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Spatiotemporal Variation in Length–Weight Relationships of Endangered Humpback Chub: Implications for Conservation and Management

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Abstract.—The largest population of endangered humpback chub *Gila cypha* inhabits the lower Little Colorado River (LCR) and the main-stem Colorado River near its confluence with the LCR in Grand Canyon, Arizona. At present, fish in both rivers spawn almost exclusively in the LCR. Flows in the main-stem Colorado River are regulated by Glen Canyon Dam, and water temperature approximates predam winter temperatures year-round. The LCR continues to provide a relatively natural hydrograph and seasonal warming patterns. Length–weight relationships among adult humpback chub from the lower Colorado River basin showed a seasonal pattern of declining condition during spring spawning season followed by recovery of condition during summer through early winter. Fish from the main stem recovered condition more rapidly after reproduction than did fish from the LCR and may have benefited from dam-mediated environmental changes. Grand Canyon Colorado River fish had the greatest weight at length of eight locations sampled in the upper and lower basins. Records since 1978 indicate a decline in condition of lower basin humpback chub coincident with a reported decline in population size in Grand Canyon. We recommend increased monitoring of all populations, including mark–recapture studies to provide population estimates during the spawning season and condition monitoring during October–November to determine more subtle changes in fish health.

The humpback chub *Gila cypha* is one of four endangered big-river fish species endemic to the Colorado River Basin; the other species are the Colorado pikeminnow *Ptychocheilus lucius*, razorback sucker *Xyrauchen texanus*, and bonytail *G. elegans*. The humpback chub was first described in 1946 (Miller 1946) and was included in the first list of endangered species in 1967 (32 FR 4001). Humpback chub persist as six populations, five in the upper Colorado River basin above Lake Powell, and one—the largest—in Grand Canyon (Figure 1; Valdez and Clemmer 1982). The Grand Canyon population consists of nine main-stem Colorado River aggregations and one aggregation in the Little Colorado River (LCR: Valdez and Ryel 1997); the LCR, with base flow of about 6.5

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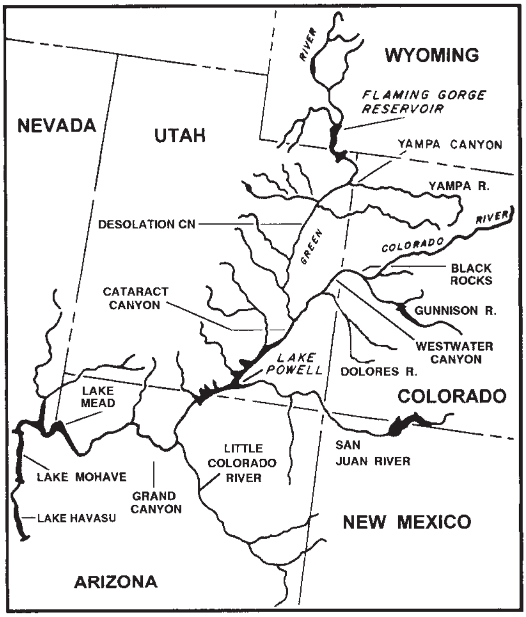

FIGURE 1.—Map showing locations of known humpback chub populations in the upper Colorado River basin (Black Rocks Canyon, Cataract Canyon, Desolation–Gray Canyon, Westwater Canyon, Yampa Canyon) and lower basin (Grand Canyon–Little Colorado River).

m^3/s, is the largest tributary of the Colorado River in Grand Canyon. The largest main-stem aggregation occurs near the confluence of the Colorado and Little Colorado rivers and is the only aggregation from which adults ascend into the LCR to spawn (Valdez and Ryel 1997). The degree of mixing of this main-stem aggregation and the apparently resident LCR aggregation is unclear (Douglas and Marsh 1996; Valdez and Ryel 1997).

Following closure of Glen Canyon Dam in 1963, year-round main-stem temperatures near the LCR confluence have ranged from 8 to 12°C (Stanford and Ward 1991), well below the 16–22°C range considered suitable for spawning and incubation of humpback chub (Hamman 1982; Marsh 1985). Water temperatures of the LCR range from 2 to 27°C (J. Korn, Grand Canyon Monitoring and Research Center, personal communication), and suitable spawning temperatures are reached in March. Because main-stem reproduction by humpback chub is precluded by cold water temperature, essentially all recruitment for the species is the result of spawning in the LCR (Valdez and Ryel 1997).

The aquatic food base of the main stem was also dramatically altered by Glen Canyon Dam; retention of particulate organic matter in Lake Powell and the change to cold, isothermal temperatures eliminated most native macroinvertebrate species (Blinn and Cole 1991). The majority of instream primary and macroinvertebrate production in Grand Canyon now occurs in the first 26 km below the dam and is accounted for primarily by the green alga *Cladophora glomerata,* the imported amphipod *Gammarus lacustris,* and several species of chironomid midges (Stevens et al. 1997). No data on the predam diet of humpback chub exist, but postdam food habit studies have shown the diet is composed primarily of aquatic macroinvertebrates (Jacobi and Jacobi 1982; Kaeding and Zimmerman 1983; Valdez and Ryel 1997). Plant material is also commonly ingested along with terrestrial macroinvertebrates and some small fish and reptiles (Valdez and Ryel 1997). Historically, humpback chub probably became engorged on periodic abundances of food washed by floods into the river or on emergences or migrations of insects, such as observed by Tyus and Minckley (1988) for Mormon crickets in the upper Colorado River basin. Humpback chub appear to be generalist, opportunistic feeders with a simple S-shaped guts and without pyloric caeca, common organs of fat storage in many fish species.

We examined length–weight relations of adult humpback chub in the Colorado River and LCR in Grand Canyon and compared these with relations for the other five known populations in the upper Colorado River basin. We recognize that flow regulation of the Colorado River by Glen Canyon Dam resulted in two distinct ecological settings for humpback chub in Grand Canyon: the dam-regulated main stem and the relatively natural LCR. We discuss the effect of these environmental differences on humpback chub condition (weight at a given length) in Grand Canyon.

Methods

Humpback chub in Grand Canyon were captured with a variety of gear, including hoop nets and trammel nets in the LCR (Gorman 1994; Douglas and Marsh 1996) and trammel nets, electrofishing, and hoop nets in the main-stem Colorado River (Valdez et al. 1993; Valdez and Ryel 1997). Humpback chub were captured during monthly field trips from July 1991 to December 1995 in the LCR and from January 1990 to November 1993 in the main-stem Colorado River. Each fish was weighed in grams and measured to total length (TL) in millimeters. Gender was determined based on expression of gametes or on the shape of the urogenital papilla (Suttkus and Clemmer 1977). Male humpback chub tend to have more pronounced, erect, and anteriorly oriented papillae than females, although the distinction is not always obvious. Egg-bearing females, the group most responsible for major intergender differences, are often noticeably gravid and robust during the breeding season. Because these females had highly variable weights during the spawning season from expulsion of egg masses, all fish identified as females were excluded from analyses, leaving only identifiable males and fish of indeterminate gender. Data from fish netted by the Arizona Game and Fish Department (1978–1996) were used, along with some of the data described above, to examine long-term trends in condition at the confluence of the main-stem Colorado River and LCR.

Fish from the LCR were partitioned into two groups: those captured 1.3–7 km from the confluence with the Colorado River (Powell Camp; N = 766) and those captured 8–14.9 km from the confluence with the Colorado River (Salt Camp; N = 1,159). Main-stem Colorado River data were limited to fish from the largest aggregation (N = 945), which extended 6.9 km upstream to 6.6 km downstream from the LCR confluence. We also analyzed length–weight data from the five upper Colorado River basin humpback chub populations: Black Rocks (Colorado River in Colorado; N = 417; 1979–1984, 1994), Cataract Canyon (Colorado River below its confluence with the Green River in Utah; N = 20; 1985–1989), Desolation and Gray canyons (Green River in Utah; N = 99; 1979–1981, 1985–1988, 1992, 1994), Westwater Canyon (Colorado River near the Utah–Colorado border; N = 137; 1991–1994), and Yampa Canyon (Yampa River in Colorado; N = 109; 1981, 1984–1989, 1993). Data sources are given in Appendix Table A.1.

Analyses were limited to fish of at least 200 mm TL, the approximate minimum length of mature adults in Grand Canyon (Valdez and Ryel 1997). All fish identified as females were excluded from the analyses. All analyses of length–weight relationships were subjected to analysis of covariance (ANCOVA; Le Cren 1951) with weight as the dependent variable, length as a covariate, and month, season, or river as group variables as appropriate. Length and weight were transformed to base-10 logarithms; transformed data met relevant assumptions. Temporal patterns of predicted weight were analyzed by month. Repeated-measures models were not used because recapture rate (from passive integrated transponder tags) in all data sets was low; successive samples were thus nearly completely independent. Two studies (Arizona State University and U.S. Fish and Wildlife Service) contributed length–weight data from the LCR. Study goals and methods differed, but study effects were not significant (ANCOVA test of study effect: lower reach, F = 1.91, df = 1, 703, P = 0.1672; upper reach, F = 3.29, df = 1, 1,090, P = 0.0701), nor was there a significant difference between upper and lower reach (ANCOVA test of reach effect: F = 3.78, df = 1, 1,794, P = 0.0520); the near significance of the latter test owed to a single month (ANCOVA test of reach effect without February 1993 data: F = 1.77, df = 1, 1,791, P = 0.1831). Lower Colorado River data were therefore pooled when LCR fish were compared with other populations.

All analyses were conducted with SAS version 6.11, PC implementation. Multiple comparisons from ANCOVA results were calculated from least-square-means comparisons, corrected for an experimentwise 5% error rate with sequential Bonferroni correction (Rice 1989). Predicted weight and 95% confidence interval for an arbitrary 300-mm TL fish (midsized adult) were calculated for each set of data to graphically compare patterns in condition without the confounding effect of weight (Cone 1989). Predictions were calculated from ANCOVA results and back-transformed into standard units. Researchers often report relative condition (Le Cren 1951) or relative weight (Wege and Anderson 1978) when analyzing length–weight data; however, ANCOVA provides better statistical properties than these ratio variables and we found no need to report a condition index per se. Our results are equivalent to an analysis of factors affecting relative condition, and we use that term when discussing weight at length. The ANCOVA approach was originally used by Le Cren (1951) and was more recently expanded by García-Berthou and Moreno-Amich (1993) to encompass multivariate analysis of covariance.

Results

Main-stem Colorado River versus Little Colorado River

Mean monthly relative condition of adult humpback chub from the main-stem Colorado River in Grand Canyon from June 1991 to December 1993 showed defined seasonal patterns with highest condition in February–April and lowest in June or July (Figure 2). Condition of LCR fish was also highest in spring, but showed a more irregular seasonal pattern and lowest condition in fall (ANCOVA test for month differences: Grand Canyon: F = 23.13,

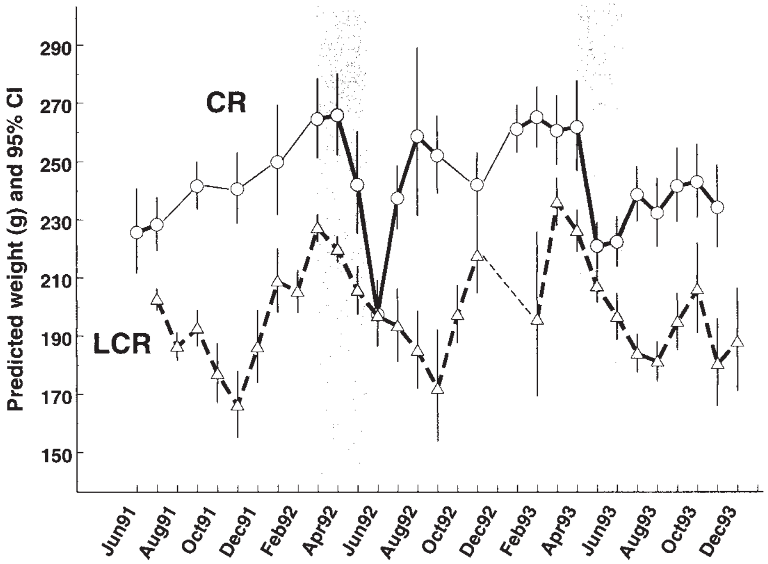

FIGURE 2.—Predicted weights and 95% confidence intervals (CI) for 300-mm TL adult male humpback chub from data collected in the Little Colorado River (LCR; $N = 1{,}797$) and Colorado River (CR; $N = 876$) in Grand Canyon, 1991–1993. Lighter-weight lines connect across periods of missing data. Shaded rectangles mark spawning seasons (March–mid-May). Predictions are back-transformed output from ANCOVA of log-transformed data; the standardized length of 300 mm is only for graphical purposes.

df = 10, 864, $P = 0.0001$; LCR: $F = 26.97$, df = 11, 1,786, $P = 0.0001$; sequential Bonferroni-corrected post hoc comparisons of average monthly condition for 1991–1993 show Grand Canyon condition higher in March–April than in June–August and LCR condition higher in March–April than in June–December).

Main-stem fish regained condition more rapidly after the breeding season than did fish from the LCR (Figure 2); on average, during 1992 and 1993, condition of main-stem fish improved slightly during the postspawning warm months (July–September) relative to the condition at the end of the spawning season (May and June), while condition of LCR fish declined slightly (ANCOVA test of season–river interaction: $F = 12.09$, df = 1, 739, $P = 0.0005$). Although condition of main-stem fish did not always increase monotonically after breeding season, condition always increased after June and remained above June levels throughout summer.

Grand Canyon Colorado River fish had significantly higher condition than LCR fish, even when monthly differences in condition pattern were taken into consideration (ANCOVA test for river differences: $F = 472.61$, df = 1, 2,101, $P = 0.0001$). Although we had statistically controlled for study differences in LCR data, we were concerned that, in comparisons with main-stem Colorado River data, pooling the LCR data might obscure meaningful differences. However, in comparing fish from each LCR study and reach combination against fish from Grand Canyon caught in the same month, we found no month in which LCR fish were significantly heavier at length than Grand Canyon Colorado River fish (ANCOVA tests of river effects, $P > 0.05$ in all cases). Accounting for length, main-stem fish were at least 10% heavier than LCR fish in 20 of 22 months compared.

Long-Term Trends in Condition

Length–weight data were collected at the confluence of the Colorado and Little Colorado rivers (the lower 1.2 km of the LCR) during most spawning seasons from 1978 to 1996. Over this period, there was a significant linear decline in predicted weight at length for humpback chub 200 mm TL and larger (multiple regression to test linear pattern over time: $t = -0.0037$, df = 1,477, $P = 0.0001$; Figure 3); no significant autocorrelation was detected in the data. Fish measured in 1990–1996, a 7-year period of relatively stable condition values, averaged 9–10% lighter than fish measured in the first 7 years of data collection (1978–1984).

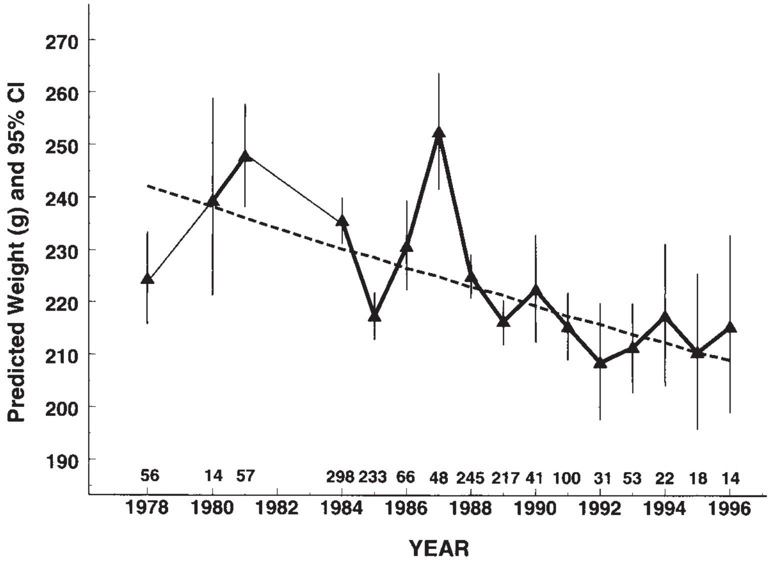

FIGURE 3.—Predicted weights and 95% confidence intervals (CI) of 300-mm TL adult male humpback chub from data collected at the Little Colorado River–Colorado River confluence, 1978–1996. The broken line shows the linear trend from a log–log analysis, back-transformed into the original units. Predictions are back-transformed output from a log–log analysis. Sample sizes are shown above the abscissa.

Comparison with Upper Colorado River Basin Populations

Length–weight relationships varied significantly among adult humpback chub from the six known populations in the Colorado River basin (Figure 4; ANCOVA test for differences among rivers: $F = 67.54$, df = 7, 6,865, $P = 0.0001$; fish length–river interaction: $F = 60.98$, df = 7, 6,865, $P = 0.0001$); all data from all studies were included in this analysis. The significance of the interaction term demonstrated that length–weight relationships differed among rivers and precluded a test of differences among rivers (Figure 4).

Discussion

Seasonal Variation in Condition

Adult humpback chub in Grand Canyon display seasonal variation in condition. We believe that this variation is associated with one or more of the following factors: onset of spawning, thermal and photoperiod regimes, and food supply.

Spawning readiness is known to coincide with good condition (Le Cren 1951; Gabelhouse 1991). In humpback chub, spawning is apparently linked to water temperature, photoperiod, and water clarity and stage (Valdez and Ryel 1997). We found that fish from the LCR and from the main-stem aggregation with access to the LCR (the aggregation shown in Figure 2) reached peak condition in January–March, just prior to spawning. Ascent into the LCR occurred primarily when LCR temperatures reached 16–22°C, generally in late March, and during descending and clearing flows of that tributary (Valdez and Ryel 1997).

However, fish in main-stem aggregations in Grand Canyon without access to the LCR reached peak condition slightly later, just before May, at approximately the time that precedes spawning by upper Colorado River basin populations (Kaeding et al. 1990; Valdez and Ryel 1997) and the time when average predam main-stem temperatures reached 16–22°C (Valdez and Ryel 1997). Under postdam conditions, main-stem fish from above and below the LCR congregate simultaneously for spawning despite constant suboptimal water temperatures, suggesting that photoperiod may cue onset of gonadal maturation and that, in the absence of seasonal tributary warming from the LCR, historic timing of gonadal maturation persists.

Rates of decline in condition during the spawning season were rapid, averaging 4–8%/month (Figure 2). These rates are somewhat higher than those reported for a chub, *Leuciscus pyrenaicus,* in the Guadalete River, Spain (approximately 4%/month; Encina and Granado-Lorencio 1997a), but lower than those reported for a barbel population (*Barbus sclateri*) in the same stream (9–11%; Encina and Granado-Lorencio 1997b). Impacts of

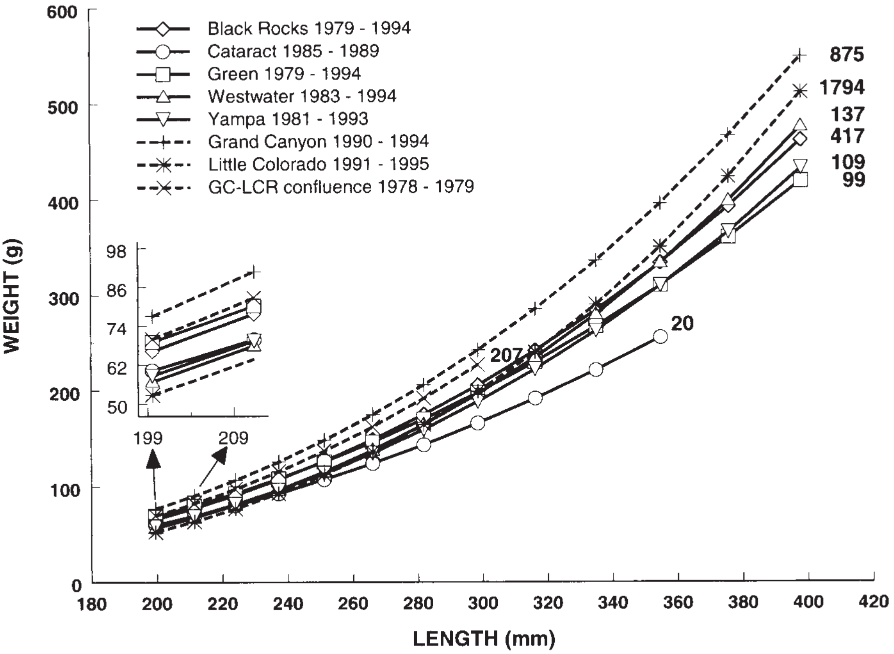

FIGURE 4.—Length–weight relationships for adult male humpback chub from five upper basin areas (solid lines) and three lower basin areas (broken lines), back-transformed from log–log regression results. All available data were pooled for each site without regard for month, year, or study. Markers on lines serve only to identify the line. Sample sizes are shown to the right of the right-most points; line length reflects range of weights in the data for the given population. Inset shows enlarged view of left end of the curves. Regressions coefficients (intercept and slope of regression of $\log_{10}$[length] on $\log_{10}$[weight]) and r^2 values are Grand Canyon–Little Colorado River (LCR–GC) confluence: −4.87, 2.92, 0.94; Little Colorado River: −5.84, 3.29, 0.96; Grand Canyon: −4.65, 2.84, 0.94; Black Rocks Canyon: −4.64, 2.81, 0.86; Cataract Canyon: −3.98, 2.51, 0.61; Green River (Desolation Canyon): −4.16, 2.61, 0.82; Westwater Canyon: −5.32, 3.07, 0.86; Yampa River: −4.88, 2.89, 0.91.

stream hydrology (e.g., spring spates) on condition of riverine fishes is unstudied; possibly these higher-energy systems lead to greater losses of condition than are reported for species inhabiting lentic systems.

River temperature may affect overall condition of humpback chub as well as recovery rates following spawning. The LCR is warm throughout the summer, and recovery rates following spawning are slower than in the colder main stem. A similarly slow recovery occurs in *Leuciscus pyrenaicus*, which inhabits seasonally warm streams and undergoes postspawning declines in condition associated with increased metabolic rate due to high water temperature (Encina and Granado-Lorencio 1997a). In addition to increased metabolism, fish in the LCR may be slower to recover condition because of low instream production and limited allochthonous input due to low rainfall in the postspawning period.

Adult humpback chub in the main-stem Colorado River in Grand Canyon exhibit the highest observed condition and the fastest recovery of weight following spawning. Historically, humpback chub were exposed to temperatures of 16–22°C from April to October and winter temperatures lower than 8–12°C. Rapid recovery of condition may reflect a more stable environment and lowered metabolic rates relative to predam circumstances. Glen Canyon Dam has eliminated high turbulent spring flows and maintained relatively cold temperatures year-round. Clear riverine flows have resulted in high productivity and a stable food base (Blinn and Cole 1991; Stevens et al. 1997; Blinn et al. 1998). For adult humpback chub, these dam-mediated changes may have a net positive effect on condition.

Food supply differs substantially among the LCR, the Colorado River in Grand Canyon, and the upper Colorado River basin. Kaeding and Zimmerman (1983) compared diets of humpback chub from the Colorado River in Grand Canyon (N = 18) and the LCR (N = 26) and reported 25 times more organisms in stomachs of main-stem fish.

Composition of stomachs was similar and chironomids and simuliids dominated these diets. More recently, *Gammarus lacustris* has been observed as an important food item, especially for fish in the vicinity of the LCR confluence (Valdez and Ryel 1997). These nonnative amphipods are relatively large macroinvertebrates introduced into Grand Canyon in 1932 and again in 1965; they are not present in the LCR or in areas occupied by humpback chub in the upper basin.

Main-stem humpback chub showed a remarkably consistent 10–20-g weight-at-length advantage over LCR fish; however, mark–recapture studies (Valdez and Ryel 1997) indicate that recruitment to the main stem is primarily from young adults reared in the LCR. Why some fish remain apparently resident in the LCR (Douglas and Marsh 1996) while others take up residence in the Colorado River remains unclear.

Apparent Decline in Condition at the LCR–Colorado River Confluence

The apparent long-term decline in condition of adult humpback chub from the LCR–Colorado River confluence area in Grand Canyon is disconcerting, particularly as it precedes an apparent decline in population size during 1991–1995 (Douglas and Marsh 1996). Historical data were available only for the LCR–main-stem confluence and other areas may show different trends; but only the confluence supports spawning humpback chub in the lower basin. Several possible explanations exist, but in all cases, evidence is sparse.

Shifts in onset of spawning might account for the apparent decline in condition observed during the 1980s in fish measured in May at the LCR–Colorado River confluence (Figure 3); year-to-year variation in condition may be explained by the proportions of fish in prespawning and postspawning condition. However, information on timing of spawning runs does not suggest that data collections were consistently or unusually late relative to spawning period in these years.

The Asian tapeworm *Bothriocephalus acheilognathi* was discovered in the LCR in 1990 (Brouder and Hoffnagle 1997) and may have contributed in some way to a decline. This parasite can emaciate the host and lead to significant losses of wild fish under conditions of stress (Granath and Esch 1983; Riggs and Esch 1987). However, the parasite cannot be conclusively detected without severe stress to the fish, and no studies have been undertaken to determine levels of tapeworm parasitism in humpback chub.

Another consideration is variability introduced by different observers. However, it seems more likely that personnel and equipment differences would contribute to increased variation in the data rather than to consistent biases through time.

Finally, it is possible that the current, apparently depressed, condition of humpback chub in the LCR–Colorado River confluence area is entirely within the range of natural variation for the species. Humpback chub may live more than 20 years (Minckley 1991), and the river in which this species evolved is capable of an immense range of conditions. We have no historic information on condition of humpback chub or on patterns of spawning success that might have occurred in a system with yearly maximum flow range of 700–56,600 m^3/s over the period of record (Dawdy 1991). A long-lived species in such a variable environment need not reproduce successfully every year in order to maintain a viable population (Douglas 1993).

Conservation and Management

Endangered species management is a conservative process in which managers are able to sacrifice few, if any, individuals, and indices of population health and trends are often based on nonlethal sampling methods and indirect measures of health and well-being. Although we cannot explain the trend in condition revealed in our analyses, careful monitoring is clearly indicated. To this end, we recommend more thorough monitoring of both population size and condition of individuals than is currently the practice. Population size is the most direct measure for documenting decline, stability, or increase in numbers of individuals. Indices such as condition factor can provide subtle evidence of a stressed or less than healthy population, but we join other investigators in recommending caution when fish condition is used to evaluate populations (Cone 1989; Springer et al. 1990).

Mark–recapture data should be collected to determine patterns of residency in the LCR and Grand Canyon and to better estimate population size. Such data and condition measurements are readily obtainable, especially during spawning season when the fish are congregated and easy to capture. However, condition during spawning is the most variable of any season; individuals may, in the course of a day, lose substantial weight by expulsion of eggs and milt. Although fish are concentrated during spawning season and easy to catch, variability of length–weight data strongly compromises the usefulness of condition measurements.

The period October–November is recommended for monitoring condition of humpback chub in Grand Canyon. This period is after the monsoon rains, and environmental conditions then are relatively stable year to year. By this time, fish have generally recovered from the stress of spawning and gender differences in length–weight relationships are minimal (Valdez and Ryel 1997), allowing data on all fish to be used. We believe this period represents a stable window through which to view humpback chub population condition. A combination of mark–recapture work during the spawning season and condition measurement combined with mark–recapture in October–November would permit continued study of seasonal changes in condition. In addition, calculation of several population estimates each year would improve overall accuracy of population assessment and allow managers to better protect this endangered species.

The various upper and lower Colorado River basin humpback chub populations differ considerably in their length–weight relationships (Figure 4). Part of this variation is certainly due to morphological variation among upper-basin populations resulting from differential genetic contributions of round-tailed chub *Gila robusta* (Dowling and DeMarais 1993, McElroy and Douglas 1995). Upper-basin populations are not all monitored consistently, and most data are collected during the postspawning summer season. We recommend instituting standardized monitoring along the lines described above at these sites, as well as in the lower basin.

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Appendix follows

Appendix: Data Available for Humpback Chub Populations

TABLE A.1.—Sources of data on humpback chub populations in the Colorado River basin.[a]

Area	River	Data years	Researcher and organization
Grand Canyon	Colorado	1991–1993	R. A. Valdez, BIO/WEST, Logan, Utah
Little Colorado River	Little Colorado	1991–1995	O. T. Gorman, U.S. Fish and Wildlife Service, Flagstaff, Arizona
		1991–1995	P. C. Marsh and M. E. Douglas, Arizona State University, Tempe
		1984–1996	D. A. Hendrickson, C. O. Minckley, W. R. Persons, H. R. Maddux, D. M. Kubly, D. A. Kinsolving, T. L. Hoffnagle, and M. J. Brouder, Arizona Game and Fish Department, Flagstaff
		1980–1981	L. R. Kaeding and M. A. Zimmerman, U.S. Fish and Wildlife Service, Grand Junction, Colorado
Colorado–Little Colorado confluence	Colorado and Little Colorado	1978–1979	S. W. Carothers and C. O. Minckley, Museum of Northern Arizona, Flagstaff
		1980–1981	L. R. Kaeding, and M. A. Zimmerman, U.S. Fish and Wildlife Service, Flagstaff, Arizona
		1984–1996	D. A. Hendrickson, C. O. Minckley, W. R. Persons, H. R. Maddux, D. M. Kubly, D. A. Kinsolving, T. L. Hoffnagle and M. J. Brouder, Arizona Game and Fish Department, Flagstaff
		1991–1995	M. E. Douglas and P. C. Marsh, Arizona State University, Tempe
Black Rocks Canyon	Colorado	1979–1981	R. A. Valdez, U.S. Fish and Wildlife Service, Grand Junction, Colorado
		1983–1984	L. R. Kaeding, B. D. Burdick and C. W. McAda, U.S. Fish and Wildlife Service, Grand Junction, Colorado
		1991–1994	W. R. Elmblad, Colorado Division of Wildlife, Grand Junction
Westwater Canyon	Colorado	1979–1982	R. A. Valdez, U.S. Fish and Wildlife Service, Grand Junction, Colorado
		1991–1994	T. Chart and M. Moretti, Utah Division of Wildlife Resources, Moab
Cataract Canyon	Colorado	1985–1989	R. A. Valdez, BIO/WEST, Logan, Utah
Desolation Canyon	Green	1979–1981, 1986	H. M. Tyus and C. A. Karp, U.S. Fish and Wildlife Service, Vernal, Utah
		1992	T. C. Modde, U.S. Fish and Wildlife Service, Vernal, Utah
		1992, 1994	T. Chart, Utah Division of Wildlife Resources, Moab
Yampa	Yampa	1986–1989	H. M. Tyus and C. A. Karp, U.S. Fish and Wildlife Service, Vernal, Utah
		1991, 1993	T. C. Modde, U.S. Fish and Wildlife Service, Vernal, Utah

[a] Personnel who collected the data may have moved, but file copies of the data are available at the offices indicated.