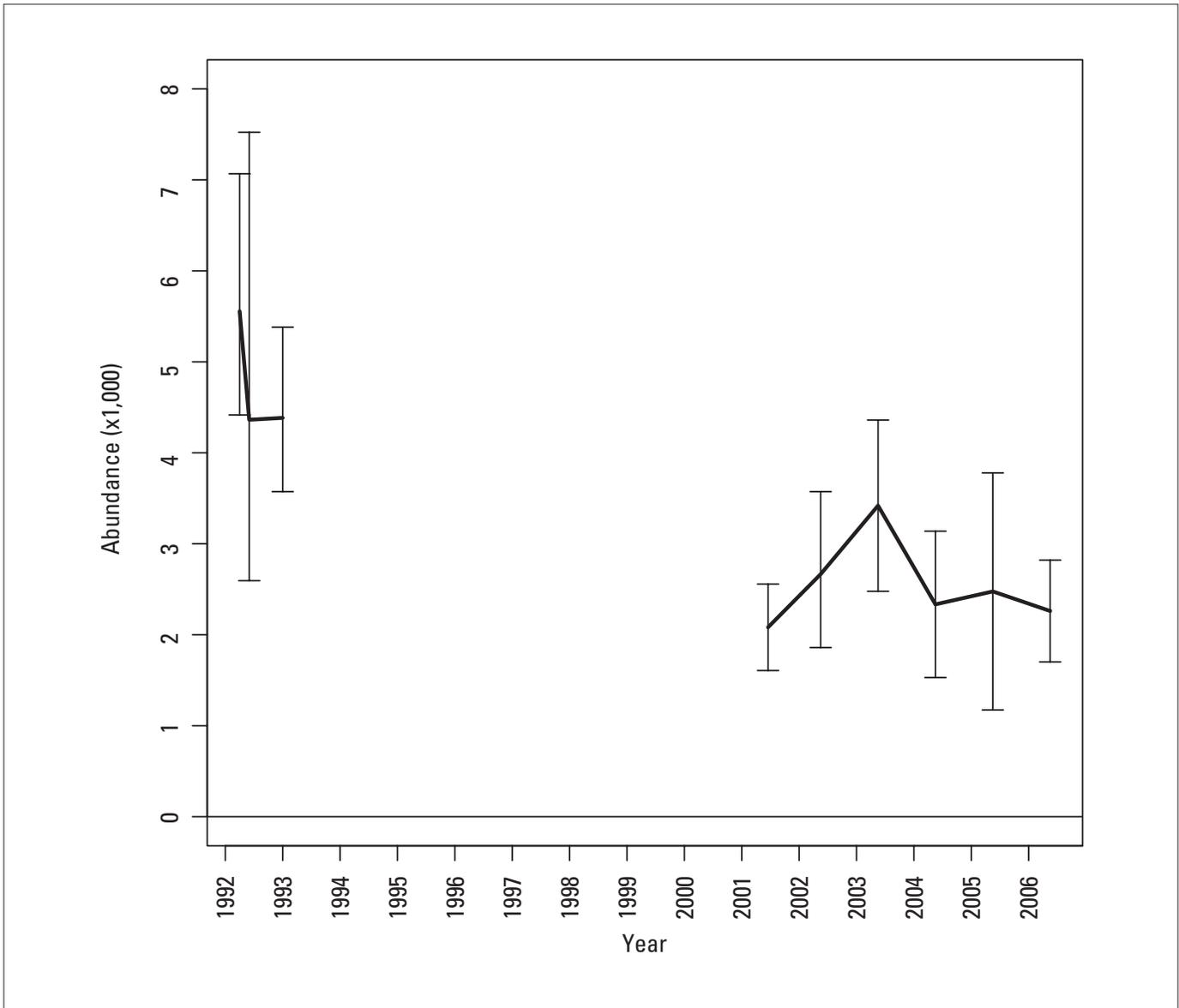


Figure 4. Mark-recapture closed population model estimates of humpback chub abundance greater than or equal to 150-mm total length in the Little Colorado River. Error bars represent 95% confidence intervals.

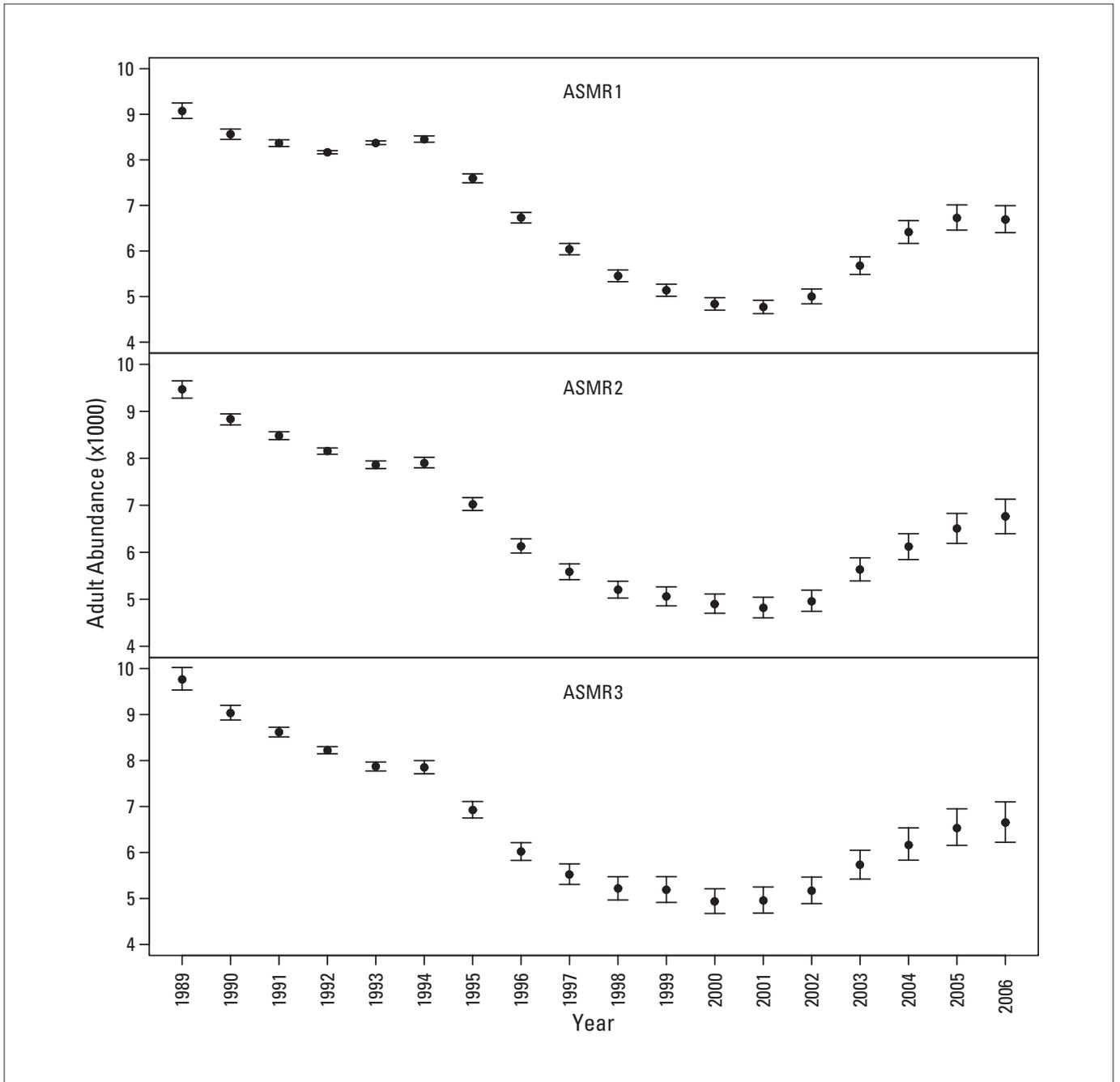


Figure 5. Humpback chub adult abundance (age-4+) estimates from the age-structured mark recapture (ASMR) models using data pooled among tag cohorts. Error bars are 95% credible intervals from 200,000 Markov-Chain Monte Carlo trials.

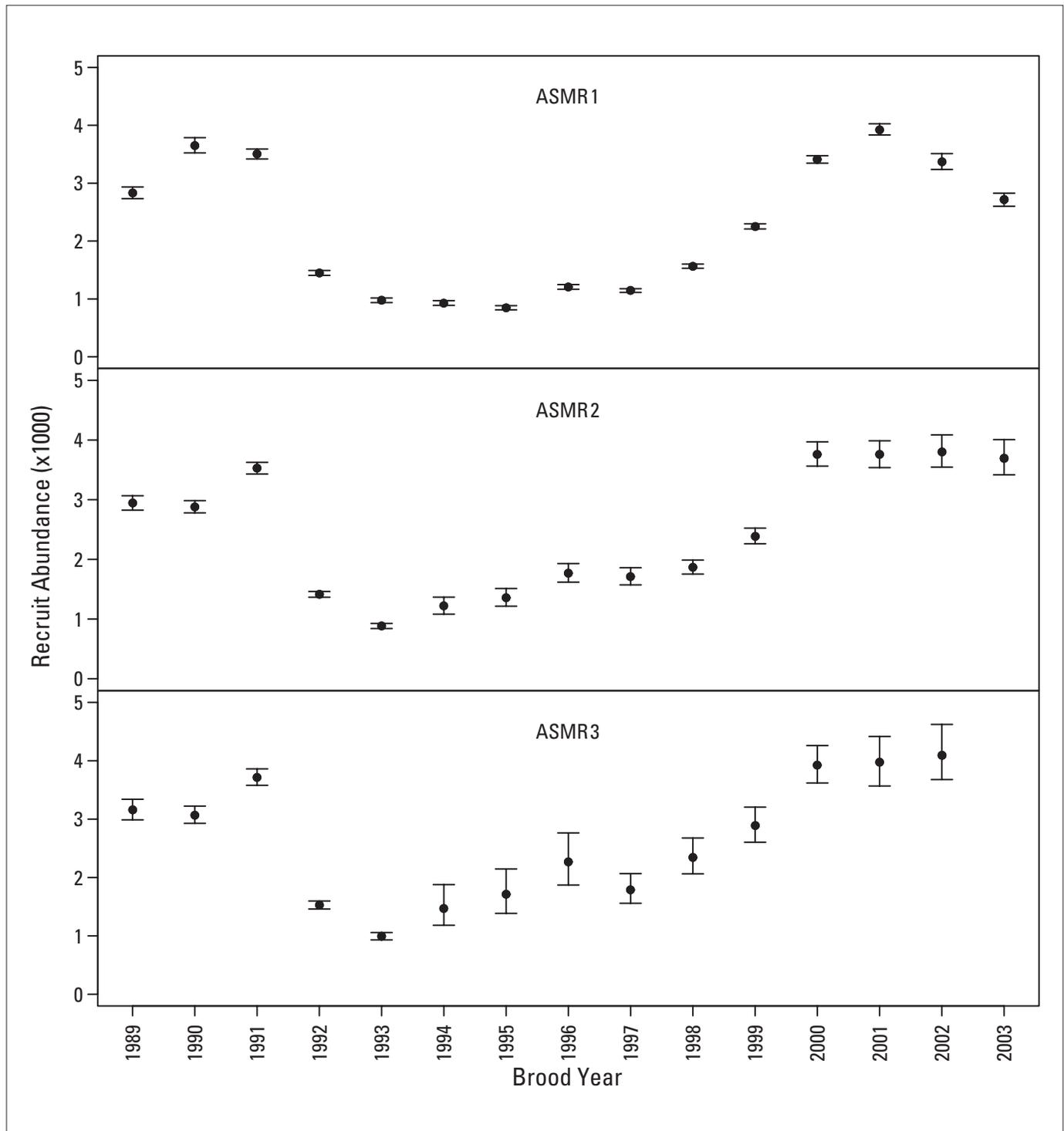


Figure 6. Humpback chub recruit abundance (age-2) estimates from the age-structured mark recapture (ASMR) models using data pooled among tag cohorts. Error bars are 95% credible intervals from 200,000 Markov-Chain Monte Carlo trials.

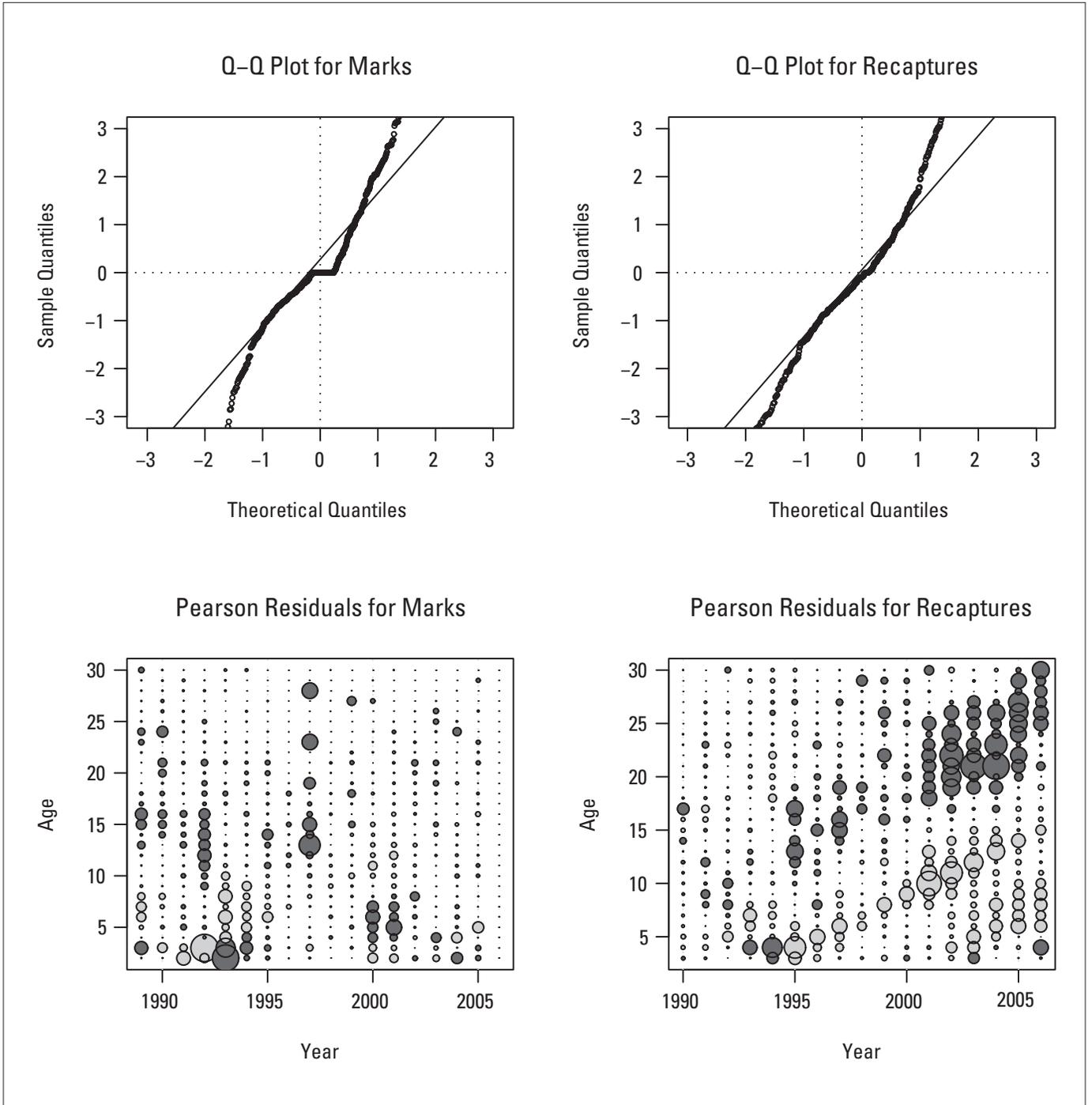


Figure 7. Quantile-quantile (Q-Q) and Pearson residual plots for age-structured mark recapture model 1 (ASMR 1) using data pooled among tag cohorts.

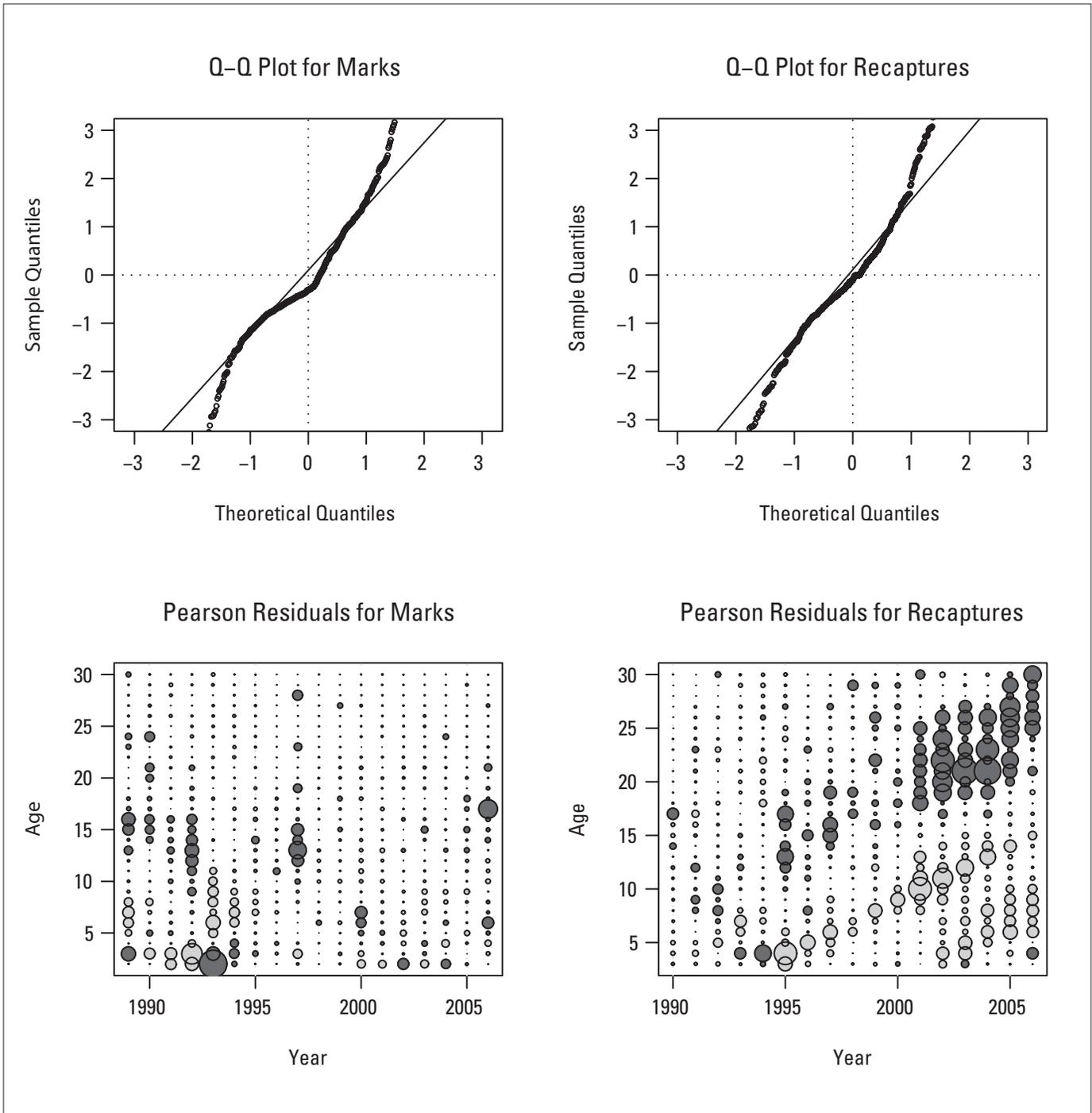


Figure 8. Quantile-quantile (Q-Q) and Pearson residual plots for age-structured mark recapture model 2 (ASMR 2) using data pooled among tag cohorts.

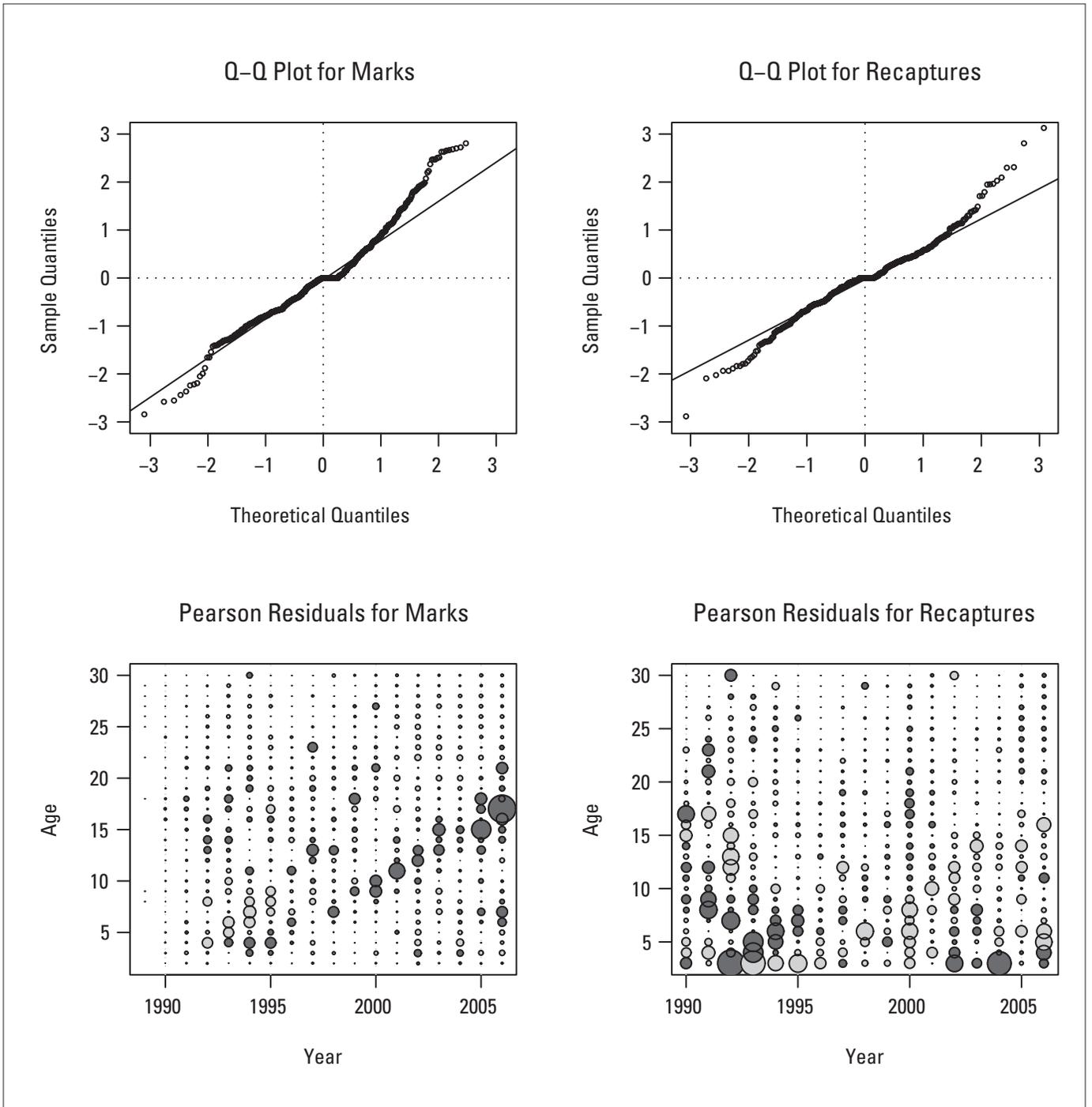


Figure 9. Quantile-quantile (Q-Q) and Pearson residual plots for plots for age-structured mark recapture model 3 (ASMR 3) using data pooled among tag cohorts.

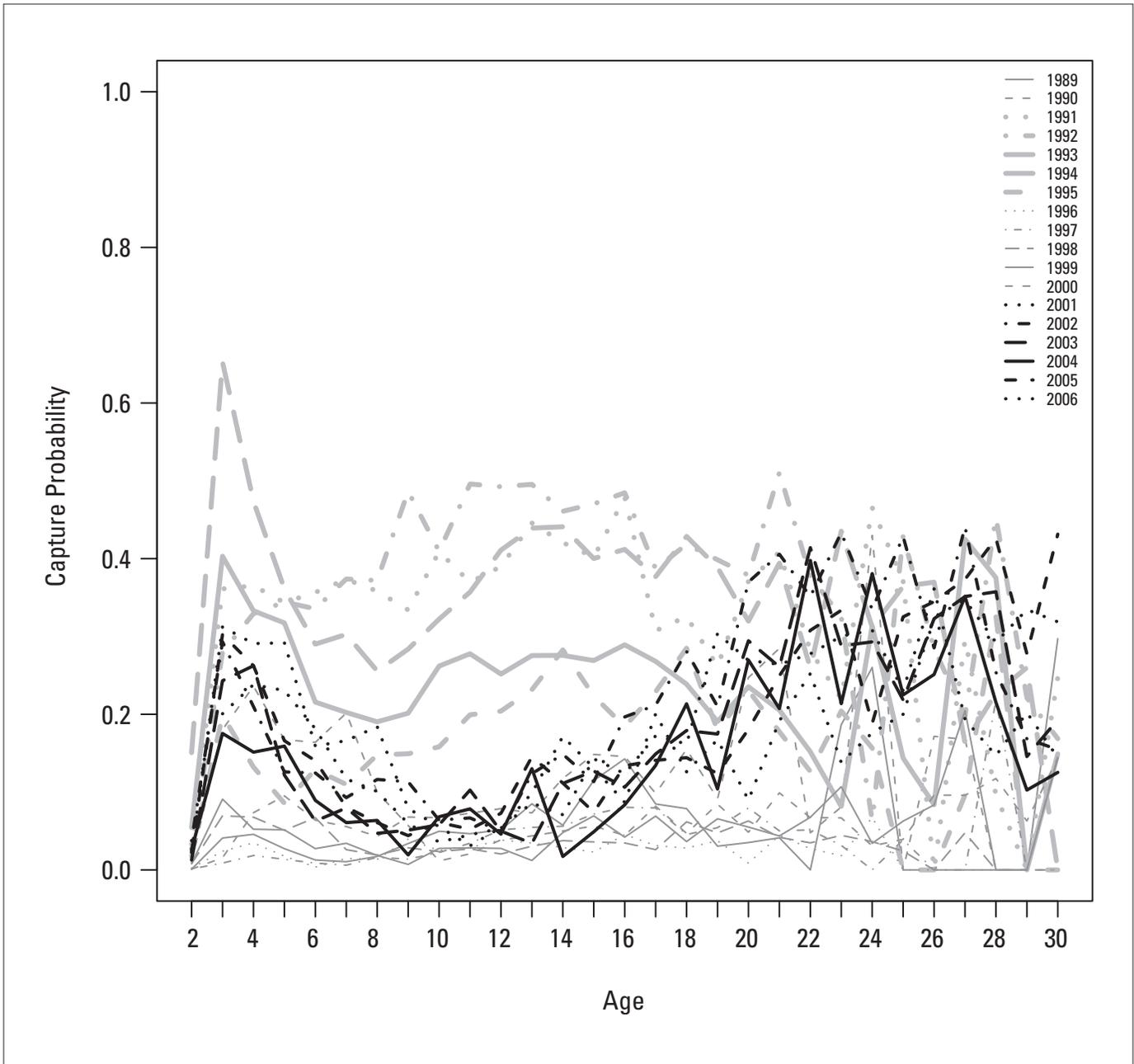


Figure 10. Humpback chub capture probability by age and year estimated from age-structured mark recapture model 3 (ASMR 3) using data pooled among tag cohorts.

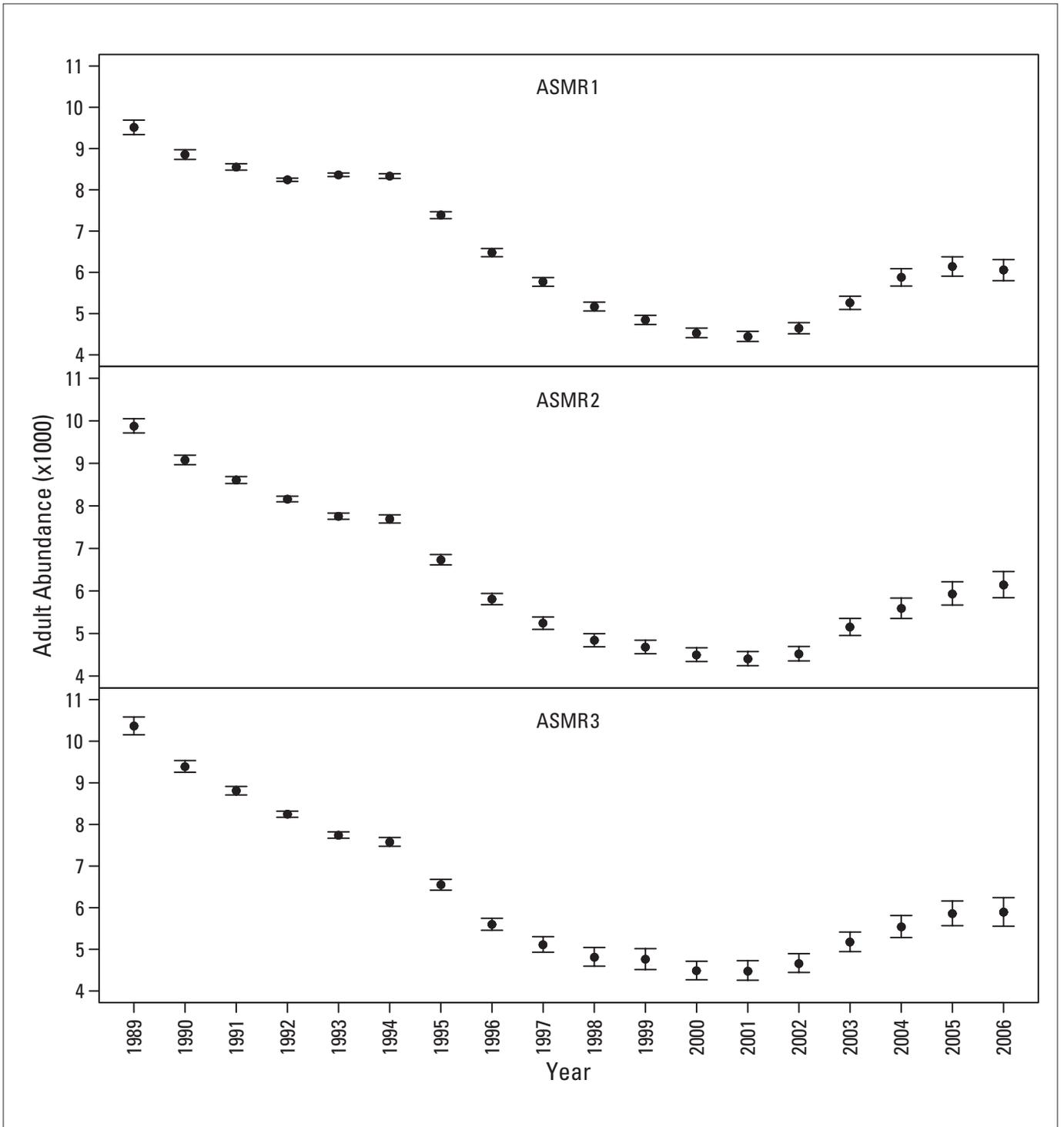


Figure 11. Humpback chub adult abundance (age-4+) estimates from the age-structured mark recapture (ASMR) models using data stratified by tag cohort. Error bars are 95% credible intervals from 200,000 Markov-Chain Monte Carlo trials.

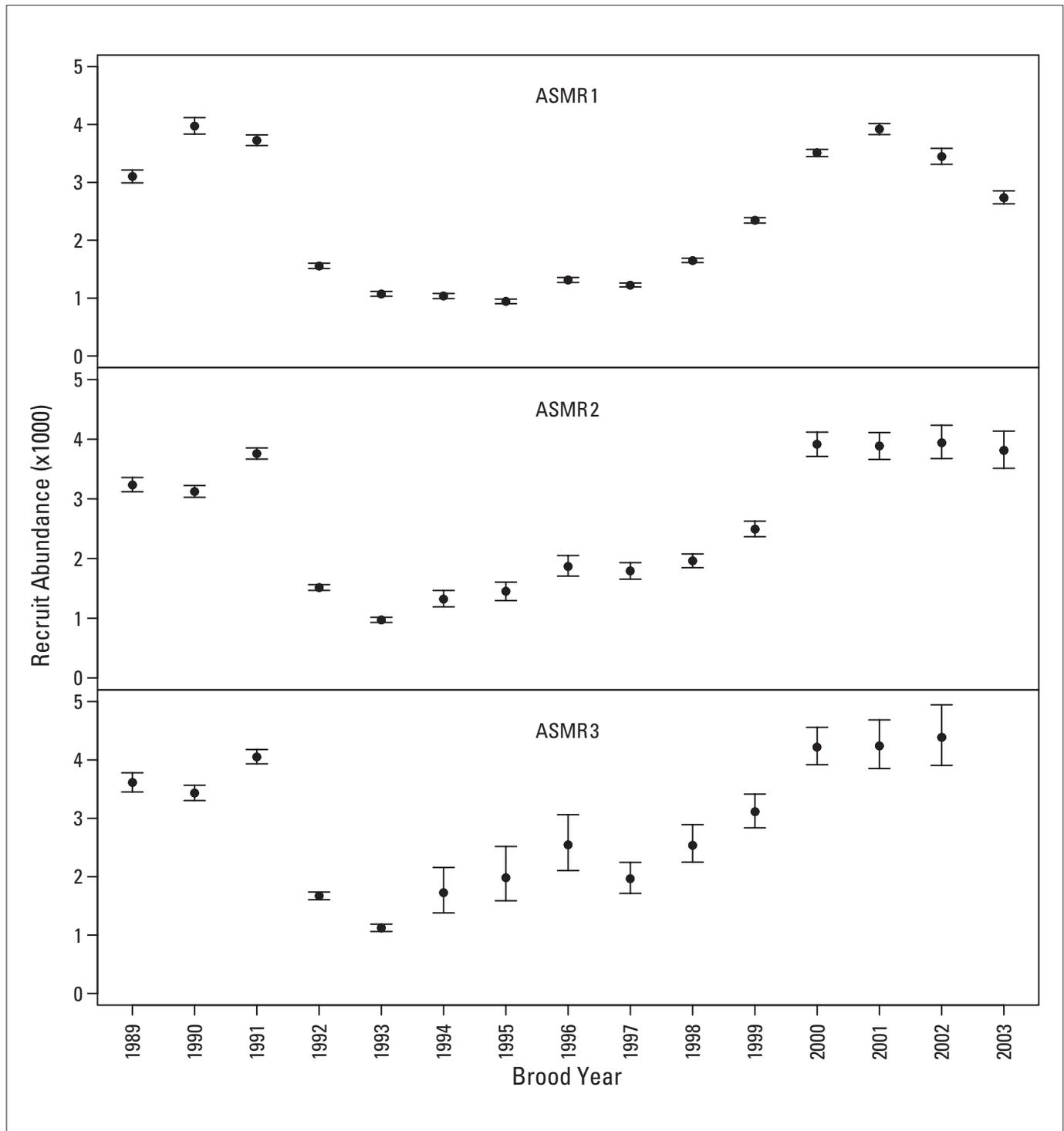


Figure 12. Humpback chub recruit abundance (age-2) estimates from the age-structured mark recapture (ASMR) models using data stratified by tag cohort. Error bars are 95% credible intervals from 200,000 Markov-Chain Monte Carlo trials.

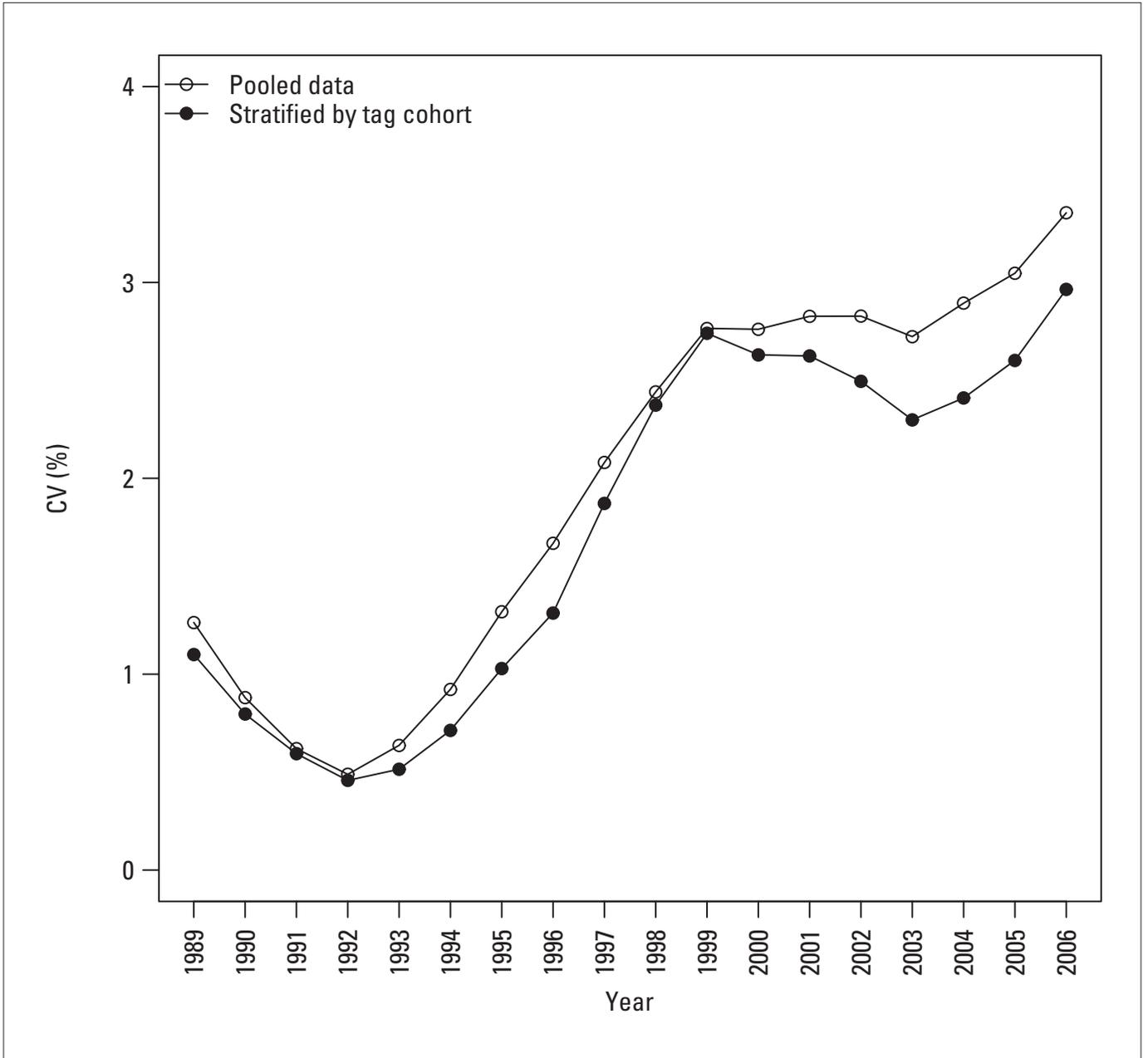


Figure 13. Coefficient of variation (CV) of humpback chub adult abundance estimates (age-4+) for data pooled among tag cohorts and stratified by tag cohorts.

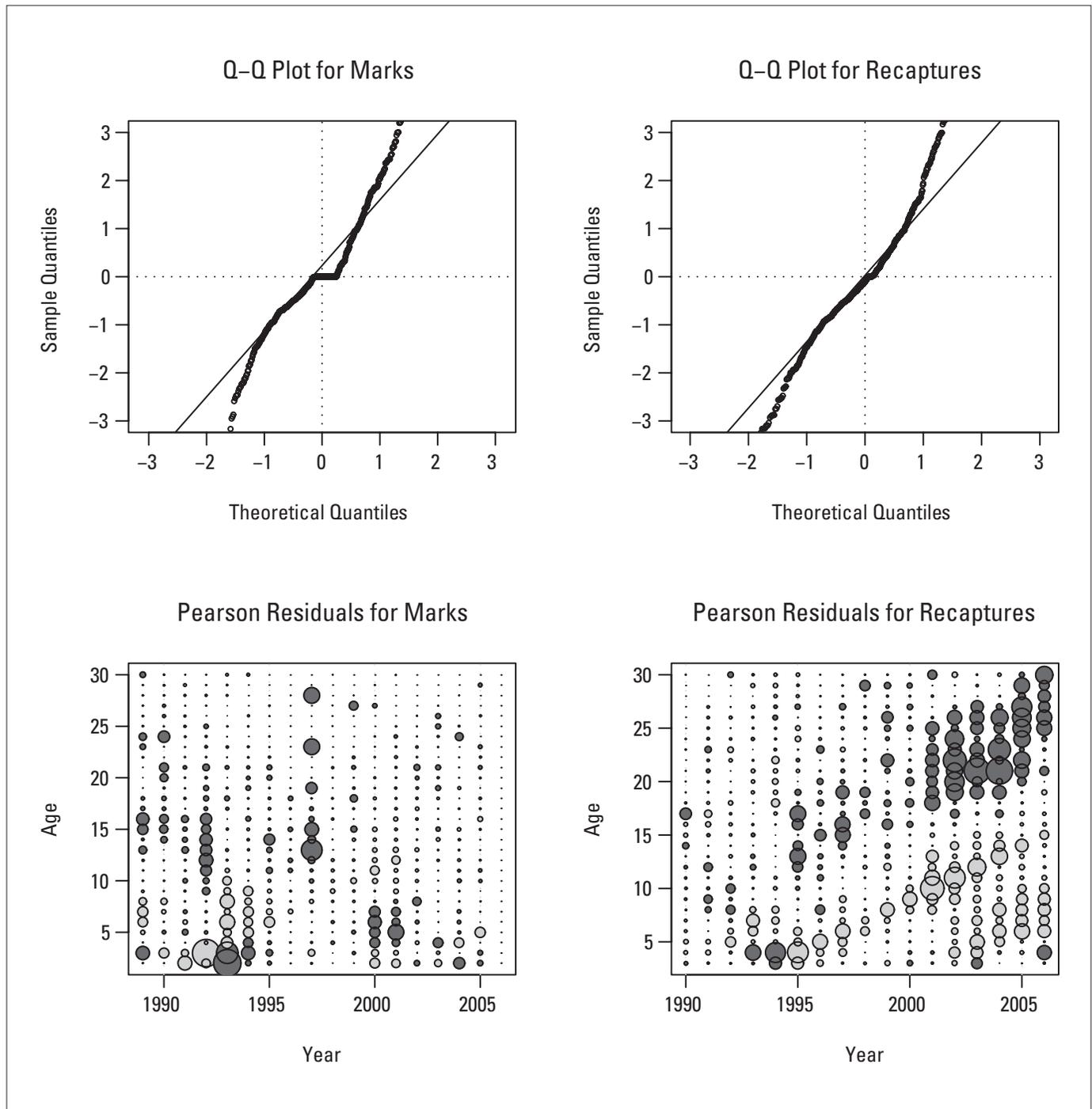


Figure 14. Quantile-quantile (Q-Q) and Pearson residual plots for age-structured mark recapture model 1 (ASMR 1) using data stratified by tag cohort.

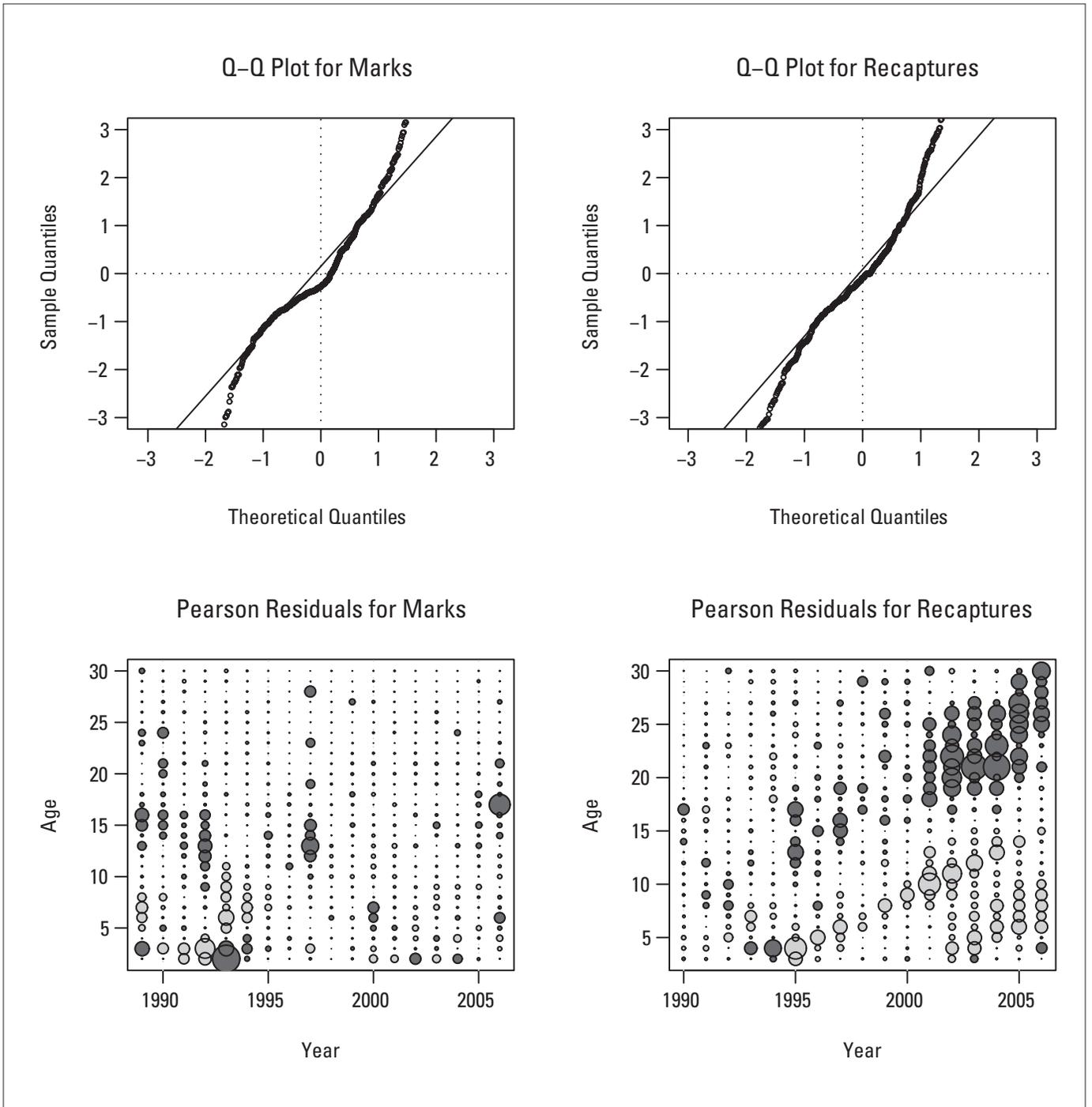


Figure 15. Quantile-quantile (Q-Q) and Pearson residual plots for age-structured mark recapture model 2 (ASMR 2) using data stratified by tag cohort.

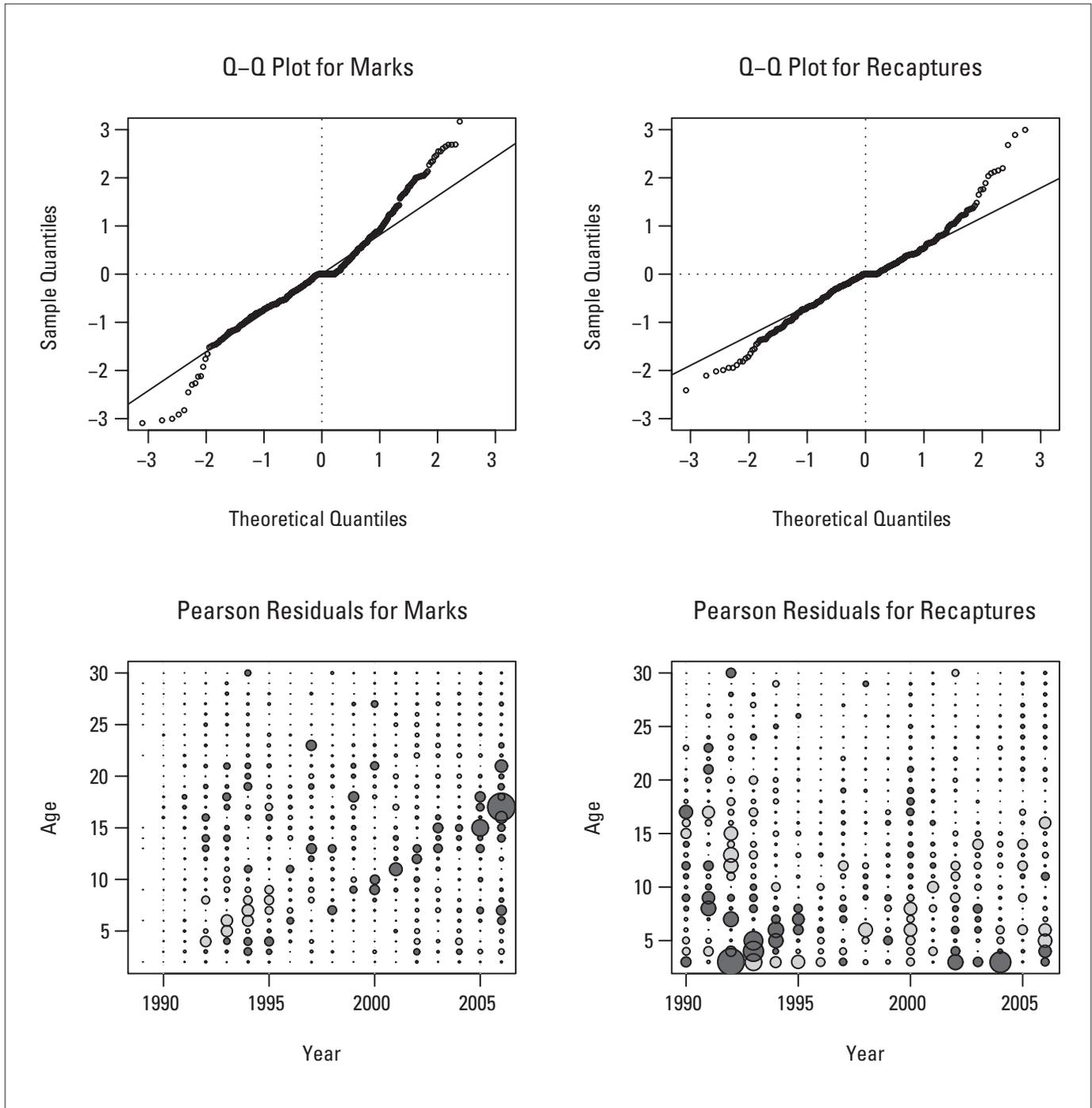


Figure 16. Quantile-quantile (Q-Q) and Pearson residual plots for age-structured mark recapture model 3 (ASMR 3) using data stratified by tag cohort.

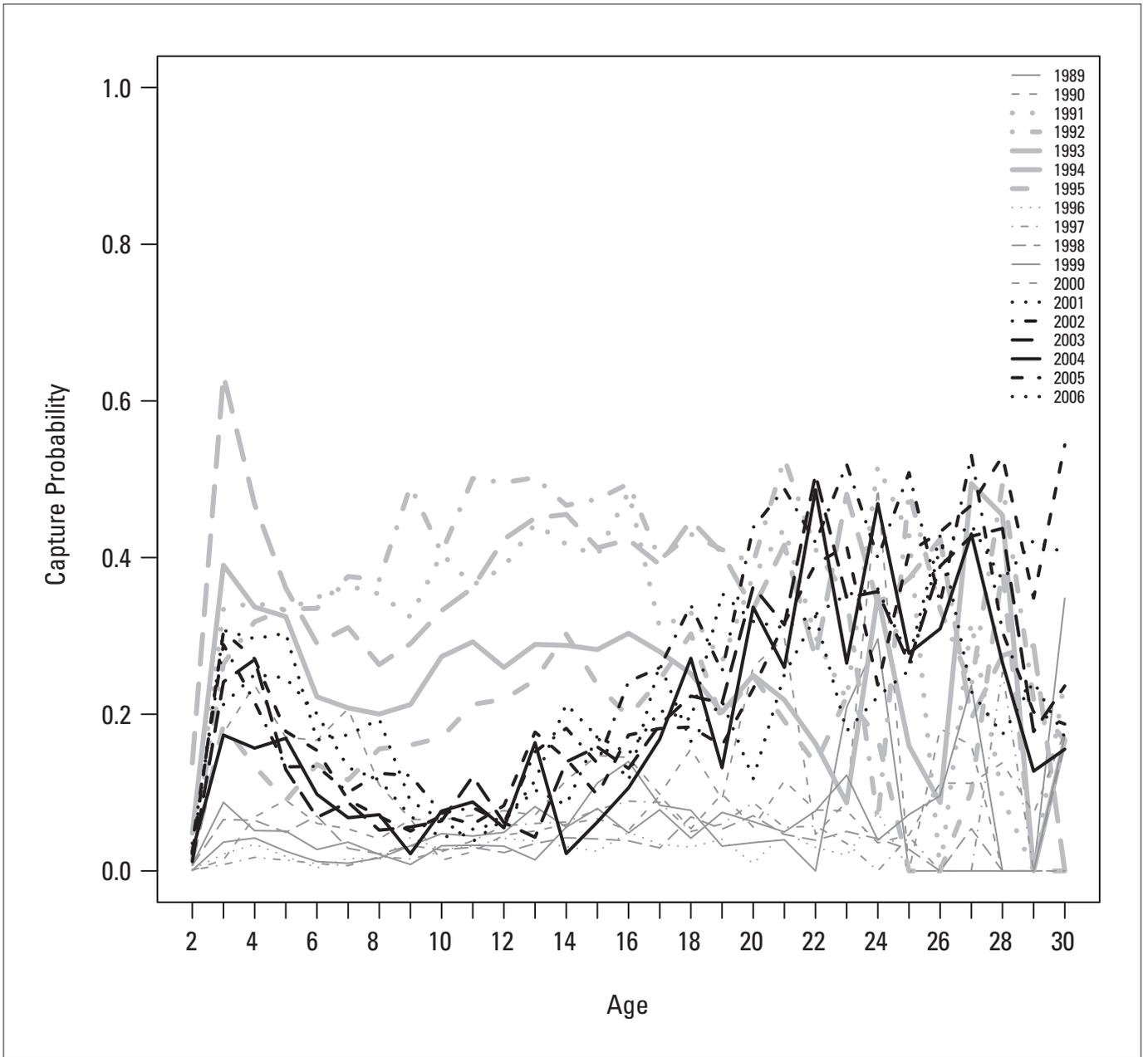


Figure 17. Humpback chub capture probability by age and year estimated from age-structured mark recapture model 3 (ASMR 3) using data stratified by tag cohort.

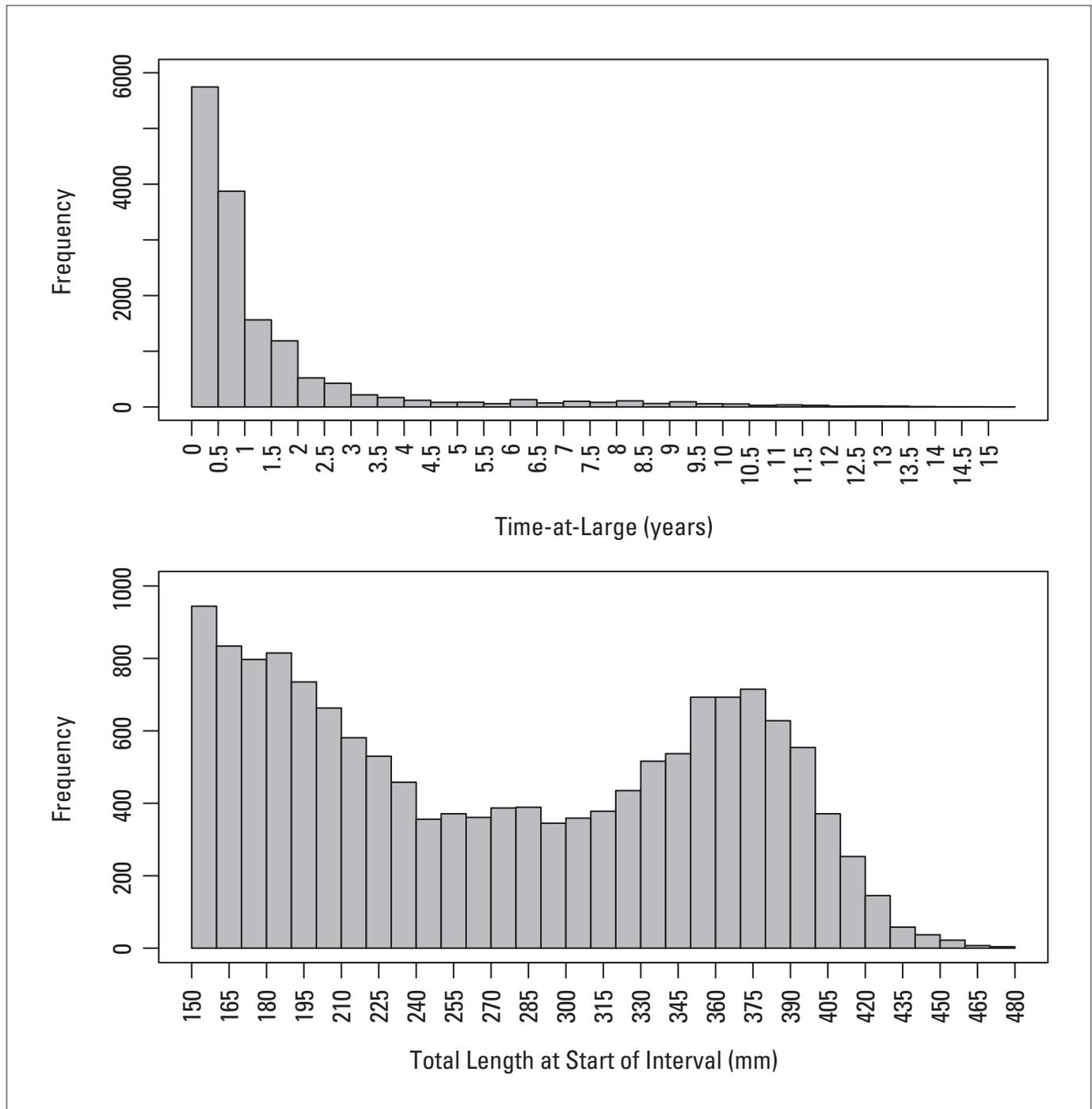


Figure 18. Frequency of humpback chub growth intervals used in the growth analysis by time-at-large (top panel) and total length at the start of the growth interval (bottom panel).

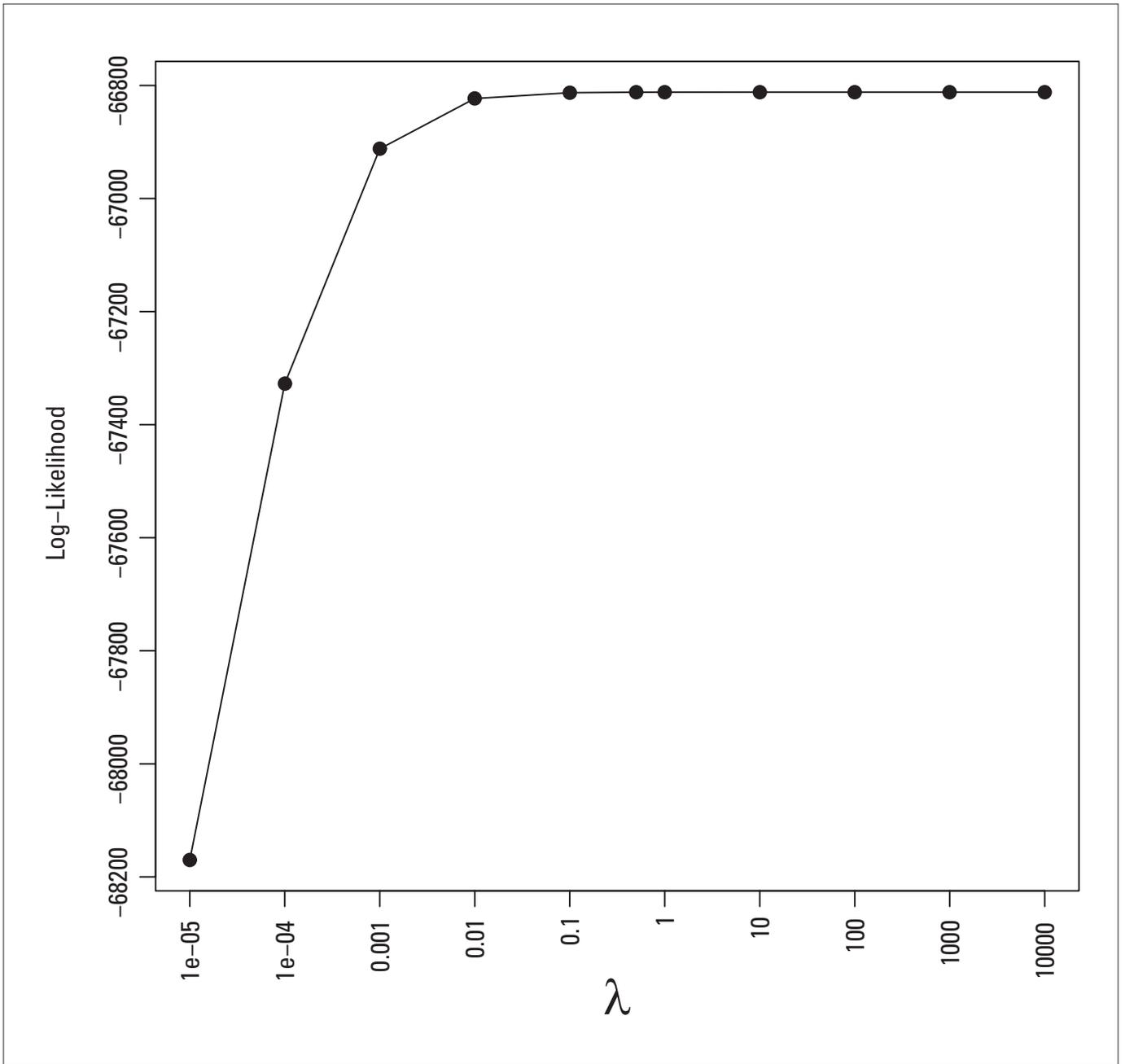


Figure 19. Log-likelihood as a function of the penalty weight (λ) on the standardized von Bertalanffy parameters for the temperature-independent growth model.

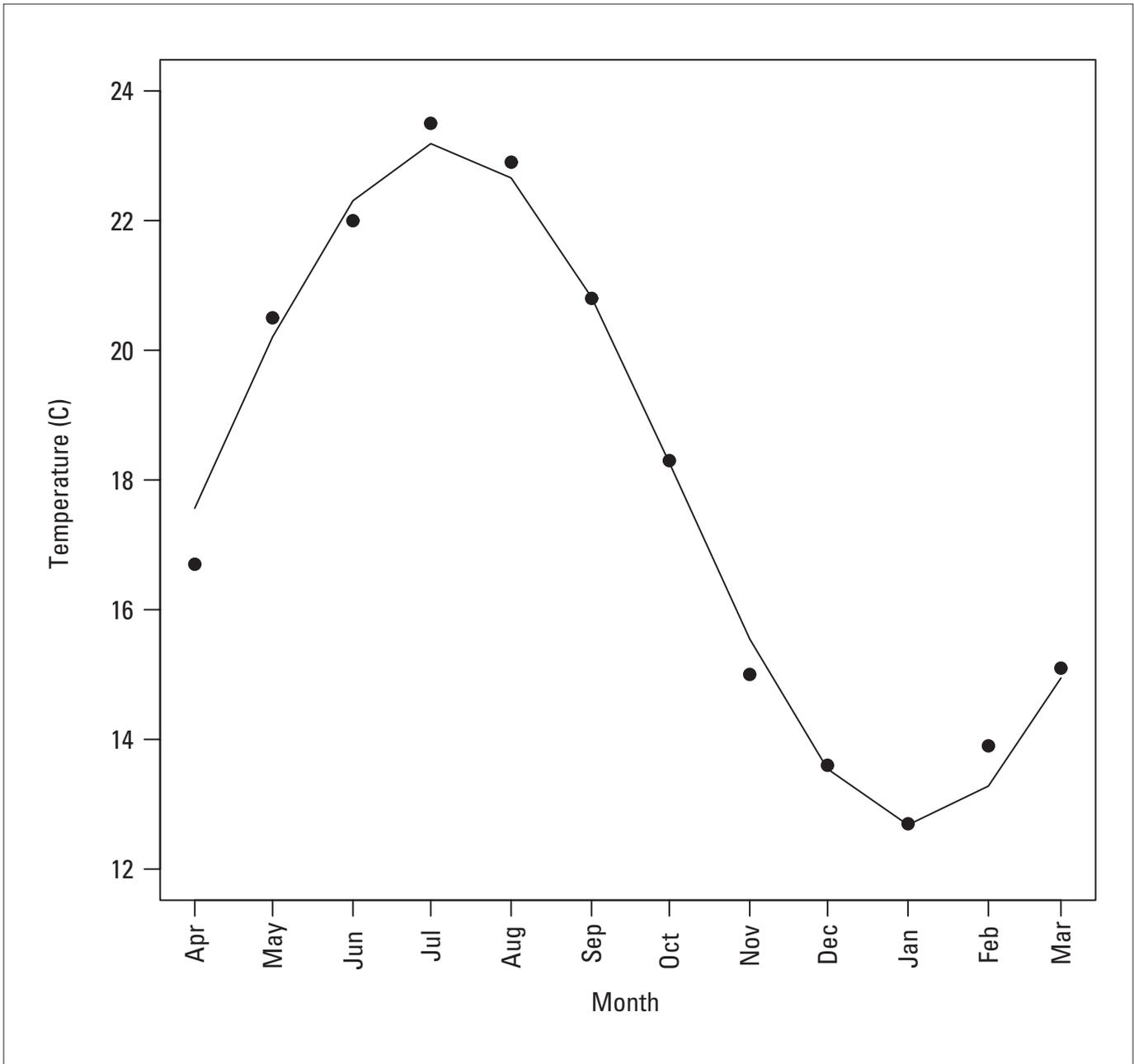


Figure 20. Fit of the sine curve to average monthly Little Colorado River water temperature. The points are the average observed monthly temperature and the line is the predicted monthly temperature.

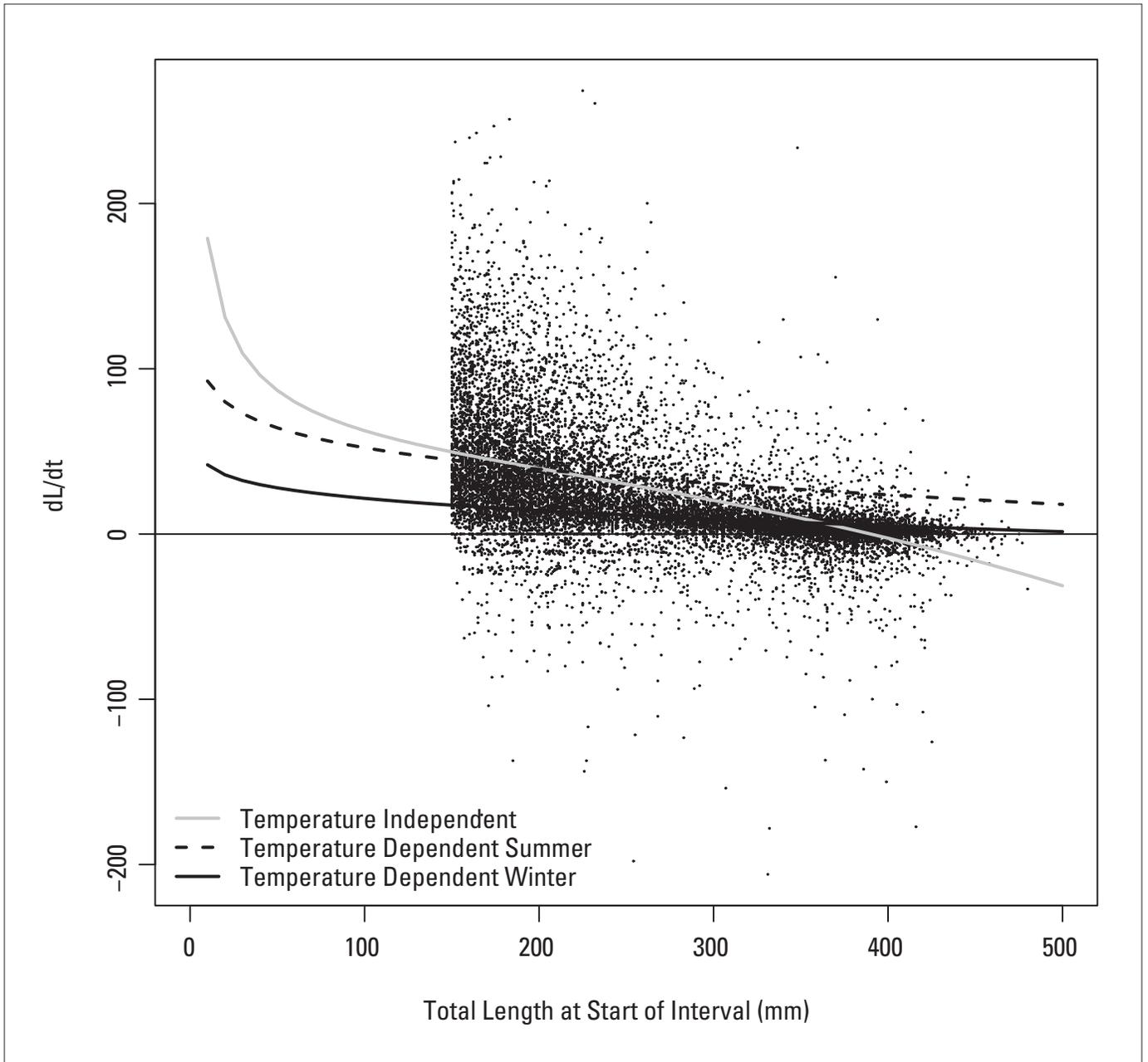


Figure 21. Fit of the temperature-independent growth model and the temperature-dependent growth model during summer and winter to all observed humpback chub growth-rate (dL/dt) data.

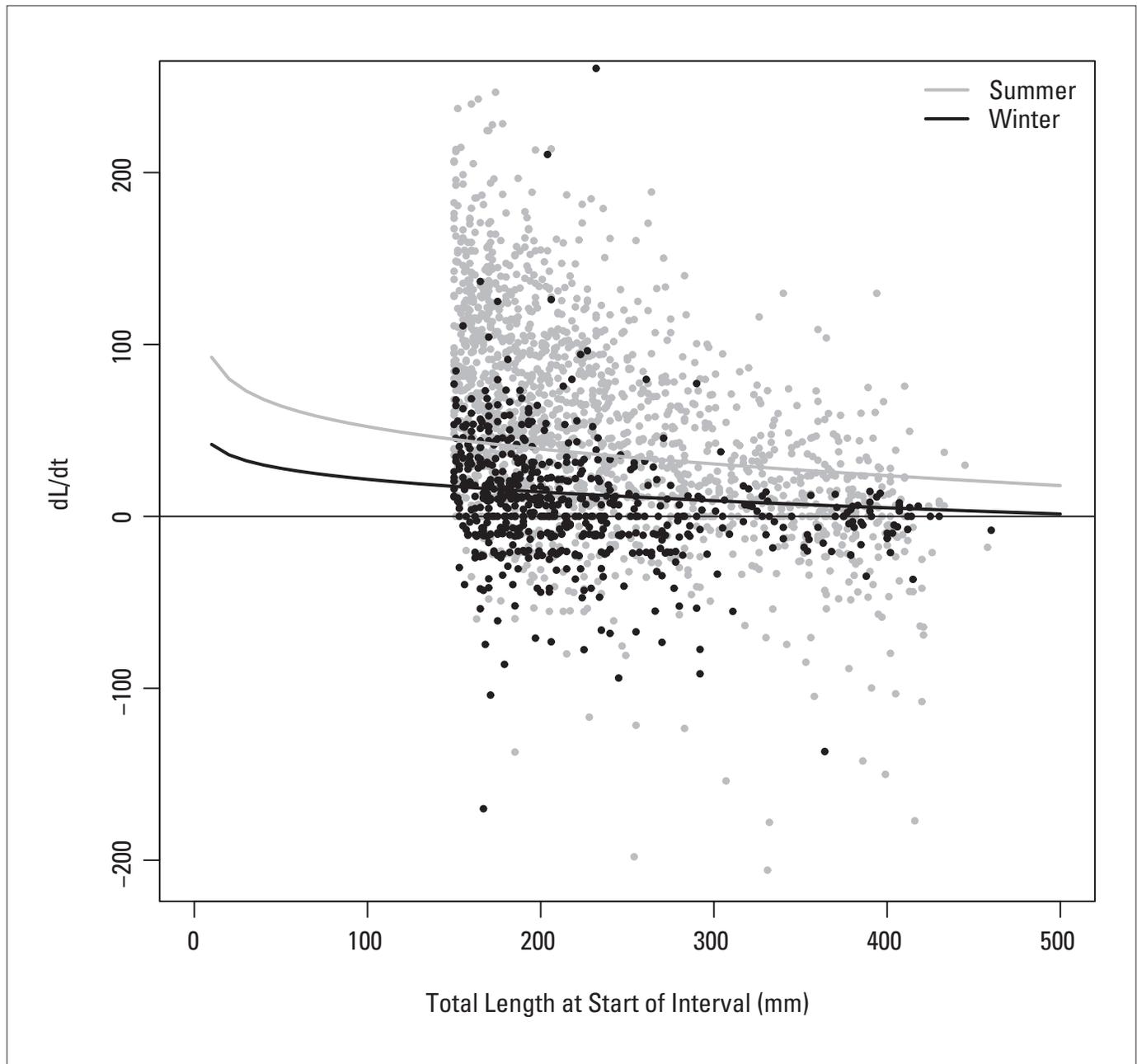


Figure 22. Fit of the temperature-dependent growth model during summer and winter to observed humpback chub growth-rate (dL/dt) data during summer and winter.

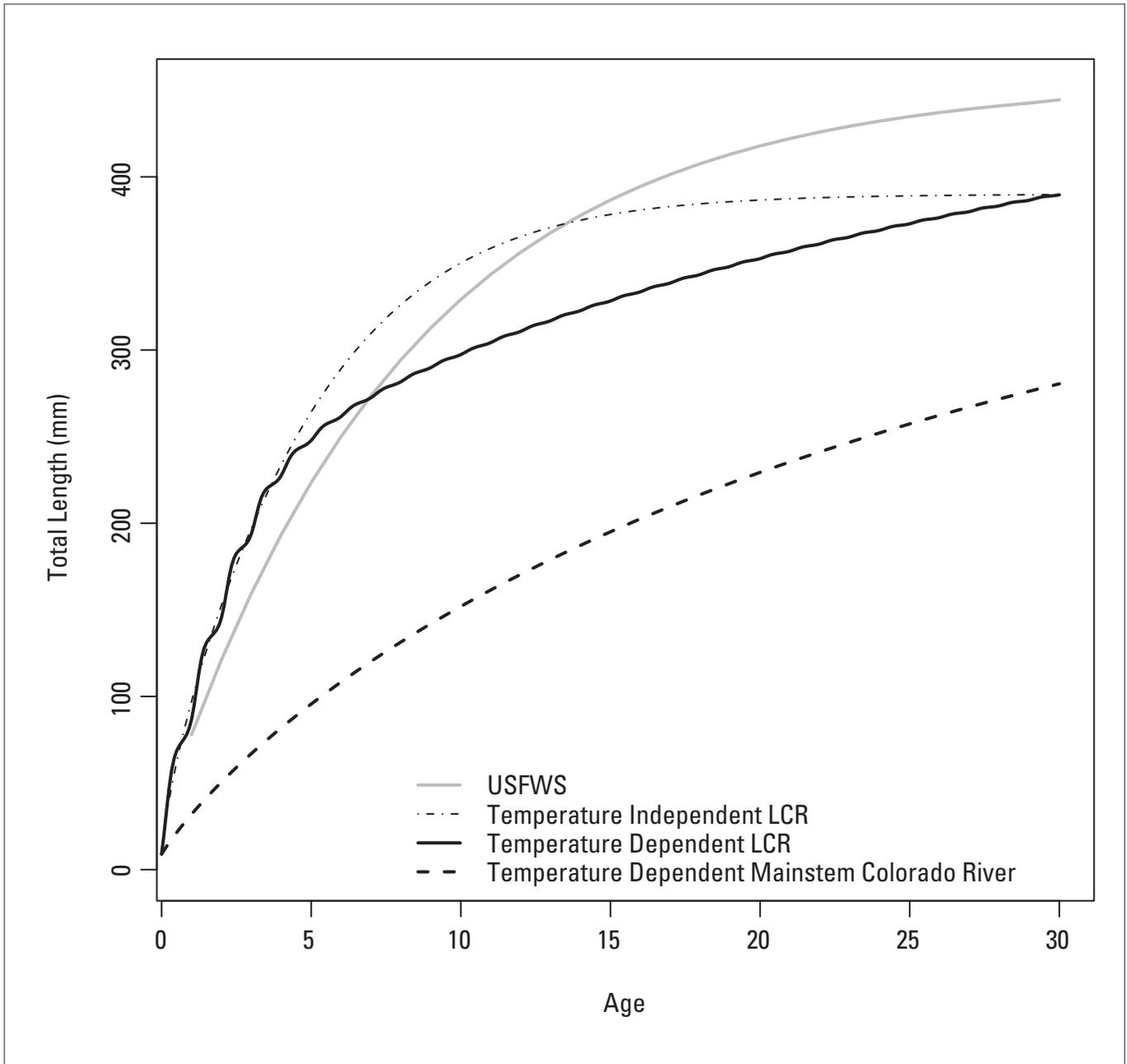


Figure 23. Predicted humpback chub length-at-age from the U.S. Fish and Wildlife Service (USFWS) growth curve, the temperature-independent growth model, the temperature-dependent growth model for the Little Colorado River (LCR) humpback chub population, and the temperature-dependent growth model for humpback chub living in the mainstem Colorado River under a constant temperature of 10°C.

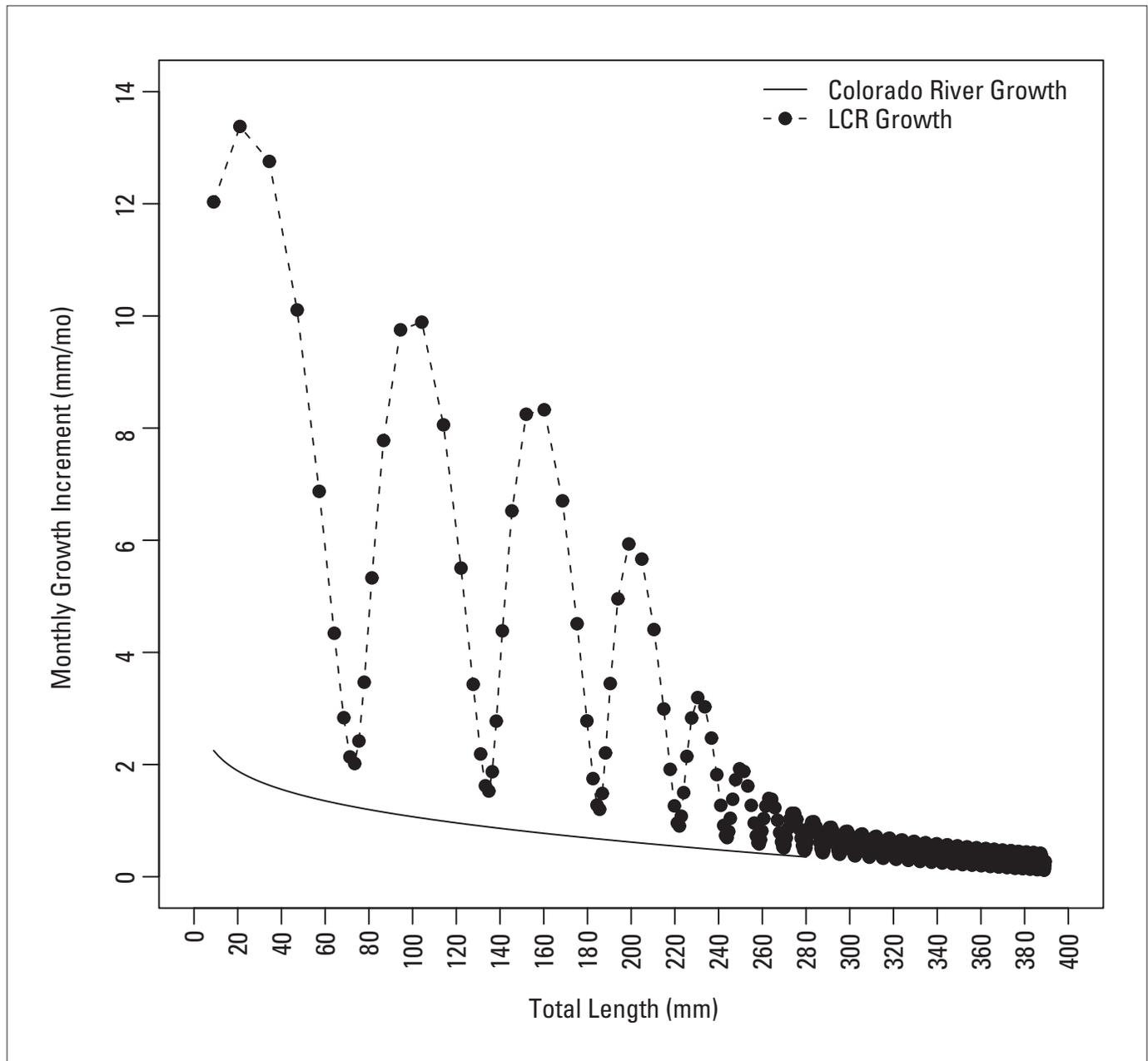


Figure 24. Predicted monthly growth rate from the temperature-dependent growth model for the Little Colorado River (LCR) population of humpback chub and for humpback chub living in the mainstem Colorado River under a constant temperature of 10°C.

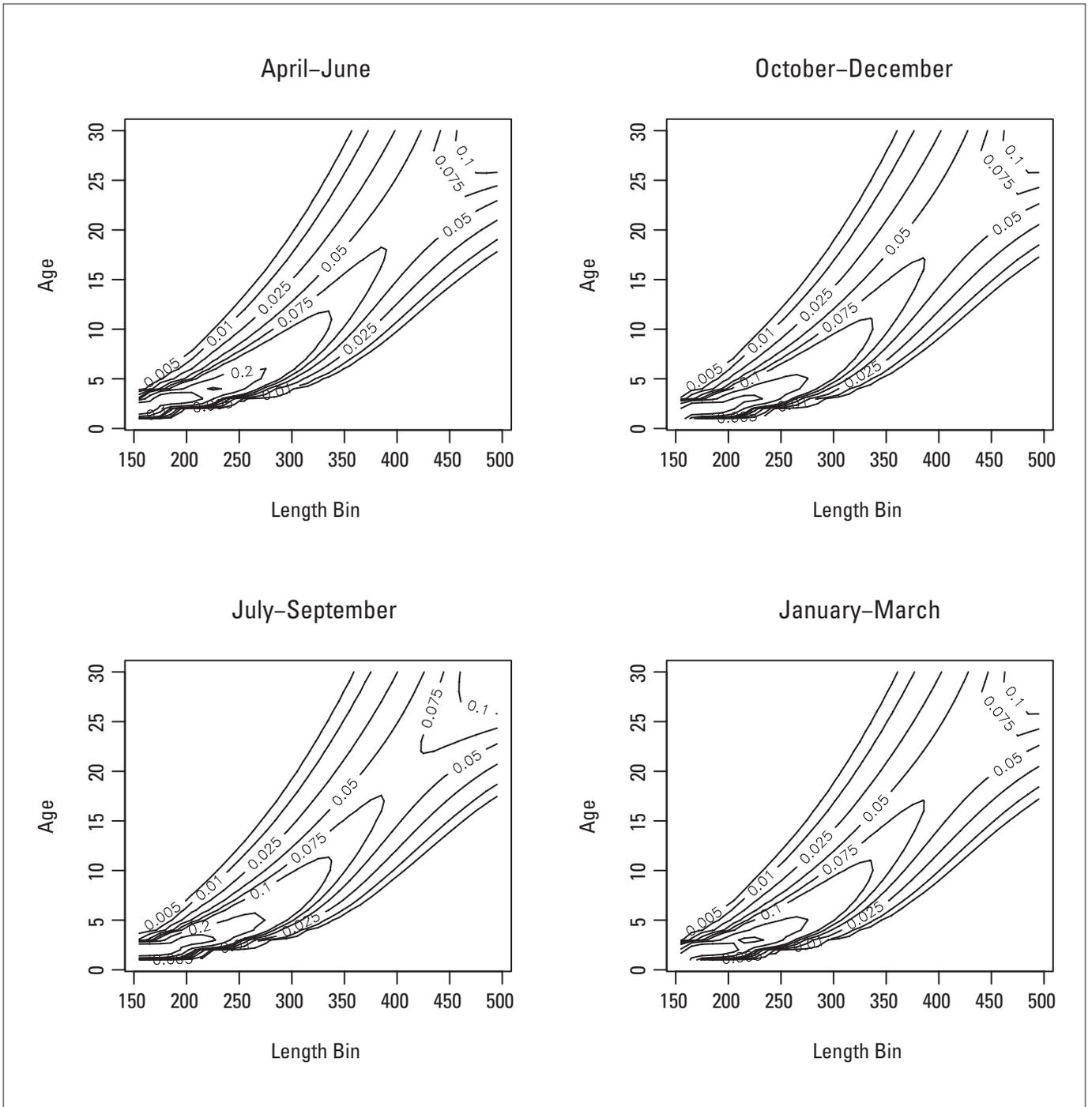


Figure 25. Seasonal probability surfaces of humpback chub age at a particular length bin. These surfaces sum to unity in the vertical dimension (i.e., for each length bin) with the height of the surface indicating the probability of a particular age given a particular length bin.

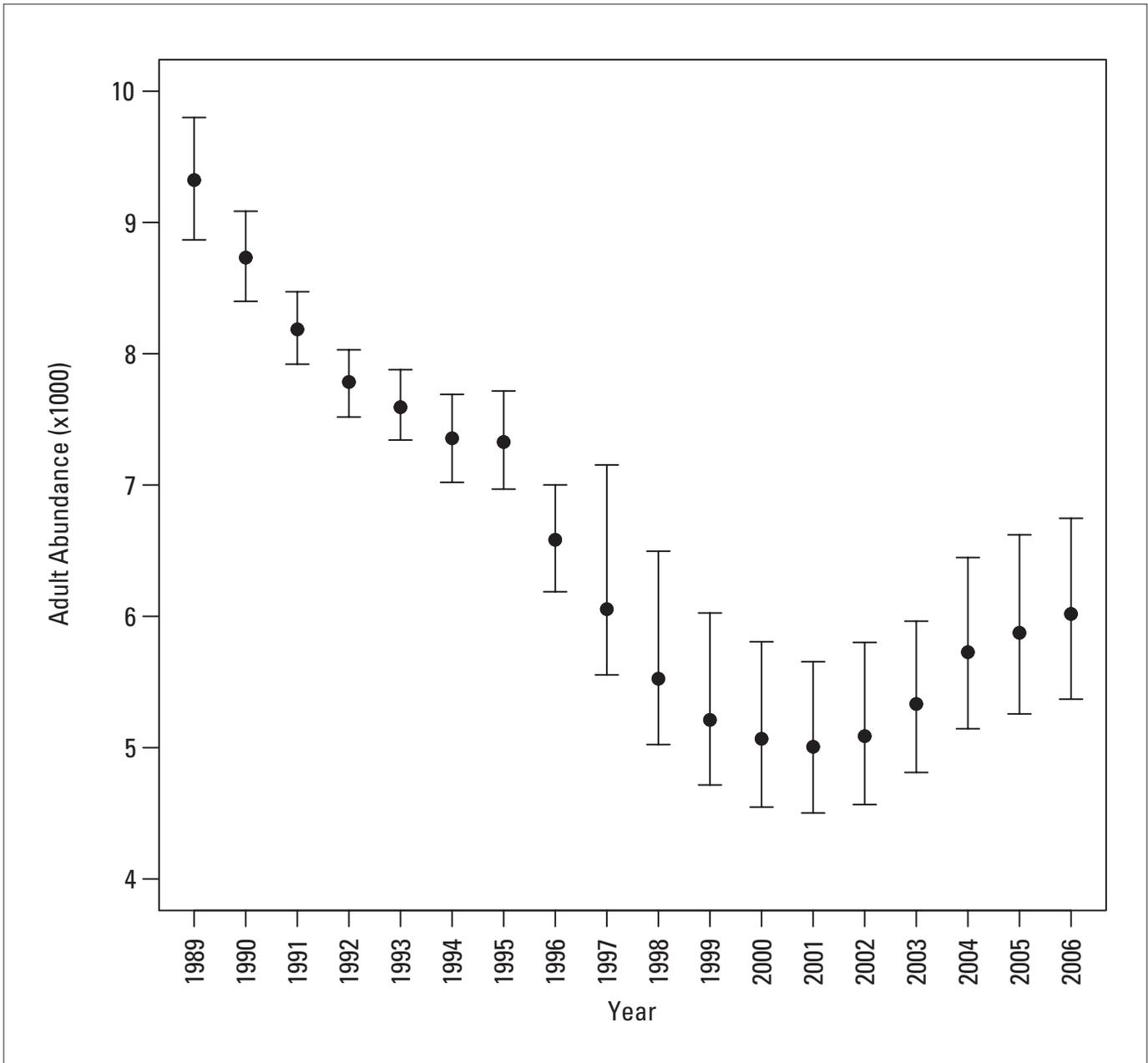


Figure 26. Estimated adult humpback chub abundance (age-4+) from the age-structured mark recapture model 3 (ASMR 3), incorporating uncertainty in assignment of age. Point estimates are mean values among 1,000 Monte Carlo trials, and error bars represent maximum and minimum 95% profile confidence intervals among 1,000 Monte Carlo trials.

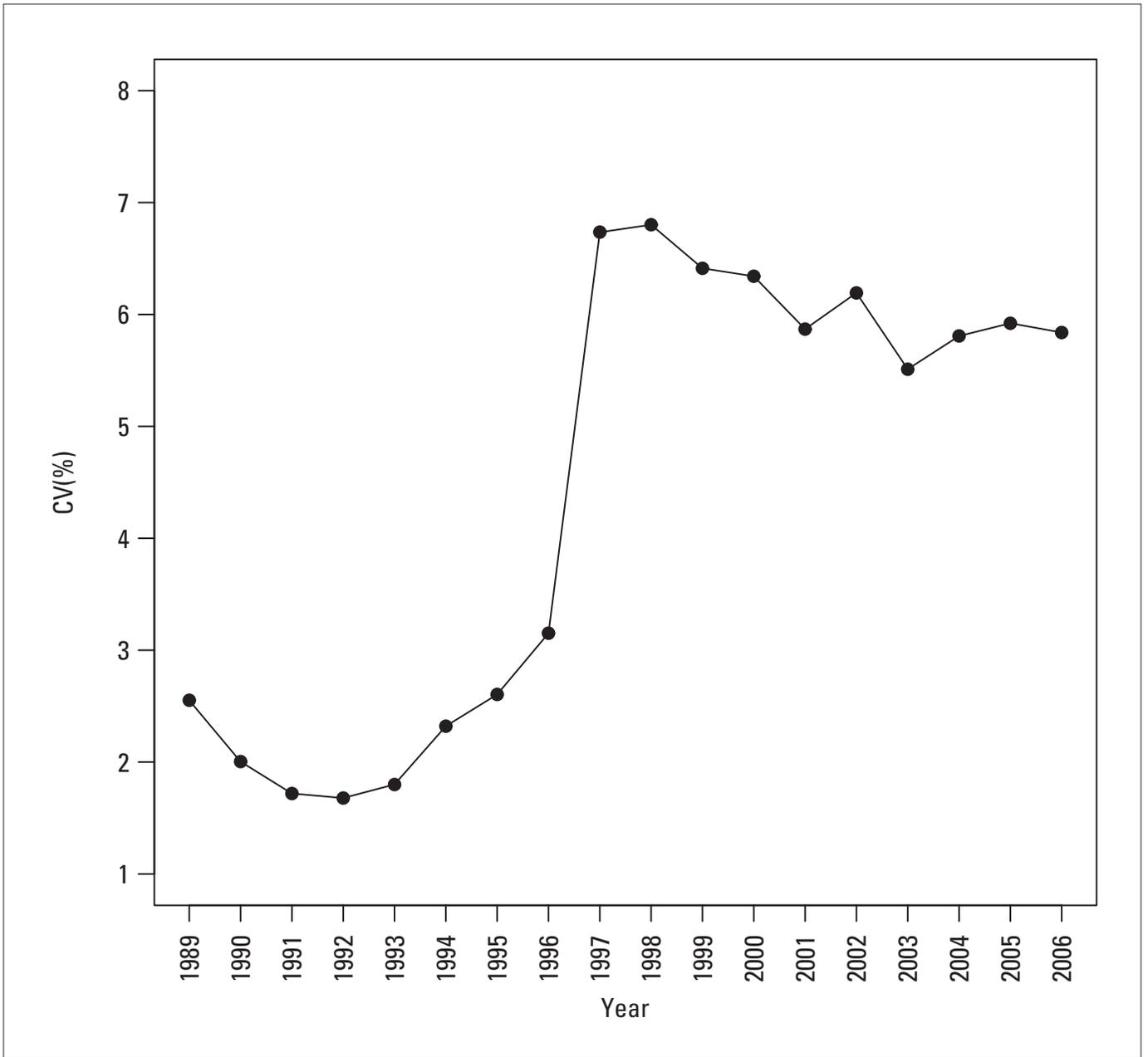


Figure 27. Coefficient of variation (CV) of humpback chub adult abundance (age-4+) estimates accounting for uncertainty in age assignment.

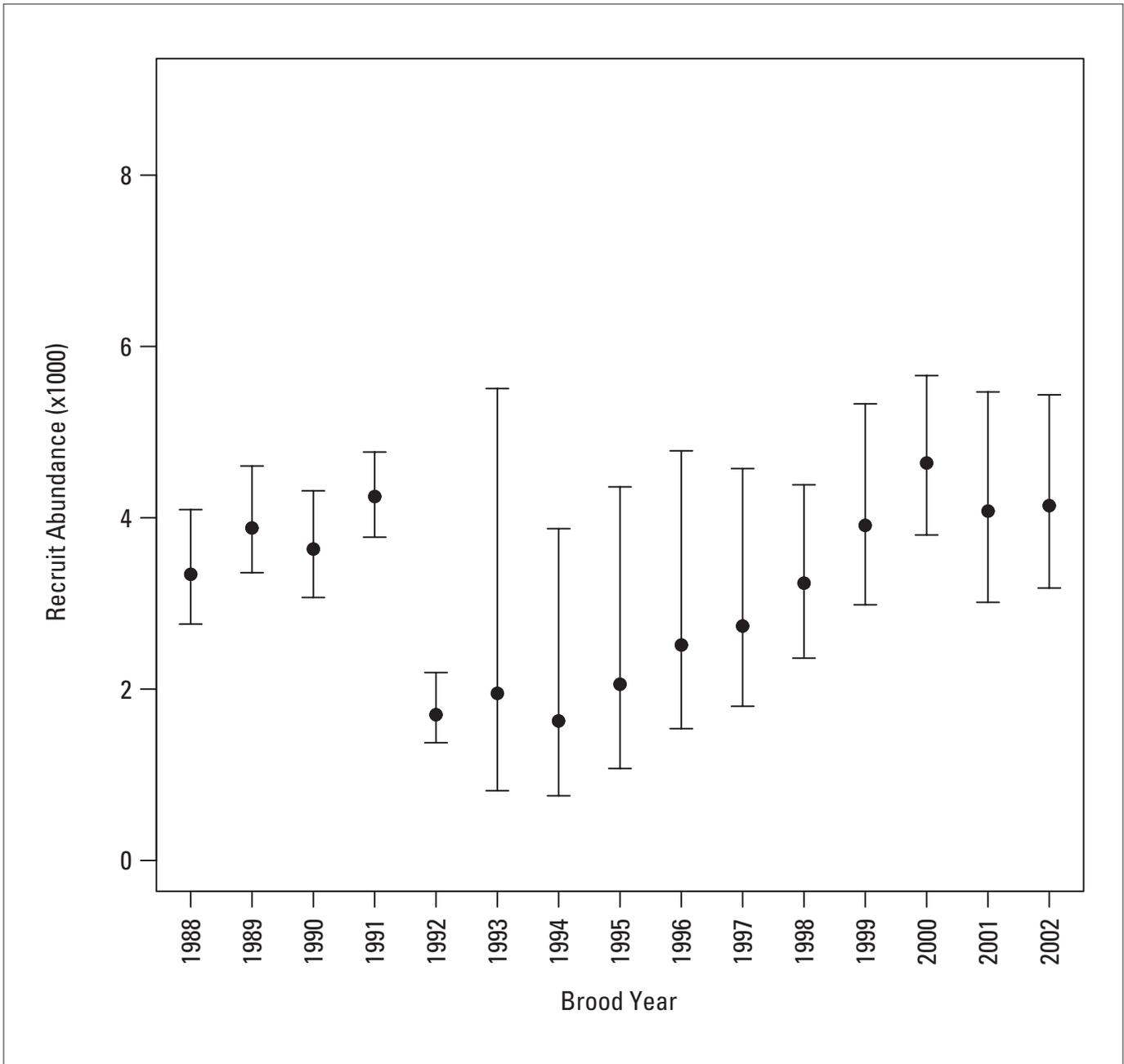


Figure 28. Estimated recruit abundance (age-1) of humpback chub from age-structured mark recapture model 3 (ASMR 3) incorporating uncertainty in assignment of age. Point estimates are mean values among 1,000 Monte Carlo trials and error bars represent maximum and minimum 95% profile confidence intervals among 1,000 Monte Carlo trials.

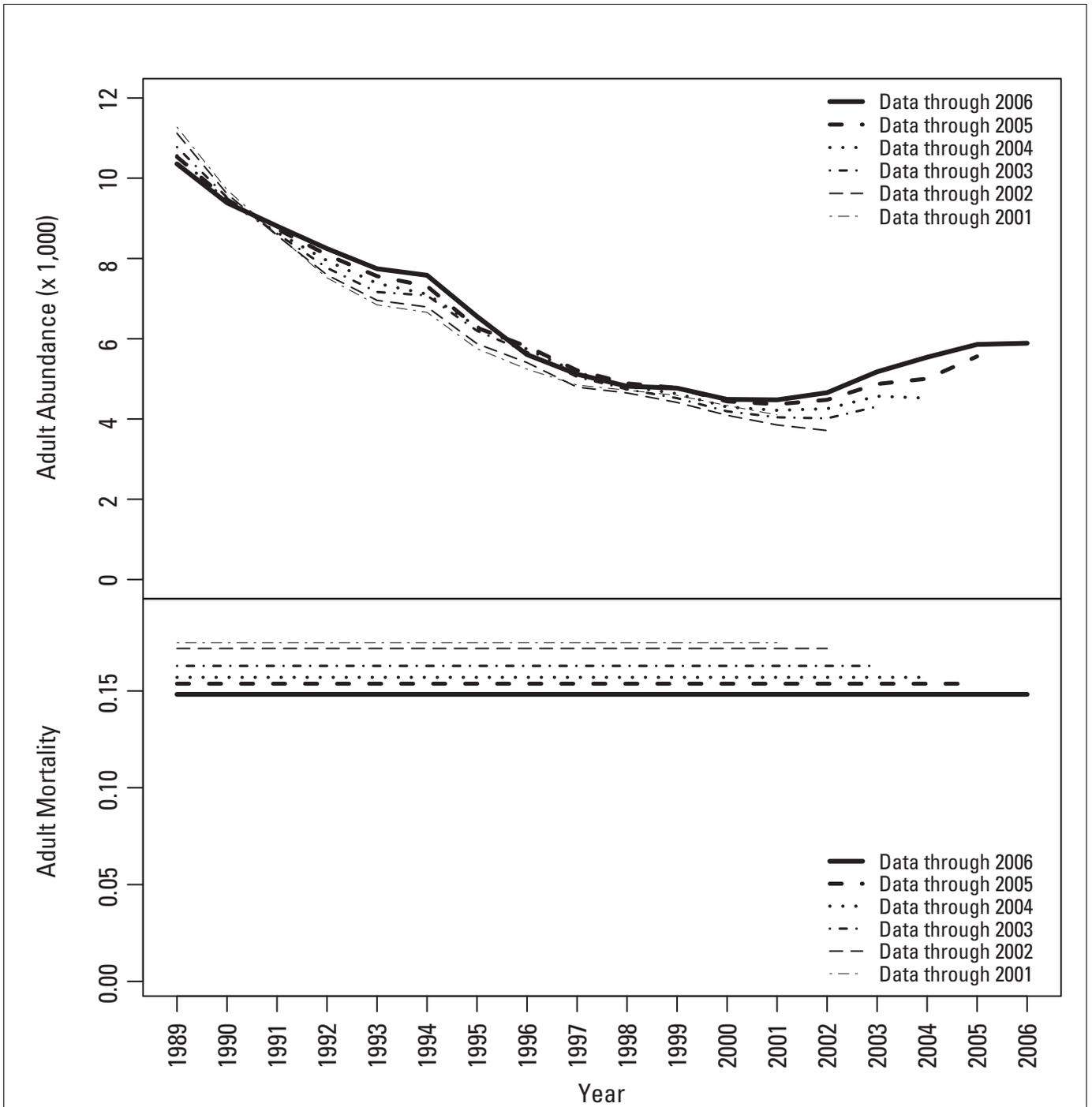


Figure 29. Retrospective analysis of adult humpback chub abundance and adult mortality rate considering datasets beginning in 1989 and ending in the year indicated in the figure legend.

Tables

Table 1. Akaike information criterion (AIC) model evaluation results among age-structured mark-recapture models fit to data pooled among tag cohorts.

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

Table 2. Akaike information criterion (AIC) model evaluation results among age-structured mark recapture models fit to data stratified by tag cohort.

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

Table 3. General growth model results for the humpback chub, temperature-independent growth model (TIGM) and the temperature-dependent growth model (TDGM).

Model	H	d	m	n	L_{∞}	σ_m^2	Q_c	L_t	AIC	# Parameters	Rank	Δ AIC
TIGM	163	0.52	.0007	1.15	391	961	--	--	133,658	6	2	38,493
TDGM	21	0.61	4.6	.89	434	2000	4.59	236	95,165	8	1	0

Table 4. Parameter correlation matrices for the humpback chub temperature-independent growth model (top table) and the temperature-dependent growth model (bottom table).

Temperature-independent growth model:

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

Temperature-dependent growth model:

	H	d	m	n	Q_c	L_t
H	1					
d	0.74	1				
m	0.88	0.94	1			
n	-0.86	-0.934	-0.99	1		
Q_c	-0.98	-0.824	-0.89	0.88	1	
L_t	0.55	0.16	0.35	-0.34	-0.46	1