Grand Canyon Monitoring and Research Center

Abundance Trends and Status of the Little Colorado River Population of Humpback Chub: An Update Considering Data From 1989–2008

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Conversion Factors

SI to Inch/Pound

Multiply	By	To obtain
	Length	
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:
°F=(1.8×°C)+32

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Executive Summary

Mark-recapture methods have been used for the past two decades to assess trends in adult abundance and recruitment of the Little Colorado River (LCR) population of humpback chub. These methods indicate that the adult population declined through the 1980s and early 1990s but has been increasing for the past decade. Recruitment appears also to have increased, particularly in the 2003-4 period. Considering a range of assumed natural mortality-rates and magnitude of ageing error, it is unlikely that there are currently less than 6,000 adults or more than 10,000 adults. Our best estimate of the current adult (age 4 years or more) population is approximately 7,650 fish.

Recent humpback chub assessments using the Age-Structured Mark-Recapture model (ASMR) and reported in 2006 (Melis and others, 2006) and 2008 (Coggins, 2008a,b) have provided abundance and recruitment trend estimates that have changed progressively over time as more data are considered by the model. The general pattern of change implies a less severe decline in adult abundance during the late 1980s through early 1990s, with attendant changes in recruitment supporting this demographic pattern. We have been concerned that these changes are not indicative of the true population and may be associated with a “retrospective” bias as additional data are included in the ASMR model. To investigate this possibility, we developed a realistic individual-based simulation model (IBM) to generate replicate artificial data sets with similar characteristics to the true humpback chub data. The artificial data have known abundance trends and we analyzed these data with ASMR. On the basis of these simulations, we believe that errors in assigning age (and therefore brood-year) to fish based on their length are likely to have caused the retrospective bias pattern seen in the assessments and to have caused both less severe trends in the adult abundance estimates and progressively more severe downward bias in estimates of adult mortality-rates. This “smearing,” or assignment of fish from a single brood-year into multiple incorrect brood-years, is a result of variation in growth rates. The IBM simulations indicate that as a result of this error source, the best estimates of abundance and recruitment for any calendar year are those obtained from data collected previous to and within a year or two after each calendar year.

Introduction

The humpback chub (*Gila cypha*) is a focal resource of the Glen Canyon Dam Adaptive Management Program (GCDAMP). This focus is primarily a result of the unique ecological role of the species as one of the few remaining endemic aquatic species within Grand Canyon and its endangered listing status under the U.S. Endangered Species Act (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 humpback chub (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; U.S. Fish and Wildlife Service, 2008).

The unique life-history attributes of HBC and the inability of scientists and managers to reconcile data collected during 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 (ASMR; Coggins and others, 2006b). This model has subsequently been used in combination with other capture-recapture and index-based assessments to provide status and trend information on the Little Colorado River (LCR) population of HBC (Coggins and others, 2006a, Coggins, 2008a,b). The ASMR approach has been subjected to a series of independent peer evaluations, both as part of the GCDAMP (Kitchell and others, 2003; written commun., David Otis, Iowa State University, 2009) and through peer review as part of the publication process. These reviews all provide support for the ASMR as an appropriate modeling approach to evaluate trends in HBC population size and recruitment patterns.

Though past reviews have supported the continued use of ASMR to assess the LCR population of HBC, Melis and others (2006) and Coggins (2008a,b) determined that retrospective analyses of past HBC mark-recapture data showed a trend of declining adult mortality estimates (and increasing estimates of adult abundance) as more data were included in the assessment. These authors suggested that such a trend was most likely a result of changes in sampling intensity through time, particularly the low sampling effort in the mid to late1990s. While we continue to view that explanation as plausible, we further hypothesize that such a trend could also be a symptom of random error in assignment of age to individual fish based on length. Such ageing error results in fish being assigned to incorrect brood-years (“smearing”)—strong brood-years appear weaker and weak brood-years appear stronger. Although Coggins (2008a,b) developed a technique to more rigorously assign age to individual fish on the basis of length than had been used in past assessments (Coggins and others, 2006a), these efforts did not evaluate how variability in growth rates of individual fish might increase the brood-year smearing identified above and bias ASMR estimates of adult mortality-rate, adult abundance, and year class strength. We used an individual-based simulation model (IBM) to investigate this hypothesis and report on the results of our investigation herein.

The primary objective of this report is to update the ASMR stock assessment model for the LCR population of HBC using data collected during 1989–2008. A secondary objective is to use IBM simulation modeling to investigate a potentially serious source of bias in assessment results. Taken together, this update provides an assessment of status and trend of the LCR population of HBC and provides additional guidance on interpretation of the results.

Methods

Humpback chub monitoring efforts began in 1987, when a standardized hoop-net sampling program was implemented in the lower reaches of the LCR. During the subsequent 20 years, four sampling periods can be generally defined that correspond to different levels of sampling effort and protocol (Coggins and others 2006a). The initial period lasted until 1991 and consisted mainly of limited hoop-netting in the lower 0.75 mi (1,200 m) of the LCR. Sampling period 2 (1991–1995) involved an intensive sampling effort in both the LCR and the mainstem Colorado River as part of an environmental impact study on the operation of Glen Canyon Dam (U.S. Bureau of Reclamation, 1995). The third sampling period began in 1996 and ended in 2000 in both the Colorado River and the LCR but with severely reduced intensities compared to period 2. Finally, a period of higher sampling intensity relative to period 3, but decreased relative to period 2, began in fall 2000 and continued through 2008. 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; Coggins 2008a,b).

The efforts described above have resulted in a large number of uniquely tagged subadult and adult HBC [>150 mm total length (TL)] that have been captured, measured, and implanted with passive integrated transponder (PIT) tags. Since 1989, more than 24,000 HBC have been captured, tagged, and released with unique identifiers. The resulting data are maintained in a central database housed at the Grand Canyon Monitoring and Research Center and are the primary data analyzed by the ASMR model.

Mark-recapture-based methods to assess population abundance and vital rates have been widely used in fisheries and wildlife studies for well over 50 years, and numerous reviews have been conducted highlighting the general approaches (for example, Seber, 1982; Williams and others, 2002). Traditional open models (for example, 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 (tagged) fish, which are repeatedly sampled to obtain time-series estimates of mark-rate (that is, the proportion of the overall population that is marked) and the number of marked fish alive in the population. These data 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. Theory related to age-structured stock assessment (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 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. While three parameterizations of the ASMR model have been described, Coggins (2008a,b) found that analysis of the HBC dataset was most appropriate using the ASMR 3 model. Following these findings, we present results only for the ASMR 3 model. A complete description of the ASMR models can be found in Coggins and others (2006b) and Coggins (2008a,b).

Simulated Humpback Chub Assessment Methods

We built an IBM simulation model to examine the effect of ageing error on ASMR parameter estimation. The simulation repeatedly samples an age-structured population with overall abundance, recruitment pattern, mortality, growth rates, and capture probability roughly similar to that estimated for the LCR population of HBC. Known numbers of 2-year-old recruits are added to the simulated population each year. Each individual is assigned a unique growth curve and survives over time with an annual probability that depends on its age. Simulated individuals are randomly captured and recaptured with length-dependent probabilities and assigned an apparent age at capture using the same function(s) used to assign age from length with the actual data. This process creates a simulated set of individual capture histories and total numbers captured/recaptured-at-age during each simulated year. These simulated mark-recapture data were then analyzed using the ASMR model to estimate age-specific abundance and adult mortality-rate.

2008 ASMR Assessment Update Methods

We used the results of the simulation modeling to structure the 2008 ASMR assessment update methods. The simulation modeling indicated that ageing error has had two major effects. First, assignment of fish to incorrect brood-years has tended to reduce temporal variability in recruitment and to positively bias estimated adult abundance trends away from the true values. Owing to this effect of ageing error, the least biased estimates of recruitment and adult abundance are those most proximal to the end of the dataset being analyzed. For example, when simulated data from 1989-2005 were analyzed, adult abundance estimates in 2005 were relatively unbiased. However, when simulated data from 1989-2008 were analyzed, 2005 adult abundance estimates were positively biased. To partially account for the retrospective bias noted in simulation trials, we present, for the analysis of the actual data, both the adult abundance time-series considering all data from 1989-2008 and the time-series considering terminal-year estimates from datasets ending 2002-2008.

The second major effect of ageing error appears to be a negative bias in adult mortality-rate (M_∞), particularly as more years of data are accumulated. This is likely related to both ageing error and a pattern of increasing recruitment in the final years of the simulation (and, we believe, in the actual HBC population). As fish from these strong year classes near the end of the recruitment time-series are incorrectly assigned to earlier brood-years, estimated mortality-rate must decline to adequately predict the catch of unmarked fish. Because adult mortality is not assumed to be time-dependent, this in turn increases the adult abundance throughout the estimated time-series. This simulation finding indicates that estimates of adult mortality-rate from the ASMR model were likely to be negatively biased when analyzing the real dataset and that a more productive approach would be to specify adult mortality-rate rather than attempt to estimate it.

Using the mark-recapture data to estimate natural mortality-rate would be preferable both from the standpoint of providing additional information on HBC life-history characteristics and for properly accounting for uncertainty in abundance estimates resulting from uncertainty in natural mortality-rate. However, our simulation results suggest that estimating natural mortality-rate within ASMR will result not only in biased terminal abundance estimates, but also will contribute to retrospective bias. Therefore we specified adult mortality $M_\infty = 0.13$ based on previous analyses and evidence from the mark-recapture data suggesting that HBC longevity likely exceeds 30 years (Coggins, 2008a,b). Although specifying natural mortality-rate in stock assessments using virtual population analysis methods is common practice (Quinn and Deriso, 1999), we also evaluated ASMR results across a range of specified adult mortality-rates ($M_\infty = 0.10–0.16$) to determine the sensitivity of model results to alternative choices of natural mortality-rate. The value of 0.13 is approximately midway between two estimates that we strongly suspect to be biased—a non-age-structured Cormack-Jolly-Seber (CJS) estimate of 0.16 and recent ASMR 3 estimates of around 0.11 (U.S. Geological Survey, unpublished data). The IBM simulations give estimates of around 0.11 when the true value is 0.13, and CJS estimates of near 0.16 when the true value is 0.13.

To account for uncertainty in the assignment of age using length, we estimated the probability of age for fish having length within a particular length interval $P(a|l)$, following methods reported by Coggins (2008a,b). Besides the mean length-at-age, the two additional parameters that are needed to construct $P(a|l)$ are the coefficient of variation in the von Bertalanffy (von Bertalanffy, 1938) L_∞

parameter (CV (L_∞)) and the adult mortality-rate (M_∞). For the ASMR assessment update, we used CV (L_∞) = 0.1 and M_∞ = 0.13. These values correspond to the CV (L_∞) used in the 2006 HBC assessment and the estimated adult mortality-rate (Coggins 2008a,b). Additionally, we examined the effect of assuming CV (L_∞) = 0.1 and CV (L_∞) = 0.2 so that we could evaluate the effect of greater variability in growth rate (CV (L_∞) = 0.2) leading to even more severe ageing error than has been assumed in previous assessments (CV (L_∞) = 0.1).

Assignment of age to individual fish was conducted using a Monte Carlo procedure, in which age was stochastically assigned to each fish on the basis of the $P(a\,|\,l)$ 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 possible 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 (age 2) was estimated using ASMR 3. Additionally, we computed 95-percent profile confidence interval estimates for adult abundance and recruitment for each dataset using numerical methods contained within the program AD Model Builder (Fournier, 2000). This procedure was repeated to generate and analyze 1,000 datasets (that is, Monte Carlo trials).

Results

Simulated Humpback Chub Assessments

The IBM simulations show that we must expect ASMR to give retrospective biases in both adult and recruit abundance time-series, becoming more apparent as more years of data are considered in the analyses (figs. 1, 2). These typical IBM simulation results demonstrate how the least biased estimates for both adult and recruit abundance are for years near the terminal-year of the dataset. Additionally, it is apparent that adult mortality-rate estimates are declining as more years are included in the analyses because the relative increase in adult abundance outpaces the relative increase in recruit abundance—this can only occur with a decrease in estimated adult mortality-rate and is exactly the same pattern that is apparent in the analysis of the actual data (Coggins, 2008a,b). Finally, it is worth noting that the retrospective bias in recruitment estimates is severe even for large departures from a general recruitment trend, as can be seen by the inability of the model to correctly estimate the large recruitment event simulated in brood-year 1989 (fig 2).

2008 Humpback Chub Assessment Update

The 2008 HBC assessment update continues to suggest an increasing trend in adult abundance since 2000-2001 (fig. 3). Our best estimate of the 2008 adult abundance is approximately 7,650 fish and represents an increase of approximately 50 percent since 2001. These estimates consider all data through 2008 and assume an adult mortality-rate of M_∞ = 0.13 and a coefficient of variation in the von Bertalanffy L_∞ CV (L_∞) = 0.1. Estimated recruitment of age 2 HBC also demonstrates an increasing trend since the mid-1990s with identical model assumptions (fig.4).

Investigation of alternative values of CV (L_∞) and M_∞ illustrates that the estimated magnitude and, to some degree, trend are affected by the specified value of these parameters (fig. 5). However, even among the most disparate assumptions of CV (L_∞) and M_∞ , the trend in adult abundance demonstrates a decline in adult abundance during the early part of the time-series, followed by recovery more recently. Considering all these parameter combinations suggests that the 2008 adult abundance is unlikely to have numbered less than 6,000 or more than 10,000 animals.

Following guidance from the simulation results and to attempt to account for retrospective bias, we also constructed adult and recruit abundance trend estimates considering datasets beginning in 1989 and ending in each year between 2002 and 2008. We summarized these findings assuming that the variability in growth rate was governed by CV (L_∞) equal to either 0.2 (figs. 6, 8) or 0.1 (figs. 7, 9). As expected, the abundance trends considering the terminal-year estimates appear to be less biased than those considering all data through 2008, consistent with the retrospective bias observed in the simulation results. Further, assuming greater variability in growth rate (and therefore ageing error), results in estimates with greater retrospective bias.

Discussion

Results from the 2008 assessment update generally agree with the last assessment update (Coggins, 2008a,b) and continue to support the hypothesis that adult HBC abundance has been increasing for most of this decade. Considering the variability in 2008 adult abundance estimates among the suite of specified values for CV (L_∞) and M_∞ (6,000–10,000 adult HBC; fig. 5), we suggest that the most robust finding in this report is the increasing trend in adult abundance, and that there is considerably more uncertainty about the 2008 absolute adult abundance estimate. The increase in adult abundance appears to be driven by a gradual increase in recruitment since approximately the mid to late 1990s (fig. 4). However, simulation results suggest that this apparent gradual increase in recruitment is quite possibly an artifact of ageing error causing recent strong cohorts to be incorrectly assigned to earlier brood-years (fig. 2). As a result, this recruitment time-series must be used with caution in any attempts to develop post-hoc hypotheses concerning management actions or environmental factors that may or may not have influenced recruitment and subsequent adult abundance.

Our simulation results suggest that the most reliable abundance and recruitment trends are likely obtained by considering the terminal-year estimates (figs. 6-9). Particularly for time-series of recruitment, these trends suggest a more stable trend in recruitment during 1993-2002, with a punctuated increase in recruitment beginning in brood-year 2003. Correspondingly, the largest increases in estimated adult abundance occur in 2007, when the 2003 brood-year matured to age 4.

It is noteworthy that the best available recruitment estimates (heavy dots in figure 9) still show evidence that an increase in recruitment started well before the increases in age 2 abundance that would be predicted to result from mechanical removal of nonnative fish or mainstem warming effects, despite our efforts to correct for upward bias and trend due to aging errors. Mainstem warming and mechanical removal effects both started in 2003 and could have begun affecting age 2 recruit abundance in 2004 and later, that is, they could have affected brood-years 2002 and later, but it appears that recruitments had at least doubled from the mid-1990s, even before the population was exposed to warmer Colorado River water temperatures and reduced nonnative abundance near the mouth of the LCR.

One possibility to explain strong 1999 and 2000 brood-years is the low summer steady flow conducted during the summer of 2000. It is conceivable that both of these brood-years, and possibly even the 1998 brood-year, benefited from this management action. However, we continue to urge caution in the use of these recruitment reconstructions to evaluate these types of post-hoc hypotheses. This warning is based on both the tenuous nature of this type of scientific reasoning (Yoccoz and others 2001), as well as our lack of confidence that these recruitment time-series are completely uncontaminated by ageing error and subsequent retrospective bias.

Guidance on Interpretation of Results and Recommendations for Future Analyses

Comments received in the review phase of this work deserve mention to aid in the interpretation of the results and to guide future assessment work on humpback chub. Reviewers pointed out that the reported statistical confidence intervals for the adult abundance and recruitment estimates are “grossly underestimated” because our assessment methodology does not recognize individual variability of fish responses to natural mortality-rate. As such, ASMR does not model process error in individual fish responses and therefore confidence intervals portray uncertainty about the expected abundance and recruitment rather than the actual values (written commun., Carl Schwarz, Simon Fraser University, 2009; written commun., Steve Martell, University of British Columbia, 2009). Additionally, recent work by Bonner (2008) indicates that this problem also exists with more traditional capture-recapture models such as the Jolly-Seber model. Though our reported confidence intervals incorporate uncertainty associated with ageing error, they do not incorporate uncertainty in natural mortality-rate because M_∞ is specified and no longer an estimated parameter in the model. This accounts for the reduction in confidence intervals presented in this report compared to those presented by Coggins (2008a,b).

We concur with the recommendations of reviewers that these issues relating to quantifying statistical uncertainty deserve further attention in subsequent assessments. In particular, we think that utilizing a negative binomial likelihood (written commun., Steven Martell, University of British Columbia, 2009) to better account for overdispersion in the data is a valid alternative model to pursue. Additionally, explicitly accounting for individual response to natural mortality-rate, considering methods recently described by Bonner (2008), should also assist in better accounting for statistical uncertainty (written commun., Carl Schwarz, Simon Frazer University, 2008). Perhaps most importantly, these comments point out that the confidence intervals reported here should not be used as a statistical “test” to infer annual differences among adult or recruit abundance estimates, because they do not adequately portray statistical uncertainty.

These issues on estimation of proper confidence intervals focus on quantifying statistical uncertainty. However, reviewers emphasized that this is likely a secondary issue compared to model uncertainty. While ASMR 3 has been shown to provide good fit to the mark-recapture data based on both Pearson residuals and AIC (Coggins 2008a,b), Schwarz (written communication, Simon Fraser University, 2009) noted that this is not unexpected owing to the large number of model parameters. Schwarz further noted that ASMR 3 is trading off complexity in mortality-rate with complexity in time- and age-specific capture probability. While this may not result in biased estimates of recruitment or adult abundance, alternative models utilizing simpler formulations of capture probability (for example, splines; Bonner 2008) and more complex time-dependent mortality formulations could provide additional insight on the sources of variability in the data. We recommend that future assessments pursue these suggestions.

Finally, reviewers expressed concern that we abandoned our attempts to estimate natural mortality-rate and instead specify this parameter as a fixed value for the purposes of estimating current abundance ($M_\infty = 0.13$). While we concur that the estimates of recruitment and adult abundance are quite sensitive to the specification of this important parameter (fig. 5), we believe that it is preferable not to attempt to estimate M_∞ using the existing ASMR 3 formulation, owing to the biases exposed through our simulation analyses. We further suggest that our choice of $M_\infty = 0.13$ is probably fairly accurate, given mark-recapture data that suggest this species likely has longevity greater than 30 years (Coggins 2008a,b). A constant natural mortality-rate of 0.13 would correspond roughly to a species having longevity of approximately 35 years (Hewitt and Hoenig, 2004).

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We would like to thank Carl Schwarz, Ken Pollock, and Steve Martell for insightful review comments and suggestions for future assessments that much improved this report. We would also like to thank Meagan Polino and Paul Alley for their efforts to track down and correct errors in the humpback chub mark-recapture database. Finally, and perhaps most deservedly, we thank the field crews past and present whose tireless efforts provide the data upon which this assessment relies completely.

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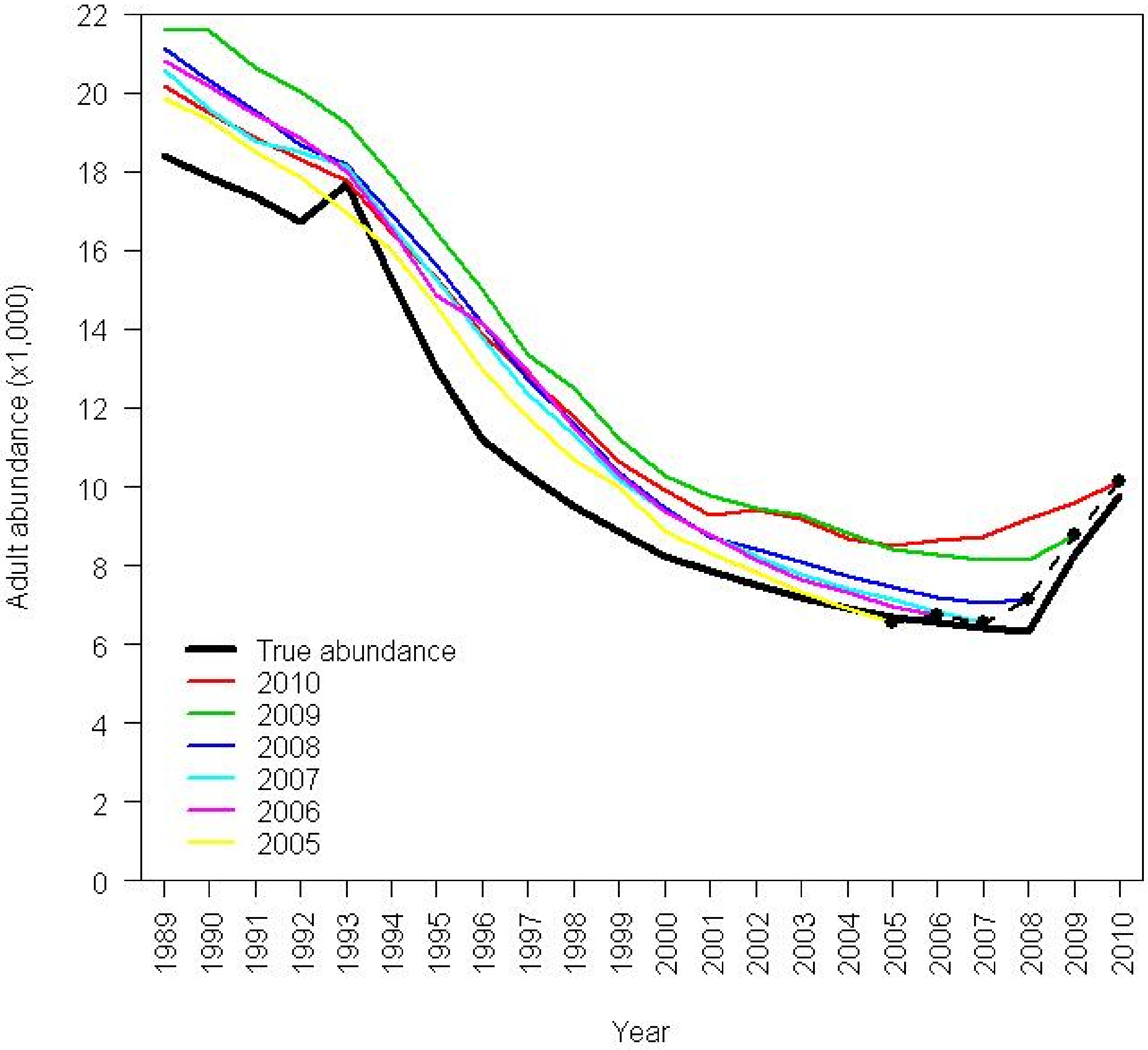

Figure 1. Typical individual-based model simulation results for simulated "true" adult abundance (heavy black line), compared to ASMR analyses of datasets ending in the year indicated in the legend. Note that the least biased adult abundance trend from 2005-2010 is to consider only the terminal-year abundance estimates from each dataset analyzed (black dots connected by dashed black line).

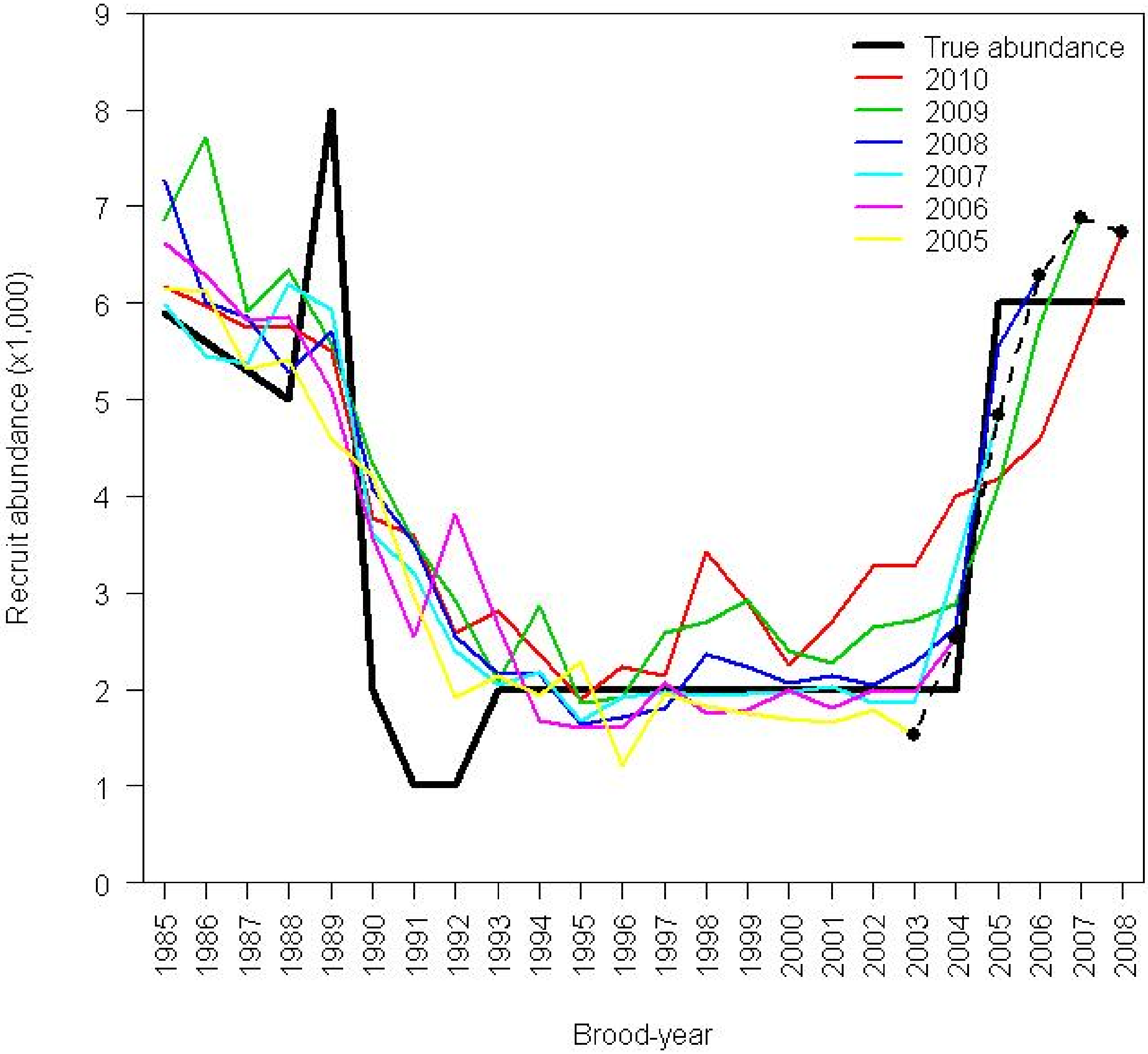

Figure 2. Typical individual-based model simulation results for simulated "true" age 2 recruit abundance (heavy black line), compared to ASMR analyses of datasets ending in the year indicated in the legend. Note that the least biased recruitment trend from brood-years 2003-2008 is to consider only the terminal-year recruitment estimates from each dataset analyzed (black dots connected by dashed black line).

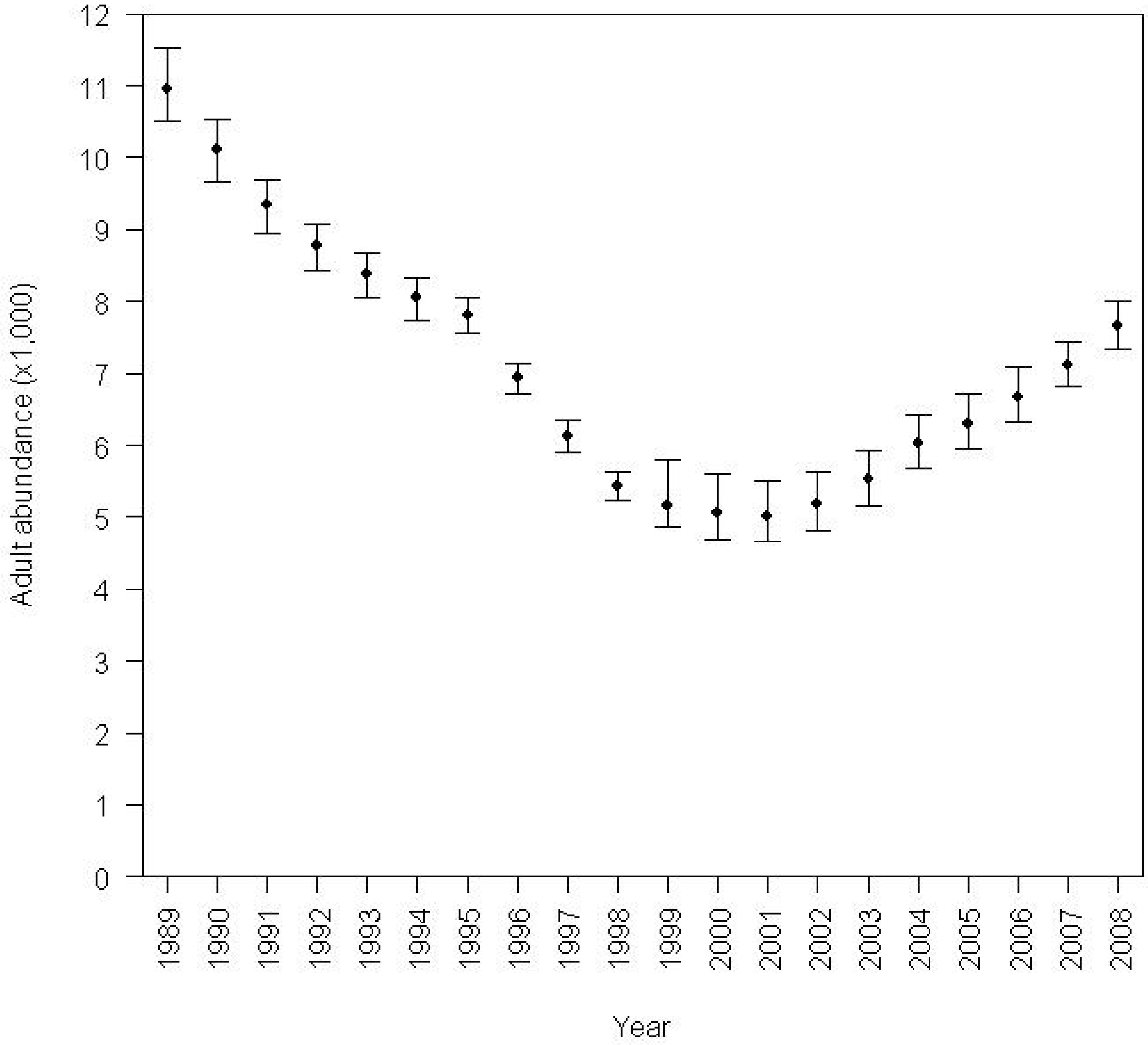

Figure 3. Estimated adult humpback chub abundance (age 4+) from ASMR, incorporating uncertainty in assignment of age. Point estimates are mean values among 1,000 Monte Carlo trials, and error bars represent maximum and minimum 95-percent profile confidence intervals among 1,000 Monte Carlo trials. All runs assume the coefficient of variation of the von Bertalanffy $L\infty$ was CV ($L\infty$) = 0.1 and adult mortality was $M\infty$ = 0.13. See "Discussion" for proper interpretation of confidence intervals.

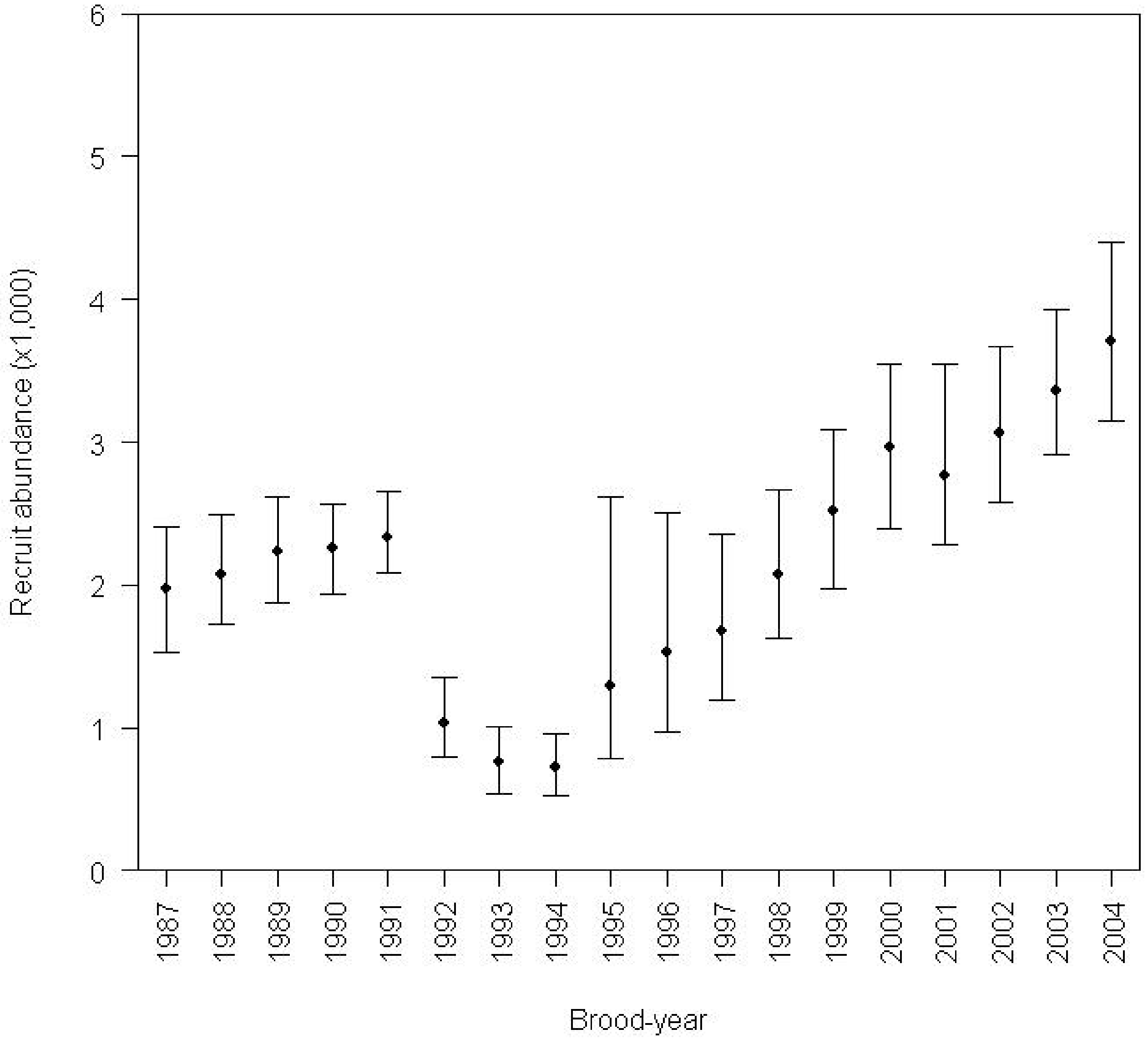

Figure 4. Estimated recruit abundance (age 2) of humpback chub from ASMR, incorporating uncertainty in assignment of age. Point estimates are mean values among 1,000 Monte Carlo trials and error bars represent maximum and minimum 95-percent profile confidence intervals among 1,000 Monte Carlo trials. All runs assume the coefficient of variation of the von Bertalanffy L_∞ was $CV(L_\infty) = 0.1$ and adult mortality was $M_\infty = 0.13$. See "Discussion" for proper interpretation of confidence intervals.

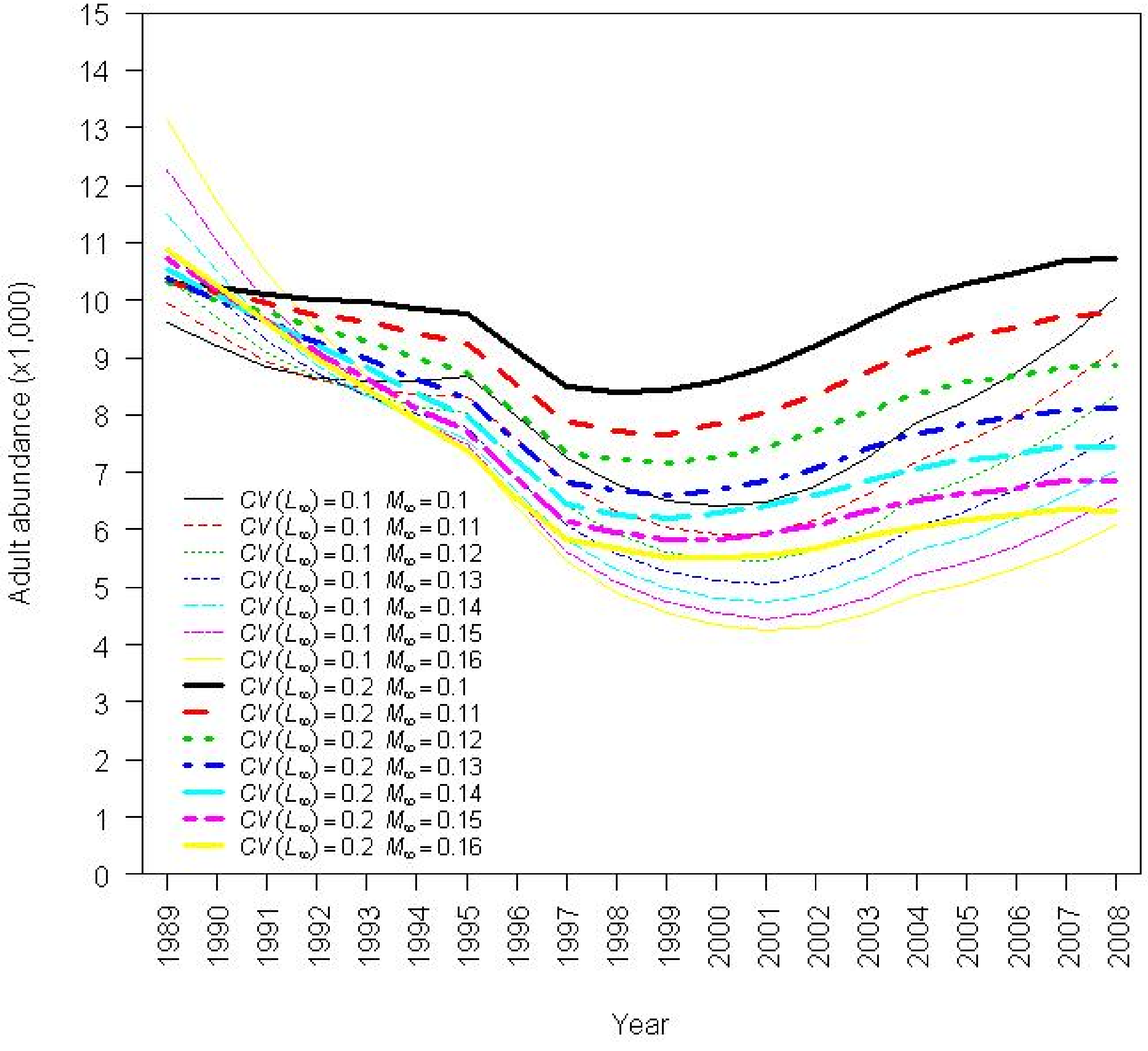

Figure 5. Adult abundance (Age 4+) from ASMR assuming coefficient of variation of the von Bertalanffy L_∞ was either $CV(L_\infty) = 0.1$ or $CV(L_\infty) = 0.2$ and adult mortality ranged between $M_\infty = 0.1$ and 0.16.

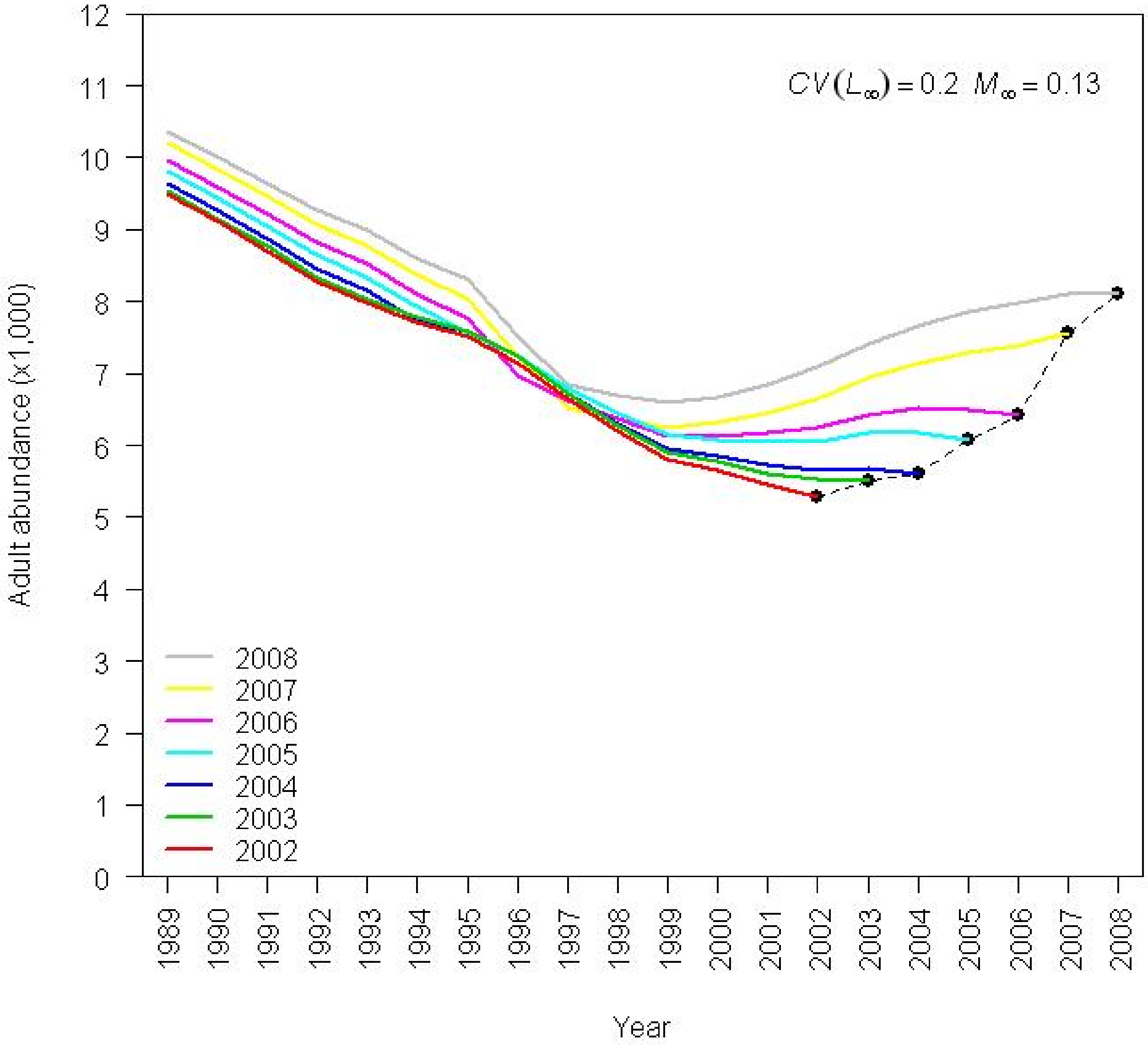

Figure 6. Adult abundance (age 4+) resulting from ASMR analyses of datasets beginning in 1989 and ending in the year indicated in the legend. All runs assume the coefficient of variation of the von Bertalanffy L_∞ was $CV(L_\infty) = 0.2$ and adult mortality was $M_\infty = 0.13$. The dashed black line is the estimated adult abundance trend from 2002 to 2008 considering the terminal-year abundance estimate for each dataset.

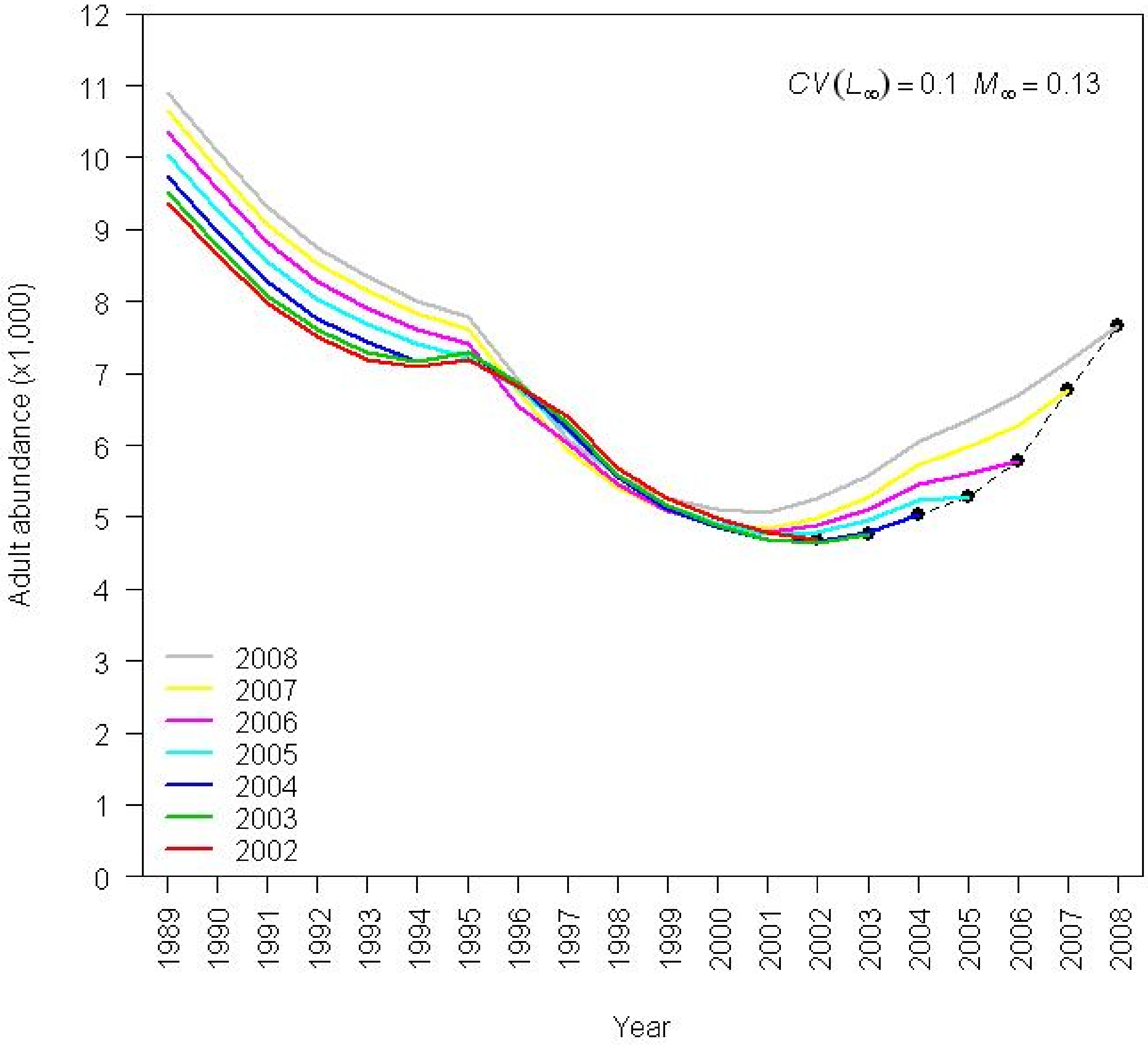

Figure 7 Adult abundance (age 4+) resulting from ASMR analyses of datasets beginning in 1989 and ending in the year indicated in the legend. All runs assume the coefficient of variation of the von Bertalanffy L_∞ was $CV(L_\infty) = 0.1$ and adult mortality was $M_\infty = 0.13$. The dashed black line is the estimated adult abundance trend from 2002 to 2008 considering the terminal-year abundance estimate for each dataset.

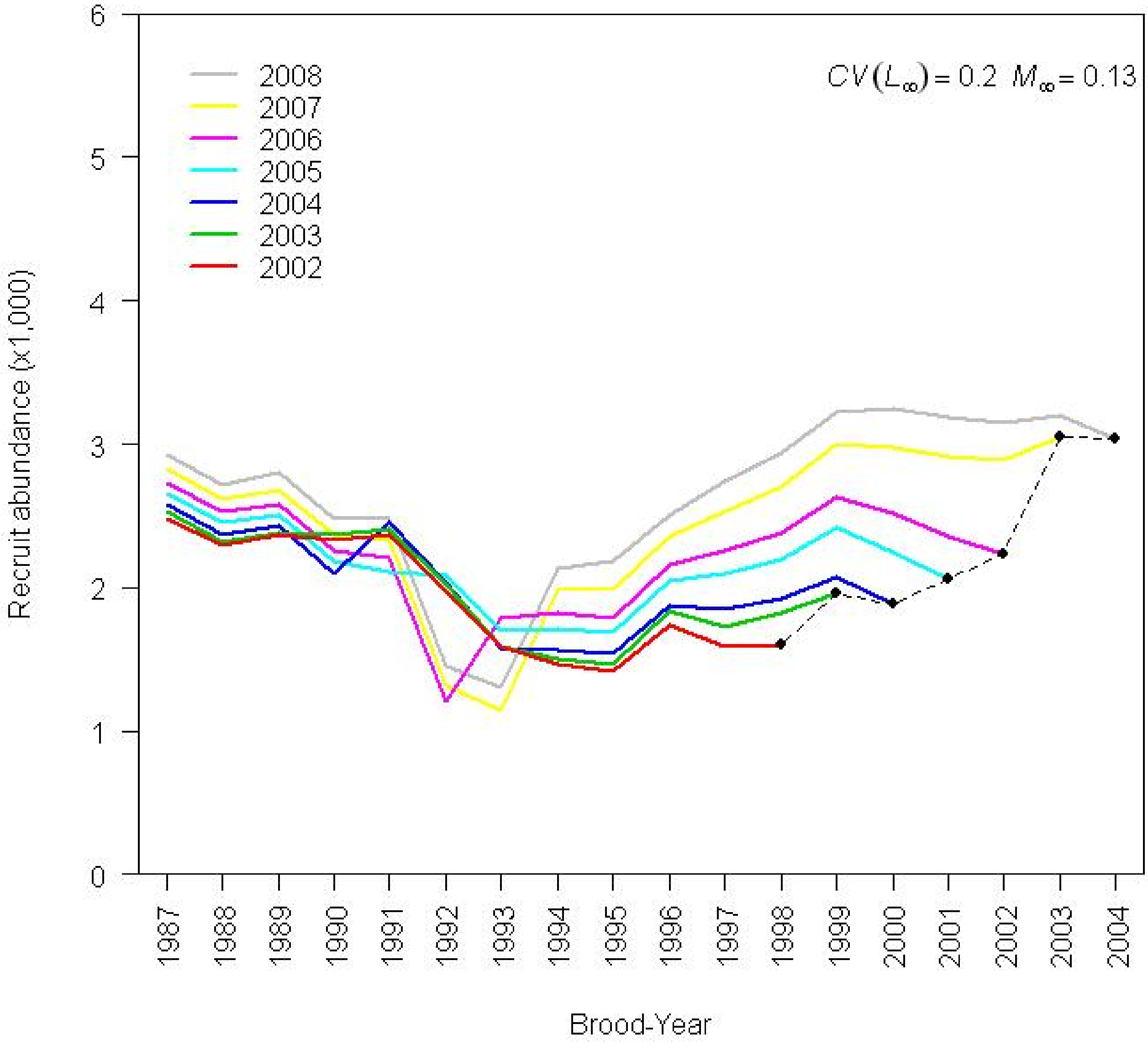

Figure 8. Recruit abundance (age 2) resulting from ASMR analyses of datasets beginning in 1989 and ending in the year indicated in the legend. All runs assume the coefficient of variation of the von Bertalanffy L_∞ was $CV(L_\infty)$ = 0.2 and adult mortality was M_∞ = 0.13. The dashed black line is the estimated recruit abundance trend from brood-years 1998-2004 considering the terminal- year abundance estimate for each dataset.

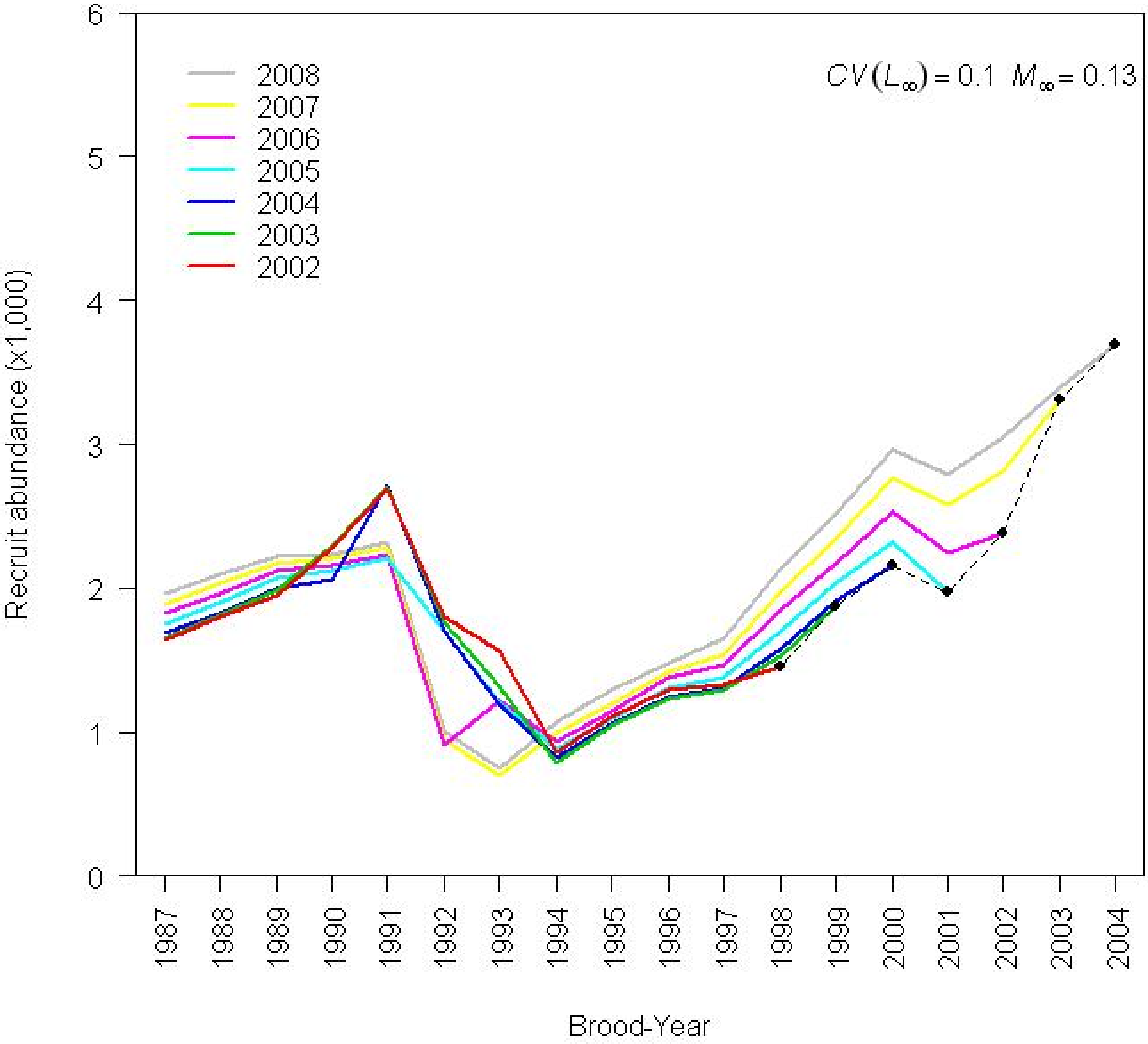

Figure 9. Recruit abundance (age 2) resulting from ASMR analyses of datasets beginning in 1989 and ending in the year indicated in the legend. All runs assume the coefficient of variation of the von Bertalanffy L_∞ was $CV(L_\infty)$ = 0.1 and adult mortality was M_∞ = 0.13. The dashed black line is the estimated recruit abundance trend from brood-years 1998-2004 considering the terminal-year abundance estimate for each dataset.

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