

Development of a Bioenergetics Model for Humpback Chub and Evaluation of Water Temperature Changes in the Grand Canyon, Colorado River

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Abstract.—The construction of Glen Canyon Dam above the Grand Canyon (Arizona) has reduced the water temperature in the Colorado River and altered the growth rate and feeding patterns of the federally endangered humpback chub *Gila cypha*. A bioenergetics model for humpback chub was developed and used to examine how warmer water temperatures in the lower Colorado River (achieved through a temperature control device [TCD] at Glen Canyon Dam) might influence their growth rate and food requirements. Parameter values for humpback chub were developed by Monte Carlo filtering and fitting to laboratory growth. Parameter bounds were established from the literature for *Gila* species, random parameter sets were selected within these bounds, and the growth of modeled humpback chub was compared with criteria from a laboratory growth experiment at 24°C. This method of parameter estimation could be applied to other imperiled fishes where physiological studies are impractical. Final parameter values were corroborated by comparison with the growth rates of humpback chub from independent field and laboratory studies. Simulations indicated that increasing water temperatures from approximately 9°C to 16°C during summer and fall, the change expected from the TCD, may have a minimal effect on humpback chub growth rate unless food availability also increases with temperature. To evaluate the effects of increased temperatures on humpback chub in the lower Colorado River, it will be essential to monitor their growth rate, the invertebrate community, and the predators of humpback chub, which are also influenced by temperature changes. Bioenergetics models for humpback chub and their predators should be helpful tools for identifying potential scenarios and evaluating the complex interactions resulting from a TCD.

The native fish community in the southwestern United States has changed dramatically over the last 100 years because of watercourse changes, introduction of nonnative species, destruction of spawning habitat, and degraded water quality (Minckley and Deacon 1991; Mueller and Marsh 2002). Humpback chub *Gila cypha* is native in the Colorado River Basin and has been listed as a federally endangered species since 1967 (USFWS 2002). Humpback chub is a large cyprinid that reaches a maximum size of about 480 mm and 1.2 kg. One of the largest populations of humpback chub occurs in the Colorado River in Grand Can-

yon below Glen Canyon Dam (USFWS 2002). Smaller populations occur above Glen Canyon Dam in the upper Colorado River, in Green River, and in Yampa River (USFWS 1990; Douglas and Marsh 1996; USFWS 2002).

Plans to facilitate the recovery of humpback chub populations have been developed and were recently revised by the U.S. Fish and Wildlife Service (USFWS 2002). These plans include specific alternatives for “downlisting” and “delisting” the species, assuming there are improvements in adult numbers, better recruitment of age-3 fish, at least three viable populations, and removal or minimization of specific threats (USFWS 2002). The most serious threats to the recovery of the Grand Canyon population include streamflow and temperature modifications caused by Glen Canyon Dam, parasitism, competition with nonnative fishes, and predation by nonnative species, especially rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* (USFWS 1990, 2002).

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Alternatives to minimize or remove threats to humpback chub recovery have been discussed and planned for over a decade (USFWS 1990). Removal of potential predators, competitors, or both is a management action that is currently underway. Rainbow trout prey on juvenile and subadult humpback chub (Valdez and Ryel 1995) and may be an important source of mortality. In 2003, over 6,000 rainbow trout were removed from the Colorado River in the reaches above and below the confluence of the Little Colorado River, a major spawning site and nursery habitat for this population of humpback chub. This removal program reduced the local trout population by about 90% (Grand Canyon Monitoring and Research Center, U.S. Geological Survey [GCMRC], unpublished).

Installation of a temperature control device (TCD) at Glen Canyon Dam is another management action being discussed. Hypolimnetic water from Glen Canyon Dam is released into the lower Colorado River causing temperatures to be 9–12°C year-round; the historic temperature range is about 2–26°C (Kaeding and Zimmerman 1983; Stevens et al. 1997). Modifications to Glen Canyon Dam being considered would enable water managers to release warmer surface water into the lower Colorado River during part of the year (USDI 1999). Warmwater releases would partially simulate the historic temperature patterns and would presumably improve the growth rates of humpback chub. Warmer water would also minimize temperature shock for juvenile humpback chub entering the Colorado River from warmwater tributaries, thus increasing their rate of survival. However, there has also been speculation that warmer water could increase competition, predation mortality, or both for humpback chub by altering the feeding patterns or increasing the growth rates of rainbow or brown trout (USDI 1999; Robinson and Childs 2001).

Predictive tools are needed to assist managers and researchers in evaluating the potential outcomes of actions such as predator removal and temperature modifications in large river systems. Models that integrate physical factors such as temperature and biological processes such as feeding rates should be especially useful, allowing managers to run divergent scenarios and eliminate actions with little chance of success. We developed a bioenergetics model for humpback chub and applied the model to simulate how water temperature changes may influence the growth rate and food requirements of humpback chub. Results are discussed in the context of management options,

needs for specific data to improve the model, and data needed to test hypotheses in the field.

Methods

Humpback chub model development and parameter estimation.—The general bioenergetics model is

$$G = C - (R + SDA + F + E),$$

where G is growth, C is consumption, R is respiration, SDA is specific dynamic action, F is excretion, and E is egestion (Jobling 1994; Hanson et al. 1997). Consumption was modeled as

$$C = C_{\max} \cdot p \cdot f(T),$$

where C_{\max} is the maximum rate of food intake for an individual of a given size, p is a proportionality constant that scales consumption according to food availability, and $f(T)$ is a temperature dependence function. The maximum rate of food intake, C_{\max} , is an allometric function of fish mass W (g), namely,

$$C_{\max} = CA \cdot W^{CB},$$

where CA and CB are fit parameters. Respiration is modeled as

$$R = (RA \cdot W^{RB}) \cdot f(T) \cdot ACT,$$

where ACT is a multiplier for fish activity and RA and RB are allometrically fit parameters. We used the warmwater form for the temperature (T) dependence of C and R (Kitchell et al. 1977; equation (2) in Hanson et al. 1997), which allows specification of optimal (CTO, RTO) and maximal (CTM, RTM) temperatures and includes a measure similar to Q_{10} , the factor by which a physiological rate increases with a 10°C increase, that approximates the rate at which the function increases over relatively low water temperatures (CQ, RQ). For C , the temperature function is

$$f(T) = V^X \cdot e^{(X \cdot (1-V))},$$

where

$$V = (CTM - T)/(CTM - CTO);$$

$$X = \{Z^2 \cdot [1 + (1 + 40/Y)^{0.5}]\} / 400,$$

$$Z = \log_e(CQ) \cdot (CTM - CTO), \text{ and}$$

$$Y = \log_e(CQ) \cdot (CTM - CTO + 2).$$

The respiration temperature function has the same form, but CTM , CTO , and CQ are replaced by RTM , RTO , and RQ , respectively. These temperature-dependence equations have been used to

TABLE 1.—Bioenergetic parameters derived from the peer-reviewed literature for cyprinids. Mass and temperature are the ranges studied or modeled. Abbreviations are as follows: CTO = optimal temperature for consumption; RTO = optimal temperature for respiration; CTM = maximum temperature for consumption; RTM = maximum temperature for respiration; CQ and RQ = the rates at which the temperature function increases at relatively low water temperatures for consumption and respiration, respectively; CA and CB = the intercept and slope of the function for the maximum rate of consumption; and NA = not available from publication. See Text for more details.

Species	Mass (g)	Temperature (°C)	CTO, RTO (°C)	CTM, RTM (°C)
Bream <i>Abramis brama</i>	71–345	9–26	25.8 ^b , –	27.8 ^b , –
Bleak <i>Alburnus alburnus</i>	<1	20	–, –	–, –
Silver bream <i>Blicca bjoerkna</i> ^c	111–211	9–26	25.8 ^b , –	27.8 ^b , –
Gibel <i>Carassius auratus gibelio</i>	857–1,144	9–26	25.8 ^b , –	27.8 ^b , –
Common carp <i>Cyprinus carpio</i>	473–1,331	9–26	25.8 ^b , –	27.8 ^b , –
Utah chub <i>Gila atraria</i>	800–1,200	6–15	–, –	–, –
	<1–41	6–22	–, 22	–, 24 ^b
Mohave tui chub <i>Gila bicolor mohavensis</i>	NA	18–30	–, 32 ^d	–, 35
Northern redbelly dace <i>Phoxinus eos</i>	1–3	5–24	26, 29	29, 32
Eurasian minnow <i>Phoxinus phoxinus</i>	<3.0	5–15	15 ^b , 15 ^b	17 ^b , 17 ^b
Fathead minnow <i>Pimephales promelas</i>	<1–6	20–25	24.0, 28.0	30.0, 33.0
Northern pikeminnow <i>Ptychocheilus oregonensis</i>	500–2,000	5–21	29.9, 21 ^b	27.0, 23 ^b
Colorado pikeminnow <i>Ptychocheilus lucius</i>	1–3	15–30	25, –	30, –
Speckled dace <i>Rhinichthys osculus</i>	<1–7	6–22	–, 18	–, 20 ^b
Roach <i>Rutilus rutilus</i>	20–239	9–26	25.8 ^b , –	27.8 ^b , –
	20–70	10–21	27, 30	30, 33

^a 1, Black and Bulkley (1985); 2, Cech et al. (1994); 3, Cui and Wooton (1988a; 1988b; 1989a; 1989b); 4, Duffy (1998); 5, He (1986); 6, Hofer et al. (1982; 1985); 7, Horppila and Peltonen (1997); 8, Keckeis and Schiemer (1990; 1992); 9, McClanahan et al. (1986); 10, Petersen and Ward (1999); 11, Rajagopal and Kramer (1974); 12, Specziar (2002); 13, Stecyk and Farrell (2002); 14, Vigg and Burley (1991).

^b No observed maximum in study; optimum was the highest tested or observed temperature; maximum was optimum plus 2°C.

^c Also known as *Abramis bjoerkna*.

^d Estimate.

^e Active oxygen consumption.

model warm- and cool-water species such as yellow perch *Perca flavescens*, fathead minnow *Pimephales promelas*, dace *Phoxinus* spp., largemouth bass *Micropterus salmoides*, and smallmouth bass *M. dolomieu* (Kitchell et al. 1977; Rice et al. 1983; Duffy 1998). Specific dynamic action (SDA) was assumed to be 0.15 (He 1986; Shuter and Post 1990). We assumed that egestion, *F*, and excretion, *E*, were constant proportions (0.1) of consumption (Hanson et al. 1997; Duffy 1998).

Since species-specific parameters were not available for humpback chub, a Monte Carlo filtering method was used to develop and test model parameters (Rose et al. 1991; Petersen and Gadomski 1994). Monte Carlo filtering is a procedure for randomly sampling within a range of parameter values in a model, running the simulation model with these parameter values to produce some output, and statistically comparing the output to a test criterion, which may be from field or laboratory studies (Rose et al. 1991). If model output is not different from the test criterion, then the particular parameter value or set of parameter values are assumed to be acceptable. Numerous iterations of the simulation model can be conducted, each with

a different random set of parameter values, eventually generating many sets of parameter values. To decide on the final parameter values among the acceptable sets, central tendency, ranking, or other techniques can be applied.

We first assumed that taxonomic relationships, especially fish in the same genus as humpback chub, could be used to set the upper and lower bounds on parameters for consumption and respiration in a bioenergetics model. Peer-reviewed literature was surveyed for energetic studies on cyprinids, particularly those studies that contained allometric and temperature-dependent functions or data. From this literature, we collated as many of the specific parameters as possible, along with the size range of fish studied and the temperature over which experiments were conducted (Table 1). For some studies we were able to use data in tables or figures to calculate specific parameters. Tabulated parameter values for *Gila* spp. were used to establish upper and lower bounds for Monte Carlo filtering. Because we did not have bounds on all parameters for *Gila* spp. (Table 1), we used fathead minnow as the next most “similar” species, knowing that fathead minnow is successful in the lower

TABLE 1.—Extended.

Species	CQ, RQ	CA, CB	RA, RB	Source ^a
Bream <i>Abramis brama</i>	1.07, –	–, –	–, –	12
Bleak <i>Alburnus alburnus</i>	–, –	0.522, –0.22	0.069, –0.31	8
Silver bream <i>Blicca bjoerkna</i> ^c	2.06, –	–, –	–, –	12
Gibel <i>Carassius auratus gibelio</i>	1.04, –	–, –	–, –	12
Common carp <i>Cyprinus carpio</i>	2.23, –	–, –	–, –	12
	–, 2.6	–, –	–, –	13
Utah chub <i>Gila atraria</i>	–, 2.2	–, –	0.03, –0.032 (22 °C)	11
Mohave tui chub <i>Gila bicolor mohavensis</i>	–, –	–, –	0.00045, –0.118	9
Northern redbelly dace <i>Phoxinus eos</i>	2.3, 2.1	0.36, –0.31	0.0148, –0.2	5
Eurasian minnow <i>Phoxinus phoxinus</i>	–, 2.83	0.110, –0.194	0.00017, –0.45	3
Fathead minnow <i>Pimephales promelas</i>	2.4, 2.6	0.149, –0.242	0.0096, –0.041	4
Northern pikeminnow <i>Ptychocheilus oregonensis</i>	2.04, 2.96	0.278, –0.197	0.00165, –0.285	2, 10, 14
Colorado pikeminnow <i>Ptychocheilus lucius</i>	–, –	–, –	–, –	1
Speckled dace <i>Rhinichthys osculus</i>	–, 1.22	–, –	0.047 ^e , –	11
Roach <i>Rutilus rutilus</i>	1.61, –	0.595, –0.27	0.065, –0.22	6, 12
	3.0, 3.1	0.3, –0.15	0.0188, –0.28	7

Colorado River, occupies a similar ecological niche in the Grand Canyon (Kaeding and Zimmerman 1983), and probably has a similar diet and physiology as small humpback chub.

For developing the *Gila* spp.–humpback chub model, the parameter bounds for optimum consumption and respiration were set from 22°C to 32°C (Tables 1, 2). We increased the upper bound of temperature for the maximum consumption or respiration parameter to 35°C (range 22–35°C), assuming that humpback chub and most *Gila* spp. had evolved in a seasonal environment that might

be warmer than parameters representing many of the cyprinids tabulated in Table 1. We had no explicit estimates of CA or CB for *Gila* spp. (Table 1), so we used an arbitrary range around values measured for fathead minnow (Duffy 1998). For the Q_{10} parameters, 2.1 was the low bound, slightly less than the 2.2 for respiration Q_{10} observed for Utah chub (Table 1), and 2.7 was the high bound, slightly higher than the respiration Q_{10} for fathead minnow. The test range for the allometric respiration parameters was slightly higher and lower than the range observed for Utah chub and Mohave

TABLE 2.—Range of parameter values used in Monte Carlo filtering for a humpback chub bioenergetics model. Parameters not included were fixed and were not determined by filtering (see Table 5). The consumption and respiration Q_{10} approximates the rate at which the function increases.

Parameter abbreviation	Description	Range
Consumption		
CA	Intercept	0.11 to 0.2
CB	Slope	–0.3 to –0.2
CQ	Consumption Q_{10}	2.1 to 2.7
CTO	Optimum temperature	22 to 32
CTM	Maximum temperature	22 to 35
p	Proportion of maximum consumption	0.0 to 1.0
Respiration		
RA	Intercept	0.0004 to 0.01
RB	Slope	–0.15 to –0.02
RQ	Respiration Q_{10}	2.1 to 2.7
RTO	Optimum temperature	22 to 32
RTM	Maximum temperature	22 to 35
ACT	Activity	0.5 to 2.0

tui chub (Table 1). Activity had bounds of 0.5–2.0, and p was allowed to range from 0.0 to 1.0 (Table 2).

A laboratory growth experiment conducted at 24°C by Gorman and VanHoosen (2000) was used to establish the test criteria for Monte Carlo filtering. Gorman and VanHoosen (2000) conducted growth experiments at three temperatures (12, 18, and 24°C) with four native fishes of the Colorado River, including humpback chub. Their experiments were conducted from January through September, starting with fish that were approximately 4 g. We used results from experiments at the highest temperature, 24°C, assuming this would give the best estimates of optimum growth for these warmwater fish. Fish were fed flaked krill, commercial pelletized feed (Silvercup #2), and thawed frozen brine shrimp three times daily (morning, midday, and early evening). Fish were offered 12% of their body weight daily, and tanks were siphoned daily to remove excess food; however, the amount of food that was uneaten was not reported. In Gorman and VanHoosen’s experiment, humpback chub started at 3.9 g and grew to 21.7 g over a 238-d period (Figure 1A).

A bioenergetics model was constructed to grow simulated fish, and Monte Carlo methods were used to sample parameters within reasonable bounds (Table 2). Simulated fish started at 3.9 g and were grown for 238 d at 24.2°C, the measured temperature (Gorman and VanHoosen 2000). To test the adequacy of a randomly drawn parameter set, the size of the modeled fish was compared to the observed size halfway through the growth period (120 d; 12.3 g) and at the end of the growth period (238 d; 21.7 g). To be acceptable and included for further analysis, a parameter set had to produce growth of modeled fish that was within one standard error of the mean observed size at the halfway point and the end of the experiment. Preliminary parameter filtering indicated that testing only the final size of fish was insufficient because certain parameter sets met the end criteria, but size trajectories were largely outside the general pattern of growth (Figure 1B).

Monte Carlo sampling of temperature-related parameters for consumption and respiration required special attention. In the formulations that we used for temperature functions, optimum and maximum temperature parameters were required and were thus sampled in the Monte Carlo program. The optimum temperature was assumed to be no greater than the temperature of the laboratory growth experiment used to fit parameters

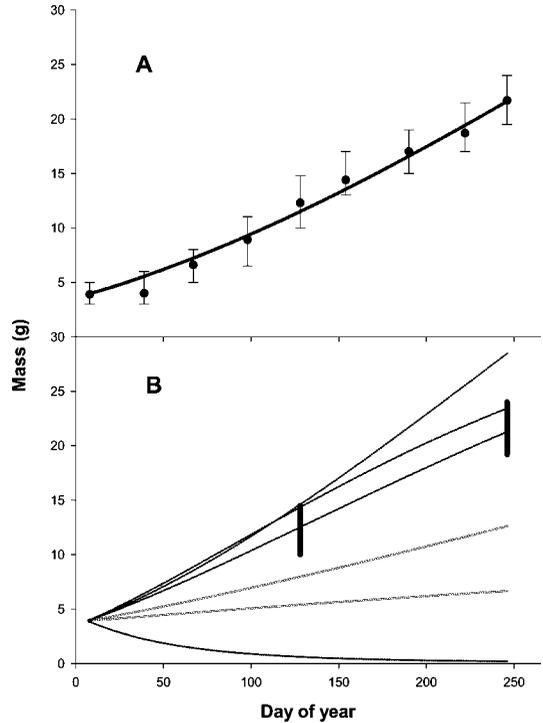


FIGURE 1.—Fit of a bioenergetics model to humpback chub growth. In panel (A) average parameter values from Monte Carlo filtering were used to simulate the growth of a subadult humpback chub (solid line), which was compared with the observed laboratory growth at 24°C (means [circles] ± SEs). In panel (B) examples of growth trajectories are shown, each with a different set of randomly chosen parameter values. In this example, two of the six trajectories met the growth criteria (vertical heavy bars), which were based on laboratory size on days 128 and 246 (see panel A). Laboratory data are from Gorman and VanHoosen (2000).

(24°C), and the optimum temperature was less than the maximum temperature, that is,

$$\begin{aligned} &\text{temperature of experiment} \\ &\leq \text{optimum temperature} \\ &< \text{maximum temperature.} \end{aligned}$$

This rule was applied to both the consumption (CTO, CTM) and the respiration (RTO, RTM) parameters. Although the optimum temperature might have been less than the temperature used in the growth experiment (24°C), Gorman and VanHoosen (2000) as well as other information suggest that optimum temperature for humpback chub is likely quite high and is above 24°C because they evolved in environments where temperatures were often above this value (Stevens et al. 1997).

Without inclusion of such a rule, it would be possible to get nonsensical parameter sets from Monte Carlo sampling, such as optimum is greater than maximum temperature because other random parameter combinations might “compensate” for temperature parameters, allowing growth to fit the test criteria.

Many parameter sets produced low or high growth rates that did not fit test criteria, whereas other parameter sets grew model fish that fit the test criteria at either the intermediate or the final time but not at both test times (Figure 1B). Some combinations of selected parameter values produced growth of humpback chub that matched size in the 24°C laboratory growth experiment (Figure 1B). Using the average parameter values from all acceptable sets, modeled growth closely matched laboratory growth (Figure 1A). Specific values of model parameters are discussed in the Results section.

Final parameter selection, model corroboration, and sensitivity.—Fitting parameters with the Monte Carlo model could be accomplished by assuming that fish in the feeding experiment have fed at either their maximum rate or some rate below the maximum rate. Although humpback chub were offered a 12% ration in the growth experiment (Gorman and VanHoosen 2000), fish might have fed below their maximum consumption rate if temperature was not optimum, there was interference competition, or the food sources were not ideal. For corroboration and final selection of parameter values, we conducted Monte Carlo sampling of parameters to fit the 24°C growth experiment under two assumptions: (1) satiation, i.e., food availability was maximum and humpback chub were feeding at their maximum consumption rate ($p = 1.0$), and (2) below satiation, i.e., humpback chub in growth experiments were feeding at some level below maximum consumption, so p was allowed to vary during parameter fitting between 0.0 and 1.0. For this second assumption, the p value was sampled as a random variable on each iteration of the Monte Carlo model, similar to other parameters.

To corroborate the humpback chub model and select final parameter values, we used independent growth rates of juvenile and subadult humpback chub from various field and laboratory sources; ran the model with appropriate diet, temperature, and fish size; and evaluated the range and average p values necessary to model observed growth. Growth under a variety of conditions that produced reasonable p values would corroborate that the

model was capable of producing a variety of growth patterns under different temperatures and conditions. An acceptable range of p values was approximately 0.2–0.8 (J. Kitchell, University of Wisconsin–Madison, personal communication). Data were not available on specific consumption rates and temperature, which might be used in a different type of corroboration of the model (e.g., Petersen and Ward 1999).

Growth rates of humpback chub in the field were from several sources. Robinson and Childs (2001) fit a von Bertalanffy growth model to juvenile humpback chub captured during 1991–1994 in the Little Colorado River (LCR), a spawning and rearing tributary of the Colorado River. We used this model to estimate size at monthly intervals and estimated p values assuming growth during the month and average LCR temperatures (taken from their Figure 1). Valdez and Ryel (1995) reported the average back-calculated size of humpback chub aged 1–4 years collected from the main-stem Colorado River, Grand Canyon, in 1992–1993. We used these sizes and average water temperature in the COR to estimate p values. Valdez and Ryel (1995) examined scales for transition checks to determine those fish that might have moved from the warm LCR ($>20^{\circ}\text{C}$) to the cold COR ($\sim 10^{\circ}\text{C}$) and concluded that there was “little or no survival of smaller fish descending from the LCR”; hence we assumed that fish used in this analysis likely grew under only the COR temperature regime. A von Bertalanffy growth model fit to recaptured humpback chub in the LCR (L. Coggins, GCMRC, unpublished analyses) was used to predict start and end size for three subadult size intervals (ages 1–4). Average water temperature in the LCR was used to model these fish. Where necessary, fork lengths (mm) were converted to mass (g) using the following regressions, which were derived from field collections of humpback chub (GCMRC, unpublished analyses). The first equation applies to main-stem Colorado River fish exceeding 150 mm in length, the second equation to main-stem Colorado River fish 30–150 mm in length, and the third equation to LCR fish 30–150 mm in length.

$$\log_{10}\text{weight} = -5.597 + 3.194(\log_{10}\text{length}),$$

$$r^2 = 0.93;$$

$$\log_{10}\text{weight} = -4.838 + 2.873(\log_{10}\text{length}),$$

$$r^2 = 0.93; \text{ and}$$

$$\log_{10}\text{weight} = -4.975 + 2.904(\log_{10}\text{length}),$$

$$r^2 = 0.90.$$

Results from laboratory growth experiments were also used in the corroboration process. Gorman and VanHoosen's (2000) experiments at temperatures different from 24°C were used in corroboration tests. Summer warming during their experiment caused the lower temperature treatment (12°C) to warm by about 2–3°C midway through the experiment. Gorman and VanHoosen (2000) concluded that there was no significant growth during the early period (~12°C; January to mid-June), but there was positive growth during the later period (14–15°C; mid-June to mid-September). Based on these results, we also separated the low-temperature treatment into two groups, a 13°C period and a 15°C period, for corroboration. Actual average temperatures for these two periods, 13.0°C and 14.8°C, were used in corroboration testing. Clarkson and Childs (2000) grew humpback chub for 90 d at 10, 14, and 20°C in the laboratory, and these results were also used in corroboration analyses.

Model sensitivity was explored in several ways. We inspected the coefficient of variation ($CV = 100 \times SD/mean$) of parameter values that met test criteria and examined the correlation coefficients of those accepted parameter sets. Sensitivity of the growth rate of juvenile and subadult humpback chub was examined by simulating growth at various temperature and food availability values. Juvenile (4.0 g) and subadult (115 g) humpback chub growth was modeled for 30 d at a given temperature (range 5–32°C) and p value (range 0.1–1.0). Daily growth rates were averaged during this period and results were presented in a response surface plot.

Bioenergetic simulations of potential temperature control device scenarios.—To demonstrate an application of the bioenergetic model for humpback chub in the lower Colorado River, we compared the growth rates and total consumption for juvenile and subadult humpback chub grown under three temperature scenarios (Figure 2): (1) pre-dam temperature conditions, (2) post-dam temperature conditions, and (3) increased temperature in May through October (TCD scenario). The TCD scenario corresponded to a potential management action that might be implemented to increase water temperature in the lower Colorado River (Figure 2). Pre- and post-dam simulations were conducted with the p equal to 0.65 (see Table 3). The TCD scenario was evaluated assuming no increase in food availability ($p = 0.65$) and with an increase in food availability due to temperature change ($p = 0.75$). Diet was constant in all simulations and growth was evaluated over a 1-year period. Diet

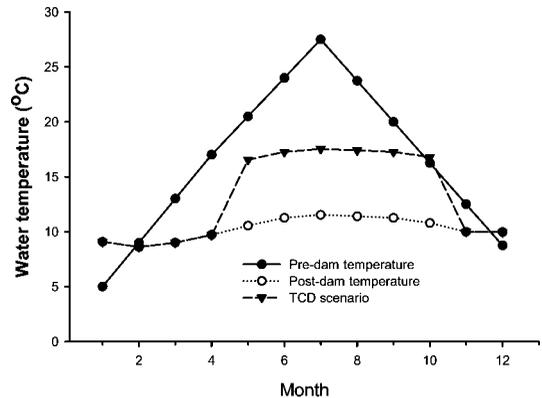


FIGURE 2.—Average monthly water temperatures in the Grand Canyon (lower Colorado River) before and after the construction of Glen Canyon Dam and for a potential temperature management scenario using a temperature control device (TCD). Temperature data are from U.S. Geological Survey at river mile 61 near the confluence with the Little Colorado River.

of humpback chub was taken from Valdez and Ryel (1995; Table 4). Energy densities of prey were from Cummins and Wuycheck (1971).

Results

Final Parameter Selection, Model Corroboration, and Sensitivity

Monte Carlo simulations with 10,000 iterations produced 273 acceptable data sets assuming satiation ($p = 1.0$) and 316 data sets assuming feeding in the growth experiment was below satiation ($0.0 < p < 1.0$). Assuming feeding was below satiation, the average value of p was 0.62 ($N = 316$).

When the two model parameter sets for humpback chub (i.e., those based on the satiation and below-satiation assumptions) were fit to field and laboratory growth, the satiation parameter values produced consistently higher food availability estimates (p) than the below-satiation parameter values (Table 3). Assuming satiation in the growth experiment, values of p in the corroboration tests ranged from 0.61 to 1.27 with an average of 1.02 (Table 3). Assuming fish were eating below satiation, p ranged from 0.34 to 0.81 and averaged 0.66 (Table 3). Values of p derived from laboratory experiments were somewhat lower than p values from field data (Table 3). Specific growth rates ranged from 0.0 to 3.0% per day; higher growth rates occurred with smaller fish and higher temperatures (Table 3). Based on the lower and more reasonable p values in this analysis, simulations in the remainder of this study used parameter val-

TABLE 3.—Corroboration results for the humpback chub bioenergetics model. The model was fit to laboratory and field growth rates and p -values (proportionality constants that scale consumption according to food availability) were determined. Two parameter sets were compared, one with satiation feeding ($p = 1.0$) and one with less than satiation feeding ($p < 1.0$).

Life stage	Period	Starting size (g)	Ending size (g)	Temperature (°C)	Specific growth rates (%/d)	Estimated p -value		Source ^a
						Parameters fit with $p = 1.0$	Parameters fit with $p < 1.0$	
Laboratory								
Juvenile	90 d	0.07	0.14	10	0.3	0.61	0.41	2
	90 d	0.07	0.32	14	0.7	0.82	0.60	2
	90 d	0.07	1.02	20	1.3	0.98	0.73	2
	146 d	3.7	3.6	12	0.0	0.66	0.34	3
	92 d	3.6	5.3	15	0.2	0.92	0.57	3
	238 d	3.5	10.1	18	0.2	0.93	0.57	3
Little Colorado River								
Subadult	May–Jun	0.01	0.06	20	3.0	1.03	0.71	4
	Jun–Jul	0.06	0.23	21	2.1	1.06	0.77	4
	Jul–Aug	0.23	0.63	21	1.4	1.04	0.81	4
	May–Jun	4.2	5.5	20	0.4	1.03	0.67	4
	Jun–Jul	5.5	7.2	21	0.4	1.06	0.69	4
	Jul–Aug	7.2	9.7	21	0.4	1.15	0.77	4
	Age 1–2	4.7	26.6	5.0–26.5	0.2	1.10	0.68	5
	Age 2–3	26.6	61.2	5.0–26.5	0.1	1.19	0.69	5
	Age 3–4	61.2	97.3	5.0–26.5	0.1	1.24	0.69	5
	Main-stem Colorado River							
	Age 1–2	5.4	19.8	9.1–11.5	0.2	1.18	0.75	1
	Age 2–3	19.8	44.9	9.1–11.5	0.1	1.27	0.77	1
Average						1.02	0.66	
Minimum						0.61	0.34	
Maximum						1.27	0.81	

^a 1, Valdez and Ryel (1995); 2, Clarkson and Childs (2000); 3, Gorman and VanHoosen (2000); 4, Robinson and Childs (2001); and 5, U.S. Geological Survey, Grand Canyon Monitoring and Research Center, unpublished.

ues that were derived by assuming feeding was below satiation in the laboratory growth experiment. Parameter values for the bioenergetic model for *Gila* spp.–humpback chub are provided in Table 5.

As expected, optimum and maximum temperatures for respiration and consumption were posi-

TABLE 4.—Energy density of prey (wet mass basis) and average contribution to diet for subadult humpback chub in the Grand Canyon. Diet is the average (ranges in parentheses) for spring, summer, and fall estimates (Valdez and Ryel 1995). Energy density is from Cummins and Wuycheck (1971).

Prey taxon or category	Diet contribution	
	Energy density (J/g)	Average composition of diet (%)
Simuliids	2,565	32 (20–39)
<i>Gammarus</i> spp.	3,389	32 (25–37)
Chironomids	2,744	7 (4–11)
<i>Cladophora</i> spp.	1,122	16 (16–17)
Other aquatic invertebrates	3,176	1 (1–1)
Terrestrial invertebrates	3,050	12 (4–19)

tively correlated (Pearson's product-moment correlation coefficient), as we included a rule that optimum temperatures could not be greater than maximum temperature. The correlation coefficient between RTO and RTM was 0.49 ($P < 0.0001$) and between CTO and CTM was 0.48 ($P < 0.0001$). The respiration intercept (RA) was strongly correlated with p (correlation coefficient 0.65; $P < 0.001$) and weakly correlated with RTO, RTM, and CA (correlation coefficient < 0.2 ; $P < 0.05$). Other correlation coefficients were not significant ($P > 0.05$).

Using the bioenergetics model, the growth rate of juvenile and subadult humpback chub was predicted to respond in a complex manner to changes in water temperature and food availability (Figure 3). When food availability was high, the maximum potential growth rate for juvenile (4 g) and subadult (115 g) humpback chub was at 27–28°C (Figure 3). At high food availability, the potential growth rate declined steadily when water temperature was below 25°C, but growth rate dropped rapidly when temperature was greater than 29°C

TABLE 5.—Final parameter values used in the bioenergetics model of juvenile and subadult humpback chub. Except for SDA, the consumption and respiration parameters, were based on Monte Carlo filtering of humpback chub growth at 24°C. The parameters for SDA, FA, and UA are from other species, so no variance was associated with these values.

Parameter abbreviation	Description	Mean (SD)	Coefficient of variation (%)
Consumption			
CA	Intercept	0.154 (0.027)	17
CB	Slope	-0.251 (0.028)	11
CQ	Consumption Q_{10}	2.39 (0.19)	8
CTO	Optimum temperature	28.1 (2.3)	8
CTM	Maximum temperature	31.5 (2.5)	8
Respiration			
RA	Intercept	0.0049 (0.0026)	53
RB	Slope	-0.084 (0.039)	47
RQ	Respiration Q_{10}	2.42 (0.17)	7
RTO	Optimum temperature	28.2 (2.3)	8
RTM	Maximum temperature	31.6 (2.4)	8
ACT	Activity	1.16 (0.41)	36
SDA	Specific dynamic action	0.15	
Excretion and egestion			
UA	Proportion of excretion	0.1	
FA	Proportion of egestion	0.1	

(Figure 3). Regardless of food availability, predicted growth rates for juvenile and subadult humpback chub were zero or negative at temperatures above approximately 31°C.

For juvenile humpback chub, the predicted growth rate was fairly constant across a broad range of temperatures (~5–25°C) when food availability was in the range of 0.4–0.6 (Figure 3A). For example, with a food availability of 0.5, growth rate varied little from 5 to 27°C. When food availability was relatively low ($p < 0.3$) growth rate was negative for all temperatures. For subadult humpback chub, growth rates were negative or zero when food availability was low ($p < 0.5$) for all temperatures examined (Figure 3B). The specific growth rates predicted across a fairly broad range of food availability and temperature is consistent with observed growth rates from laboratory and field studies (compare Figure 3 and Table 3), suggesting the model is operating within the expected range.

Bioenergetic Simulations of a Potential Temperature Control Device Scenario

Before the completion of Glen Canyon Dam in 1963, average monthly water temperature through the Grand Canyon ranged from about 5°C to 27°C (Figure 2). Since the dam was constructed, water temperature has varied across a narrow range (9–12°C; Figure 2). Bioenergetic model simulations suggest that before the dam was built, juvenile humpback chub may have grown from 4 to 22 g

during 1 year; since the dam, 4-g juveniles grow to only 12 g (Table 6). Over twice as much food was required to achieve the high rate of growth under high temperatures prior to dam construction (Table 6). When we assumed an increased summer–fall temperature from a TCD and average ($p = 0.65$) food availability, juvenile size at the end of 1 year increased 33% compared with the size predicted with post-dam temperatures (12 g versus 16 g; Table 6). Juvenile humpback chub would have to eat about 76 g of food (+58% relative to post-dam average conditions) to achieve this increase in size. With a slight increase in prey availability ($p = 0.75$), juvenile humpback chub grew to 24 g (+100%), requiring 106 g of prey (+121%; Table 6). Predicted growth of subadult humpback chub differed little between pre-dam, post-dam, and increased temperature scenarios. The food required to maintain this constant size varied from 378 g for post-dam conditions to 516 g (+37%) and 709 g (+88%) in the increased temperature and pre-dam conditions, respectively, due to the higher temperatures in these simulations. If prey availability increased ($p = 0.75$) during a TCD application, subadult humpback chub grew to 158 g (+28% relative to post-dam average conditions), requiring 657 g of prey (+74%; Table 6).

Discussion

Bioenergetics Model Development

Estimating bioenergetic parameters using the Monte Carlo sampling procedure was relatively

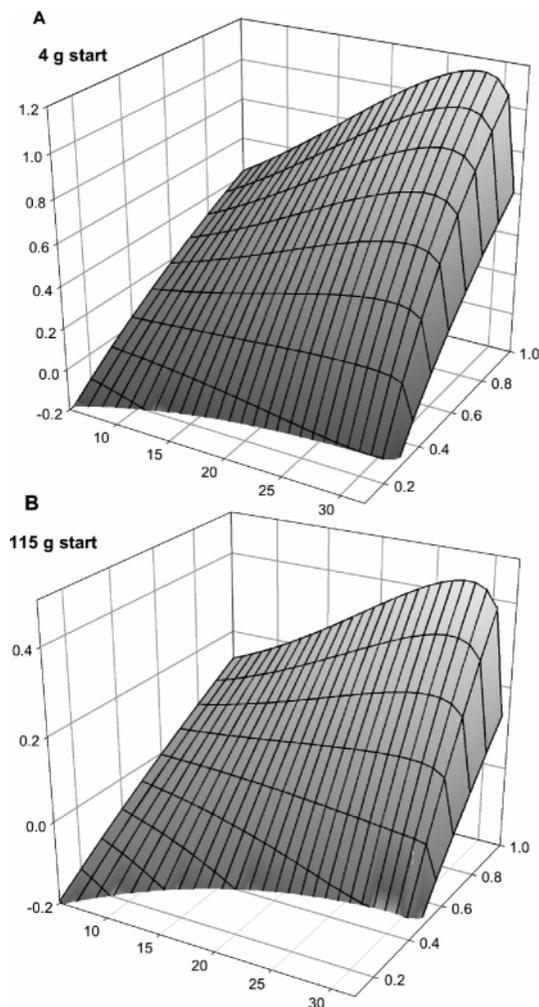


FIGURE 3.—Effect of varying food availability (p ; range, 0.1–1.0) and temperature (range, 5–32°C) on the growth of a (A) juvenile (starting size, 4 g) and (B) subadult (starting size, 115 g) humpback chub based on a bioenergetics model. Growth simulations were run over 365 d. Growth rates are hypothetical.

simple, and this methodology may have applications for other rare species. For many rare or imperiled species, researchers face problems obtaining collecting permits, obtaining a sufficient sample size because of limits on the total number of individuals that can be collected, and sampling an appropriate size range of fish from field populations. Laboratory work with endangered species may also be subject to strict regulations on the types of experiments that are allowed and the mortality rate for experimental groups. Rare, endangered, or imperiled species are, however, often of great concern to conservation and management

agencies, and thus bioenergetic models and analyses would be useful in decision making. The approach that we used relied upon fitting the model parameters to temperature-dependent growth, so we did not completely avoid some of the issues mentioned above. Growth experiments at different temperatures are, however, relatively easy to conduct, and mortality of test animals is usually low. The model we developed was further corroborated using values of p derived from observed growth rates of humpback chub in independent laboratory and field studies. Using the existing literature to obtain ranges in parameter values (such as those listed in Table 1 for cyprinids) for bioenergetics modeling provides a useful supplement to field and laboratory experiments.

Using growth experiments and Monte Carlo filtering to fit model parameters provided an alternative to simple “borrowing” of parameters from related species. Based on the coefficients of variation in humpback chub parameters fit with Monte Carlo sampling (Table 5), laboratory experiments on respiration rates (RA and RB), activity (ACT), and perhaps maximum consumption (CA and CB), could improve or corroborate this parameter set. The intercept and slope for respiration had high coefficients of variation (>45%; Table 5), suggesting a wide range of these parameter values were acceptable. Except for the ACT multiplier, the coefficients of variation for other parameters were much lower (<20%; Table 5), suggesting narrower ranges and variability for acceptable parameter values. Many other bioenergetic models have been shown to be highly sensitive to respiration and consumption parameters (e.g., Bartell et al. 1986; Duffy 1998; Petersen and Ward 1999). Laboratory or field experiments that provide specific estimates for these parameters could improve the humpback chub bioenergetics model.

The high correlation between RA and food availability is probably a result of the very broad range for RA that we allowed during Monte Carlo sampling. The bounds for RA allowed this parameter to vary by several orders of magnitude whereas other parameters were much more restricted (Table 2). When high values of RA were randomly selected, only parameter sets with quite high values of p would fit the test criteria of the growth experiment, thus the strong positive correlation between these parameters. The narrower range for other parameters did not allow for such a broad range of p values, causing lower correlation coefficients.

Corroboration of this model was indirect, using

TABLE 6.—Predicted growth and consumption for juvenile and subadult humpback chub in the Colorado River below Glen Canyon Dam based on a bioenergetics model and four temperature and food scenarios. Model fish were grown for 1 year. The start size for juvenile fish was 4 g; for Subadult was 115 g. Food availability (p) was 0.65 except for one simulation in which it was assumed to have increased to 0.75.

Predicted response (g)	Temperature and food scenario			
	Pre dam temperatures, $p = 0.65$	Post dam temperatures, $p = 0.65$	Increased temperature (May–Oct), $p = 0.65$	Increased temperature (May–Oct), $p = 0.75$
Juvenile				
Final size	22	12	16	24
Consumption	123	48	76	106
Subadult				
Final size	124	123	124	158
Consumption	709	378	516	657

p values and the potential response of growth rates to various conditions. Stronger corroboration testing might be done by comparing feeding rates from the field with model-predicted feeding rates; however, such data are difficult to obtain, are often highly variable, and depend themselves on various assumptions about times of feeding, temperature, prey size, and other factors (Adams and Breck 1990). We were able to simulate observed growth rates with reasonable p values at a broad range of temperatures and in two habitats where humpback chub occur (the Colorado and Little Colorado rivers), so the model and parameter estimates should be a useful tool for scientists and managers.

Temperature Control Device Implications

Water temperature has been identified as a possible cause of declines of native fishes in the Grand Canyon (Minckley 1991), and warmer water temperatures have been shown to improve the condition and swimming ability and to increase the growth rate of native fishes (Clarkson and Childs 2000; Meretsky et al. 2000; Ward et al. 2002). The implementation of a TCD on Glen Canyon Dam that will increase water temperatures 5–10°C in the Colorado River may also increase the growth rate of humpback chub if food availability increases simultaneously. Our simulations suggested that humpback chub growth rates were relatively constant at water temperatures between 5 and 25°C if food availability was constant at moderate levels. Higher growth rates were predicted at increased water temperature coupled with increased food availability. Water temperature can strongly influence consumption by fish, and individuals cannot feed at the same rate at low temperatures as they can at higher temperatures. Consumption typically peaks at an optimum temperature but declines

drastically above this optimum temperature (Jobling 1994). Therefore, a ration that produces positive growth at low temperatures is not likely to produce similar growth at high temperatures, and growth rate can decline with increased temperature and no concomitant change in ration. An evaluation of any management action for humpback chub that alters temperature must take into account prey availability and consumption across the range of expected temperatures.

Temperature changes following implementation of a TCD will likely cause complex changes at several trophic levels in the lower Colorado River, and these changes should be closely monitored (Poff et al. 1997). In particular, the abundance and species composition of invertebrates, the primary food base for fishes in the Grand Canyon (Valdez and Ryel 1995), should be monitored if a TCD is implemented. In other river systems, the response of invertebrate populations to increased temperatures has been mixed. An increase in water temperature of 2.3°C caused a decrease in the densities of invertebrates in a Canadian stream experiment, although growth rate of the invertebrates increased (Hogg and Williams 1996). At Flaming Gorge Dam in Utah, an increase of summer water temperature from 6 to 12°C did not change the taxa richness of invertebrates (Vinson 2001). Compared with other unregulated rivers in the region, the Colorado River in Grand Canyon has had a relatively depauperate invertebrate community following closure of Glen Canyon Dam (Stevens et al. 1997), suggesting the cool, stenothermal regime may have decreased species diversity and abundance. Although water temperature may be the most important variable in determining local invertebrate community dynamics in streams (Vannote and Sweeney 1980), other factors such

as turbidity and periphyton abundance may also be influential (Gore 1977; Vannote and Sweeney 1980). Temperature effects on nutrient cycling and production rates of invertebrates within the lower Colorado River will likely have a strong impact on humpback chub food sources.

Temperature is only one of the many hypothesized causes of native fish declines in the Colorado River, with flow regimes and nonnative fish introductions also influencing native fish populations. Abundant nonnative fishes such as fathead minnow, channel catfish *Ictalurus punctatus*, common carp, rainbow trout, and brown trout may be the most important factor in native fish declines (Minckley 1991). Warmer temperatures in the river may cause increased growth rates and possibly increased main-stem spawning by nonnative species that currently co-occur with humpback chub (Clarkson and Childs 2000; Robinson and Childs 2001). Warmer main-stem water temperatures may also increase the probability that fish such as striped bass *Morone saxatilis* will migrate up the Colorado River from downstream reservoirs, possibly increasing predation on humpback chub and other native fishes (Valdez and Leibfried 1999). The most proximate threat to humpback chub from nonnative predation is brown trout whose current mode of distribution is near Bright Angel Creek. Large brown trout have been observed feeding on adult humpback chub (L. Coggins, GCMRC, personal communication). Brown trout are also more tolerant than are rainbow trout to increased temperatures and are adapted to forage under low light conditions (Robinson and Tash 1979; Young 1999), commonly observed in the lower Colorado River.

The impacts of a TCD would directly influence the growth rates of predators such as rainbow trout and brown trout along with the rate of growth of small humpback chub that are prey to these predators. The size of prey that predators such as rainbow trout consume is often limited to a specific size range (Ware 1972; Vogel and Beauchamp 1999), so faster growth of prey can limit the duration of time that they are vulnerable to the predator. With increasing temperatures or variations in food availability in the lower Colorado River, this "window of vulnerability" would presumably shorten if the growth rate of juvenile humpback chub increased. The window of prey vulnerability depends upon growth rates of both the predators and their prey, which may differ with an altered temperature regime. Valdez and Ryel (1995) made some estimates of the maximum size of humpback

chub that could be consumed by brown trout, rainbow trout, and channel catfish of varying sizes, but they did not estimate the period of vulnerability during the year. Bioenergetic or other growth models could be used to evaluate further specific temperature and food scenarios and the potential importance of prey-to-predator size ratios (Cowan et al. 1996). If a TCD is installed and operated, predator and prey sizes should be monitored so specific predation hypotheses can be tested.

The model that we fit and applied is largely driven by water temperature and the diet of humpback chub and thus does not take into account some conditions that are believed to be important for the growth and survival of humpback chub in the lower Colorado River. Turbidity, for example, increases substantially below the Little Colorado River during certain periods and may reduce primary productivity (and therefore food availability, consumption, or both) through increased light attenuation (SWCA 1998). Asian tapeworms *Bothriocephalus acheilognathi* have also been observed in up to 78% of humpback chub and may represent a new threat in Grand Canyon, perhaps reducing the growth rate of native fishes (Clarkson et al. 1997; Brouder 1999). Turbidity and parasitic effects cannot be directly simulated with the bioenergetics model that we employed, although the model could be modified to incorporate these types of variables. Individual-based models, in particular, have been used to examine how turbidity or light influences foraging rate in fishes (Peterson and Gadomski 1994; Vogel and Beauchamp 1999). Beyers et al. (1999) have shown how stress or parasites might be modeled using a bioenergetics framework. As the specific objectives evolve for humpback chub recovery in the lower Colorado River, models and analyses that account for such factors as turbidity and stress may be necessary.

The bioenergetic modeling approach was applied to explore a few of the potential interactions and produced some nonintuitive results that can be used to develop testable hypotheses. Bioenergetic or modified models that consider turbidity and predator-prey size ratios could also be used with nonnative fishes such as rainbow trout and brown trout that have well-developed energetic parameter sets.

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