The Southwestern Naturalist 52(2):234–242 June 2007

COMPARATIVE GROWTH AND CONSUMPTION POTENTIAL OF RAINBOW TROUT AND HUMPBACK CHUB IN THE COLORADO RIVER, GRAND CANYON, ARIZONA, UNDER DIFFERENT TEMPERATURE SCENARIOS

Craig P. Paukert* and James H. Petersen

U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, 205 Leasure Hall, Division of Biology, Kansas State University, Manhattan, KS 66506 (CPP)

U.S. Geological Survey, Western Fisheries Research Center, Columbia River Research Laboratory, 5501 Cook-Underwood Road, Cook, WA 98605 (JHP, deceased)

**Correspondent: cpaukert@ksu.edu*

Abstract—We used bioenergetics models for humpback chub, *Gila cypha*, and rainbow trout, *Oncorhynchus mykiss*, to examine how warmer water temperatures in the Colorado River, Grand Canyon, Arizona, through a proposed selective withdrawal system (SWS) at Glen Canyon Dam, would affect growth, consumption, and predation rates. Consumption by the rainbow trout population was at least 10 times higher than by the smaller humpback chub population. Water temperature increases of 6°C during autumn increased growth of humpback chub and likely increased their survival by reducing the time vulnerable to predation. Water temperature increases caused by drought in 2005 did not alter humpback chub growth as much as the SWS. Increased temperatures might cause changes to the invertebrate community and the distribution and abundance of other warmwater nonnative fishes. The implications on the entire aquatic community need to be considered before any management action that includes increasing water temperatures is implemented.

Resumen—Usamos modelos bioenergéticos para el cacho corcovado (*Gila cypha*) y la trucha arcoiris (*Oncorhynchuys mykiss*) para examinar cómo las aguas más tibias del Río Colorado en el Gran Cañón en Arizona, debido al sistema propuesto de sacar agua selectivamente (SWS) en la presa Glen Canyon, influirían las tasas de crecimiento, consumo y depredación. El consumo por la población de la trucha arcoiris fue por lo menos 10 veces mayor que el por la población menor del cacho corcovado. El aumento de la temperatura del agua de 6°C durante el otoño aumentó el crecimiento del cacho corcovado y probablemente aumentó su supervivencia al reducir el tiempo en que estaba vulnerable a la depredación. Los aumentos de la temperatura del agua causados por la sequía en 2005 no cambiaron el crecimiento del cacho corcovado tanto como el SWS. Es posible que los aumentos de temperatura causen cambios a la comunidad invertebrada y también a la distribución y abundancia de otros peces no nativos de aguas tibias. Se deben tomar en cuenta las repercusiones a la comunidad acuática entera antes de implementar cualquier acción de manejo que incluya subir la temperatura del agua.

Native Colorado River fishes have declined dramatically because of the altered hydrologic and thermal regime and subsequent proliferation of nonnative fishes (Minckley, 1991). The Colorado River, Grand Canyon, has the largest remaining aggregation of the federally endangered humpback chub, *Gila cypha* (U.S. Fish and Wildlife Service, 2002). These fish spawn in a warmwater tributary, the Little Colorado River, 124 km below Glen Canyon Dam. They also reside in or migrate (or drift as larvae) to the mainstem Colorado River, where they encounter cold, stenothermic temperatures near 9 to 12°C caused by hypolimnetic releases from Glen Canyon Dam (Kaeding and Zimmerman, 1983; Gorman and Stone, 1999; Paukert et al., 2006).

The fish community in the Colorado River, Grand Canyon, has been substantially altered by nonnative fish introductions and coldwater releases from Glen Canyon Dam, which was completed in 1963. The upper river reach is primarily an introduced rainbow trout, *Oncorhynchus mykiss*, fishery, with few native fish remaining. However, the Little Colorado River reach 124 river km below Glen Canyon Dam contains substantially more native fishes and has the highest abundance of humpback chub in Grand Canyon (Coggins et al., 2006; Paukert et al., 2006). Rainbow trout are the most abundant fish in the mainstem Colorado River in Grand Canyon, comprising over 77% of the total electrofishing catch (although native fish still occur in these downstream reaches), with an estimated population size of over 440 fish per river km near the Little Colorado River (R. S. Rogers et al., 2003, unpublished report, Grand Canyon Monitoring and Research Center, Flagstaff, Arizona). Rainbow trout might compete with humpback chub for food resources; both species feed on aquatic invertebrates (Valdez and Ryel, 1995), and studies on the energy requirements and condition of rainbow trout have suggested that they are food limited (McKinney and Speas, 2001). In addition, rainbow trout have been known to consume humpback chub and, therefore, might be an important source of humpback chub mortality (Marsh and Douglas, 1997).

In addition to the concern about predation and competition by nonnative fishes on native fishes, there has been discussion of accessing warmer reservoir water to achieve warmer water temperature in Grand Canyon by implementing a selective withdrawal system (SWS) on Glen Canyon Dam to benefit the native, warmwater fish community (U.S. Department of the Interior, 1999). Water temperatures from Glen Canyon Dam from 1992 to 2002 ranged from 9 to 12°C (Petersen and Paukert, 2005) because of the hypolimnetic releases from the dam, whereas historical temperatures ranged from 2 to 26°C (Stevens et al., 1997). These cooler water temperatures have possibly reduced native, warmwater fish recruitment and have made the system more suitable for nonnative, coolwater fishes, such as rainbow trout and brown trout, *Salmo trutta*. The proposed water temperature increase from a SWS might increase growth rates of native, warmwater fish, provide suitable temperatures for spawning in the mainstem Colorado River, and minimize thermal shock of drifting larvae (Ward et al., 2002) when native fish from the warmer Little Colorado River enter the mainstem Colorado River at early life stages. However, in 2005, lower water levels in Lake Powell (immediately upstream of Grand Canyon; impounded by Glen Canyon Dam) resulted in reduced reservoir water levels and placement of warmer surface water near the penstock withdrawal zone, thus increasing water temperatures in Grand Canyon near the Little Colorado River up to 17°C, compared to 11°C from the 10-year (1993–2002) September average.

We used bioenergetics models to simulate how water temperature changes might alter the consumption of rainbow trout and humpback chub. Specifically, we wanted to determine the growth of these 2 species, and if warmer water temperatures (from a SWS or naturally caused by warmer water released from Glen Canyon Dam during drought) can reduce the period of vulnerability of humpback chub to predation by rainbow trout.

Table 1—Energy density and average contribution (percent by weight) of diets of humpback chub, *Gila cypha*, and rainbow trout, *Oncorhynchus mykiss*. Humpback chub diets are from Valdez and Ryel (1995) and Petersen and Paukert (2005). Rainbow trout diets were estimated from Grand Canyon Monitoring and Research Center, unpublished data. Energy densities are from Cummins and Wuycheck (1971), with unidentified fish from Hanson et al. (1997).

		Average diet composition (%)	
	Energy density (J/g)	Humpback chub	Rainbow trout
Simuliids	2,565	32	61
Gammarus	3,389	32	8
Chironomids	2,744	7	4
Cladophora	1,122	16	0
Other aquatic invertebrates	3,176	1	12
Terrestrial invertebrates	3,050	12	13
Unidentified fish	4,186	0	2

Methods—We conducted a series of simulations with bioenergetics models (Hanson et al., 1997) of humpback chub and rainbow trout to evaluate the effects of warmer water temperatures on the consumption and growth of these fishes. Model parameters for humpback chub were from Petersen and Paukert (2005), and parameters from Railsback and Rose (1999) were used for the rainbow trout model. Diets of humpback chub were from Petersen and Paukert (2005), and rainbow trout diets were from U.S. Geological Survey (Grand Canyon Monitoring and Research Center [GCMRC], unpublished data; Table 1). Energy densities were obtained from Cummins and Wuycheck (1971; Table 1).

We estimated per capita consumption for rainbow trout and humpback chub under varying temperature

TABLE 2—Annual growth rates for humpback chub, *Gila cypha*, and rainbow trout, *Oncorhynchus mykiss*, in the Little Colorado River (LCR) and main-stem Colorado River (COR), Grand Canyon, Arizona. Observed growth is from the field observations, whereas predicted growth is from the bioenergetics models using a constant proportion of maximum consumption (p-value) = 0.35 for rainbow trout (RBT) and p = 0.65 for humpback chub (HBC).

Species	River	Temperature (°C)	Start size (g)	Observed growth (g)	Predicted growth (g)	Reference
HBC	LCR	5 to 26	4.7	21.9	27.7	Petersen and Paukert, 2005
		5 to 26	26.6	34.6	42.9	Petersen and Paukert, 2005
	COR	9 to 12	5.4	14.4	13.0	Petersen and Paukert, 2005
		9 to 12	19.8	25.1	20.8	Petersen and Paukert, 2005
RBT	COR	9 to 12	292[1]	78[1]	66	McKinney and Speas, 2001

[1] Estimated from length-weight regressions (Grand Canyon Monitoring and Research Center, unpublished data) and figure 3 in McKinney and Speas (2001).

regimes by determining total annual consumption for an individual of each species by using the bioenergetic parameters listed above. These simulations were run with a 300 g (about 300 mm total length [TL]) rainbow trout at a constant proportion of maximum consumption (p-value; Hanson et al., 1997) of 0.35, whereas the humpback chub model was run with a 115 g chub (about 250 mm TL) at a constant p-value of 0.65. These fish sizes represented common sizes of rainbow trout and humpback chub in Grand Canyon (Valdez and Ryel, 1995; GCMRC, unpublished data), and the p-values reflected realistic growth that was similar to field observations (Table 2). All simulations used the 10-year mean water temperature (1993 to 2002) for January–June and December, but used a series of 1°C increments in mean monthly water temperatures from July to November, the period when a potential SWS would increase water temperatures (i.e., fall warming scenario). In addition, total population consumption and total consumption of fish was estimated by multiplying the per capita consumption by the estimated population size. Rainbow trout population size was estimated at 6,499 fish in the Colorado River within the 16-km area adjacent to the Little Colorado River in January 2003 (GCMRC, unpublished data), whereas the humpback chub population estimate was 3,419 fish >150 mm TL in March and April 2003 in the Little Colorado River (R. Van Haverbeke, 2004, unpublished report, GCMRC, Flagstaff, Arizona).

We assessed size vulnerability of humpback chub to predation by using the estimated growth of 6 sizes of rainbow trout (initial weights of 37, 80, 145, 236, 356, and 408 g), which represent trout from 150 to 400 mm TL (in 50-mm increments) and encompass 99% of all rainbow trout sizes in Grand Canyon during January to March 2003 (GCMRC, unpublished data). Bioenergetics models for humpback chub used 5 sizes of chubs (3, 8, 17, 31, and 51 g), which represent humpback chub from 70 to 190 mm (in 30-mm increments) and encompass 94% of all juvenile chubs collected in the mainstem Colorado River, January to March 2003 (GCMRC, unpublished data). Simulations were run at the post-dam mean water temperature scenario (Petersen and Paukert, 2005), 2005 water temperatures, and the fall warming temperature scenario (i.e., 6°C increase in water temperatures from July to November) (Fig. 1).

We ran simulations for all size combinations of rainbow trout and humpback chub, resulting in 30 simulations (6 rainbow trout sizes by 5 humpback chub sizes) for each temperature scenario. We then estimated size vulnerability by calculating the prey to predator size ratio for rainbow trout and humpback chub for each day of the 365-day simulations. Valdez and Ryel (1995) found, based on diet studies and predator length and prey body depth ratios, that a 339 mm rainbow trout (~325 g) can consume a maximum of a 135 mm humpback chub (~19 g), suggesting that a humpback chub weight to rainbow trout weight ratio >0.058 (19/325 g; 0.398 when using length) would not be vulnerable to predation. Therefore, a prey to predator ratio ≤0.058 (g/g) would suggest the prey (humpback chub) is vulnerable to predation. This ratio

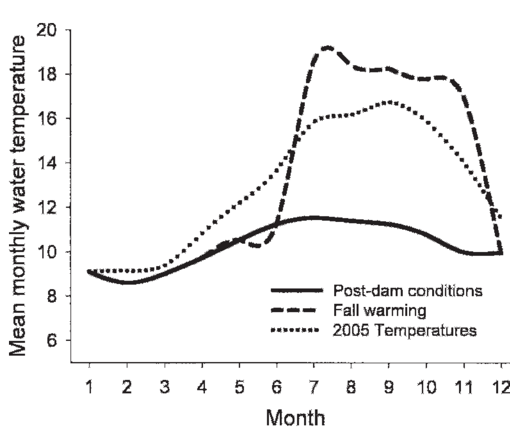

FIG. 1—Water temperature (°C) scenarios used for the bioenergetics simulations for humpback chub, *Gila cypha*, and rainbow trout, *Oncorhynchus mykiss*, in the Colorado River, Grand Canyon, Arizona. Temperatures are from the Colorado River near the Little Colorado River confluence.

TABLE 3—Average and temperature-dependent annual consumption (kg) by humpback chub, *Gila cypha*, and rainbow trout, *Oncorhynchus mykiss*, in the Colorado River, Grand Canyon, Arizona, using bioenergetic simulations. Constant proportion of maximum consumption p-values were set at 0.35 for rainbow trout and 0.65 for humpback chub. Water temperatures were modeled using the 10-year mean (1993 to 2002) for January through June and for December, but increased each month in 1°C increments from July through November, the months when a proposed selective withdrawal system on Glen Canyon Dam would increase water temperature in the Colorado River. Numbers in parenthesis for rainbow trout are the per capita and population consumption (kg) of fish.

July to November water temperature	Humpback chub		Rainbow trout	
	Per capita	Population[1]	Per capita	Population[2]
10-year mean	0.400	1,368	2.863 (0.057)	18,608 (372)
1°C increase	0.418	1,429	3.011 (0.060)	19,570 (391)
2°C increase	0.439	1,501	3.144 (0.063)	20,432 (409)
3°C increase	0.460	1,573	3.257 (0.065)	21,167 (423)
4°C increase	0.483	1,651	3.348 (0.067)	21,762 (435)
5°C increase	0.508	1,737	3.418 (0.068)	22,214 (444)
6°C increase	0.534	1,826	3.468 (0.069)	22,536 (451)
7°C increase	0.562	1,921	3.500 (0.070)	22,746 (455)
8°C increase	0.593	2,027	3.520 (0.070)	22,876 (458)
9°C increase	0.624	2,133	3.533 (0.071)	22,962 (459)
10°C increase	0.657	2,246	3.546 (0.071)	23,046 (461)

[1] Based on a population estimate of 3,419 fish >150 mm (Van Haverbeke, 2004, in litt.).

[2] Based on a population estimate of 6,499 fish (Grand Canyon Monitoring and Research Center, unpublished data).

was similar to other studies of salmonid predation on other fishes (0.19 to 0.62 based on length; Jude et al., 1987; Elrod and O'Gorman, 1991; Nowak et al., 2004). Although this indicates a potential maximum prey size that rainbow trout can consume, the actual sizes of native fish in Grand Canyon consumed by trout might be smaller (Marsh and Douglas, 1997), so our analyses suggest maximum consumption. The number of days this prey:predator ratio was equal to or under 0.058 was calculated for each simulation. To determine how many days humpback chub were more or less vulnerable to predation compared to ''current'' conditions (post-dam), the difference in the number of days vulnerable for the 2005 temperature scenario and the fall warming scenario were subtracted from the post-dam scenario.

RESULTS—Per capita annual consumption was 5.4 to 7.2 times higher for rainbow trout compared to humpback chub, depending on temperature (Table 3). Rainbow trout per capita annual consumption was relatively stable (2.8 to 3.5 kg) for all simulations. Humpback chub per capita annual consumption ranged from only 0.400 to 0.657 kg, with increased consumption at higher temperatures (Table 3). Total population consumption typically was 18,600 to 23,000 kg for rainbow trout, whereas humpback chub consumption was always less than 2,300 kg. Therefore, rainbow trout population consumption was at least 10 times higher than humpback chub consumption across all temperature warming scenarios. Consumption of fish by rainbow trout also increased with temperature. Population consumption ranged from 372 kg for the 10-year mean water temperature to 461 kg for a 10° increase. Although the proportion of fish in the diet of rainbow trout was low, total population consumption was relatively high given the low abundance of humpback chub in Grand Canyon.

Comparing post-dam to the fall warming (SWS) scenario, the growth rate and final size after one year were decreased for adult rainbow trout but increased for juvenile humpback chub (Fig. 2). As an example, a 145 g rainbow trout grew to 251 g (73% increase) and a 236 g rainbow trout grew to 356 g (51% increase) at the post-dam mean water temperatures, but only grew to 241 g for the 145 g trout (66% increase) and 337 g for the 235 g trout (43% increase) with the fall warming scenario (Fig. 2a, 2b). Conversely, a 3 g humpback chub grew to 13 g (339% increase) and an 8 g chub grew to 23 g (191% increase) at the post-dam mean water temperatures, but grew to 18.6 g (521% increase) for the 3 g chub and 30 g (277% increase) for the 8 g chub under the fall warming scenario (Fig. 2c, 2d). Under 2005

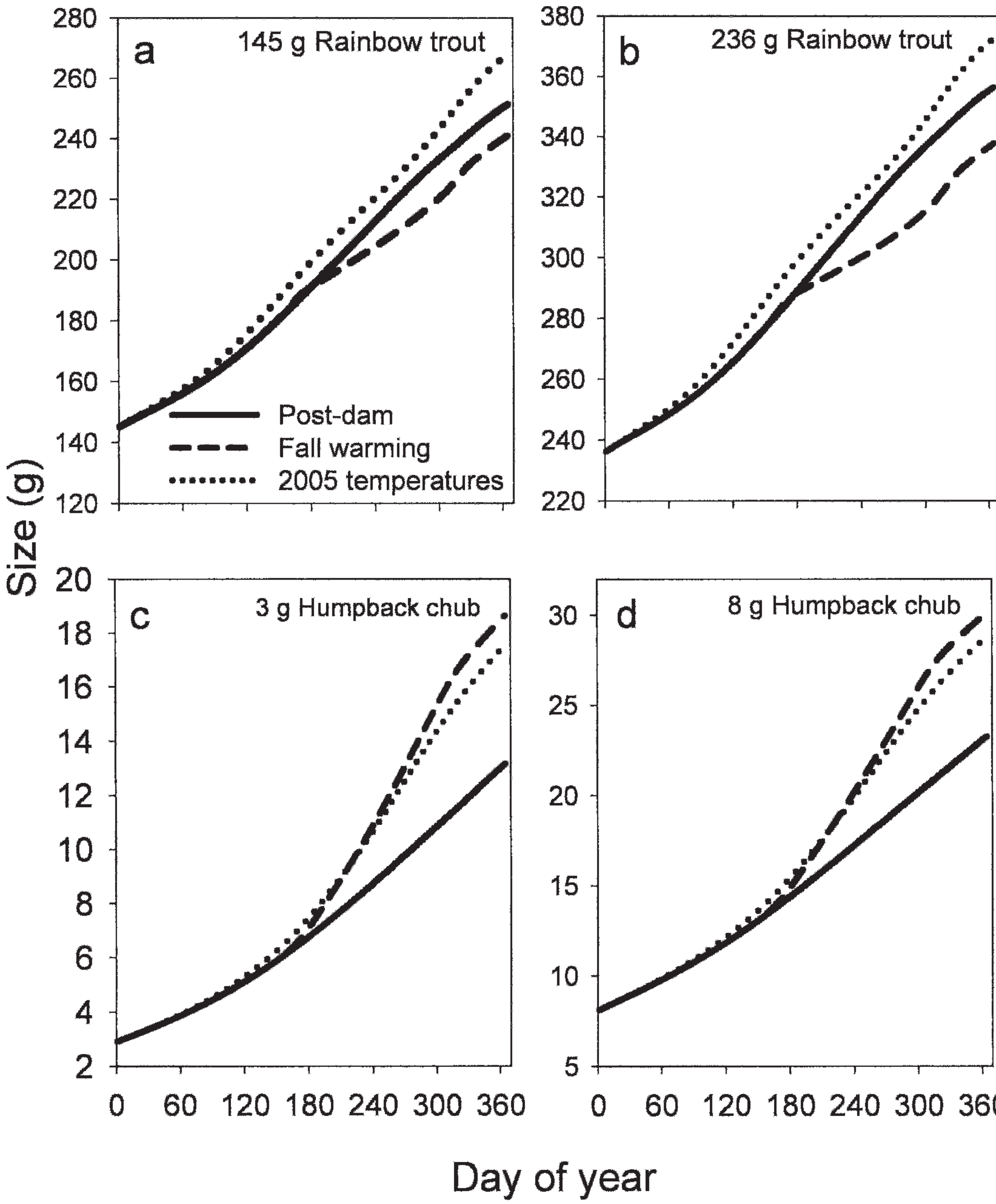

FIG. 2—Simulated annual growth of a 145 g (250 mm total length [TL]) rainbow trout, *Oncorhynchus mykiss* (a), 236 g (300 mm TL) rainbow trout (b), 3 g (70 mm TL) humpback chub, *Gila cypha* (c), and 8 g (100 mm TL) humpback chub (d) under the 10-year (1993 to 2002) mean water temperature, fall warming scenario, and the 2005 water temperatures in the Colorado River, Grand Canyon, Arizona.

water temperatures, adult rainbow trout of 145 and 236 g increased 85 and 58%, respectively, and juvenile humpback chub of 3 and 8 g increased 484 and 287%, respectively. Therefore, the scenario that increased juvenile humpback chub growth the greatest (fall warming) caused the lowest growth scenario for adult rainbow trout, although growth increases at 2005 temperatures were approaching growth of humpback chub at the fall warming scenario.

TABLE 4—Difference in the number of days that humpback chub, *Gila cypha*, were vulnerable to predation by rainbow trout, *Oncorhynchus mykiss*, for 2 temperature warming scenarios: fall warming and 2005 temperatures (drought year) compared to the post-dam (1993 to 2002) water temperatures, Colorado River, Grand Canyon, Arizona. Values are for the starting weights for humpback chub and rainbow trout. Positive values indicate an increase in the number of days vulnerable to predation with the warming scenario, whereas negative values indicate a decrease in the number of days vulnerable.

	Rainbow trout start size						
Humpback chub start size	37 g (150 mm)	80 g (200 mm)	145 g (250 mm)	236 g (300 mm)	356 g (350 mm)	508 g (400 mm)	Net days vulnerable
			Fall warming				
3 g (70 mm)	0	7	−107	0	0	0	−100
8 g (100 mm)	0	0	0	−76	−73	0	−149
17 g (130 mm)	0	0	0	0	1	−123	−122
31 g (160 mm)	0	0	0	0	0	0	0
51 g (190 mm)	0	0	0	0	0	0	0
			2005 water temperatures				
3 g (70 mm)	0	5	−69	0	0	0	−64
8 g (100 mm)	0	0	0	−61	0	0	−61
17 g (130 mm)	0	0	0	0	1	−95	−94
31 g (160 mm)	0	0	0	0	0	0	0
51 g (190 mm)	0	0	0	0	0	0	0

Humpback chub of the sizes modeled were rarely vulnerable to small (≤80 g) rainbow trout. Conversely, small (3 g) humpback chub were always vulnerable to larger (356 g) rainbow trout during some part of the year, regardless of the temperature scenario used to simulate growth. When compared to the post-dam temperatures, the fall warming scenario reduced the days vulnerable to rainbow trout predation by 0 to 149 d, depending on initial humpback chub size (Table 4). The 2005 water temperatures also resulted in fewer days vulnerable to predation when compared to the post-dam temperatures; the reduction in the number of days vulnerable ranged from 0 to 94 d. Neither the fall warming nor 2005 temperature scenario resulted in fewer days vulnerable to predation when comparing the largest rainbow trout and largest humpback chub. Across all humpback chub and rainbow trout sizes, there were 3,159 d vulnerable to predation during the 10 y mean water temperatures. The fall warming scenario reduced the number of days vulnerable by 371 (11.7%; 371/3,159 d vulnerable across all predator sizes), and the 2005 temperatures reduced the number of days vulnerable by 219 d (6.9%; 219/3,159; Table 4).

DISCUSSION—Competition for food resources between rainbow trout and humpback chub might be detrimental to humpback chub recovery. Diet studies have also suggested that both of these fishes consume aquatic invertebrates (Kaeding and Zimmerman, 1983; Valdez and Ryel, 1995; McKinney and Speas, 2001) and, therefore, might be competitors. Because the rainbow trout population might consume over 10 times the biomass of the humpback chub population, removal of nonnative competitors might improve growth rate or recruitment success of native fishes by increasing the amount of food available to native fish in the system, assuming the fish population in Grand Canyon is food limited (Shannon et al., 1996). In addition, the humpback chub population estimate was for fish in the Little Colorado River (R. Van Haverbeke, 2004, unpublished report, GCMRC, Flagstaff, Arizona), and substantially fewer chub might be present in the mainstem Colorado River (Valdez and Ryel, 1995), so our consumption estimates for mainstem humpback chub might be high, thus increasing the magnitude difference in the rainbow trout and humpback chub consumption.

Warming water temperatures, either by installation of an SWS or by warmer water temperature releases caused by drought, will likely change the growth rates of both rainbow trout and humpback chub. Our results suggested that both of these species would grow in all temperature scenarios. However, the largest increases in growth occurred at the fall warming scenario (i.e., increases up to 18°C for July down to 17°C for November) for humpback chub, and the 2005 temperatures (peak increases to 17°C) for rainbow trout. Coldwater releases from Glen Canyon Dam have been implicated in the reduced growth of warmwater, native fish (Robinson and Childs, 2001), and our results suggested that substantial increases in water temperature (e.g., 6°C with a proposed SWS) will be more beneficial (in terms of growth) to the native humpback chub and less beneficial to the nonnative rainbow tout. Although drought has increased water temperatures, these increases actually increased growth of rainbow trout (and humpback chub) compared to the 10-year mean water temperature. Therefore, the most benefit to humpback chub would the temperature scenario from an SWS, because only warming temperature through drought still had benefits to rainbow trout.

Predation often is limited by gape size of the predator, so these fish (i.e., rainbow trout) can only consume prey up to a certain size (Ware, 1972). Therefore, if the prey exhibits faster growth, it can more quickly attain a size too large to be vulnerable to predators, thus reducing this window of vulnerability (Wesp and Gibb, 2003; Petersen and Paukert, 2005). Our analyses suggested that increasing water temperature would reduce the window of vulnerability for smaller humpback chub up to about 149 d per year, depending on rainbow trout and humpback chub size and assuming growth rates of both the predators and their prey respond only to the altered temperature regime. The most dramatic benefits occurred for rainbow trout ≥145 g (250 mm) coupled with humpback chub ≤17 g (130 mm). The drought-caused temperature warming in the Colorado River in 2005 decreased the days vulnerable to predation less than the proposed water temperature modifications from an SWS, suggesting there could still be some benefit gained, even during drought conditions.

It remains to be seen if altered temperature regimes in Grand Canyon will alter the invertebrate abundance and composition. Our simulations assume that food availability remained constant across temperatures (i.e., p-value will be the same regardless of temperature). Invertebrate responses to temperature changes in other river systems have not been consistent (Hogg and Williams, 1996; Vinson, 2001) and warrant further study (Barko and Hrabik, 2004). However, aquatic invertebrate taxa richness and relative abundance was relatively similar before and after an SWS device was installed on Flaming Gorge Dam, Utah (Vinson, 2001), which suggests that food availability to fishes (and therefore consumption) after an SWS might be similar to pre-SWS conditions, although Stevens et al. (1997) speculated that increased summer temperature in Grand Canyon might increase invertebrate diversity and production. The Colorado River, Grand Canyon, has low aquatic invertebrate biomass (Stevens et al., 1997), and stream trout are commonly food limited (Filbert and Hawkins, 1995), suggesting aquatic invertebrate biomass might be a critical link in the potential competition between nonnative and native fishes in this system. This is particularly true if food is a limiting factor to fishes in Grand Canyon (Shannon et al., 1996). A thorough understanding of invertebrate community and biomass changes to altered flows and temperatures is needed to fully understand these effects on riverine fishes (Stevens et al., 1997). A monitoring program to detect changes in invertebrate abundance and composition (or a surrogate, such as fish growth) is needed to assess the impact of an SWS (or other factors, such as drought) on the aquatic biota of the Colorado River.

Recovery of humpback chub in Grand Canyon likely will need to include several management actions in addition to increasing water temperatures. Removal of nonnative fishes is underway in Grand Canyon. In 2003, over 6,000 rainbow trout (about 90% reduction) were removed from the Colorado River near the Little Colorado River confluence (GCMRC, unpublished data). Our modeling results suggested that this removal might free over 18,000 kg of invertebrates that can be used by native fish, assuming food is a limiting resource (Filbert and Hawkins, 1995; Shannon et al., 1996). In addition, these removal efforts also have possibly reduced the biomass of fish consumed by rainbow trout by over 370 kg. Although results of the nonnative fish removal efforts on native fishes are currently speculative, it appears that humpback chub recruitment has increased since removal efforts began (GCMRC, unpublished data). Removal of nonnative fishes, coupled with management actions to increase growth and recruitment of native fishes (e.g., an SWS) also might be instrumental in controlling any additional invasive species that might benefit from increased temperatures. All of these efforts might concurrently aid in native fish recovery in the Colorado River.

The full impacts of temperature warming in Grand Canyon will undoubtedly be associated with complex ecological interactions between water temperature, productivity and aquatic invertebrate abundance and composition, and fish population dynamics. Warming the water in Grand Canyon will not affect just rainbow trout, humpback chub, and the aquatic invertebrates. The implementation of an SWS might cause complex changes in the aquatic community, such as increased abundance of other nonnative fishes, including brown trout, fathead minnow (*Pimephales promelas*), and channel catfish (*Ictalurus punctatus*), all of which are well established in the Colorado River in Grand Canyon. Management actions need to be identified that would also address high-risk issues, such as future invasion of nonnative warmwater fishes and potential competition for food resources these nonnative fishes might create. Our simulations provide a framework for future hypothesis testing on the various implications of warming in large river systems. Any management action to alter the water temperature should carefully consider the effects of that action on the entire aquatic community.

This manuscript could not have been completed without the suggestions and encouragement of J. Kitchell. Staff at the Southwest Biological Science Center (L. Coggins, D. Fenn, S. Gloss, and J. Lovich), and the Western Fisheries Science Center (J. Seelye and L. Thorsteinson) provided financial assistance, encouragement, and suggestions. S. Hueftle provided temperature data. The manuscript benefited from reviews and discussions from B. Persons, D. Speas, S. Rogers, O. Gorman, and 2 anonymous reviewers.

Literature Cited

Barko, V. A., and T. R. Hrabik. 2004. Abundance of Ohio shrimp (*Macrobrachium ohione*) and glass shrimp (*Palaemonetes kadiakensis*) in the unimpounded upper Mississippi River. American Midland Naturalist 151:265–273.

Coggins, L. G., Jr., W. E. Pine, III, C. J. Walters, D. R. Van Haverbeke, D. L. Ward, and H. Johnstone. 2006. Abundance trends and status of the Little Colorado River population of humpback chub. North American Journal of Fisheries Management 26:233–245.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations of ecological energetics. International Association of Theoretical and Applied Limnology Special Communication 18:1–158.

Elrod, J. H., and R. O'Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979–1987. Transactions of the American Fisheries Society 120:290–302.

Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. Transactions of the American Fisheries Society 124:824–835.

Gorman, O. T., and D. S. Stone. 1999. Ecology of the spawning humpback chub, *Gila cypha*, in the Little Colorado River near Grand Canyon, Arizona. Environmental Biology of Fishes 55:115–133.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Bioenergetics model 3.0 for Windows. University of Wisconsin, Madison, Sea Grant Institute, Technical Report WISCU-T-97-001.

Hogg, I. D., and D. D. Williams. 1996. Response of stream invertebrates to a global warming thermal regime: an ecosystem-level manipulation. Ecology 77:395–407.

Jude, D. J., F. J. Tesar, S. F. Deboe, and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Transactions of the American Fisheries Society 116:677–691.

Kaeding, L. R., and M. A. Zimmerman. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado rivers of the Grand Canyon. Transactions of the American Fisheries Society 112:577–594.

Marsh, P. C., and M. E. Douglas. 1997. Predation by introduced fishes on endangered humpback chub and other native species in the Little Colorado River, Arizona. Transactions of the American Fisheries Society 126:343–346.

McKinney, T., and D. W. Speas. 2001. Observations of size-related asymmetries in diet and energy intake of rainbow trout in a regulated river. Environmental Biology of Fishes 61:435–444.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? In: Committee to Review Glen Canyon Environmental Studies, editors. 1991. Colorado River Ecology and Dam Management. National Academy Press, Washington, D.C. Pages 124–177.

Nowak, G. M., R. A. Tabor, A. J. Warner, K. L. Fresh, and T. P. Quinn. 2004. Ontogenetic shifts in habitat and diet of cutthroat trout in Lake Washington,

Washington. North American Journal of Fisheries Management 24:624–635.

Paukert, C. P., L. G. Coggins, and C. F. Flaccus. 2006. Distribution and movement of humpback chub in the Colorado River, Grand Canyon, based on recaptures. Transactions of the American Fisheries Society 135:539–544.

Petersen, J. H., and C. P. Paukert. 2005. Development of a bioenergetics model for humpback chub and evaluation of water temperature changes in Grand Canyon, Colorado River. Transactions of the American Fisheries Society 134:960–974.

Railsback, S. F., and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Transactions of the American Fisheries Society 128:241–256.

Robinson, A. T., and M. R. Childs. 2001. Juvenile growth of native fishes in the Little Colorado River and a thermally modified portion of the Colorado River. North American Journal of Fisheries Management 21:809–815.

Shannon, J. P., D. W. Blinn, P. L. Benenati, and K. P. Wilson. 1996. Organic drift in a regulated desert river. Canadian Journal of Fisheries and Aquatic Sciences 53:1360–1369.

Stevens, L. E., J. P. Shannon, and D. W. Blinn. 1997. Colorado River benthic ecology in Grand Canyon, Arizona: dam, tributary, and geomorphological influences. Regulated Rivers: Research and Management 13:129–149.

U.S. Department of the Interior. 1999. Glen Canyon Dam modifications to control downstream temperatures: plan and draft environmental assessment. U.S. Department of the Interior, Bureau of Reclamation, Upper Colorado Region, Salt Lake City, Utah.

U.S. Fish and Wildlife Service. 2002. Humpback chub (*Gila cypha*) recovery goals: amendment and supplement to the Humpback Chub Recovery Plan. U.S. Fish and Wildlife Service, Mountain-Prairie Region, Denver, Colorado.

Valdez, R. A., and R. J. Ryel. 1995. Life history and ecology of the humpback chub (*Gila cypha*) in the Colorado River Grand Canyon, Arizona. Contract Number 0-CS-40-09110, U.S. Department of the Interior, Bureau of Reclamation, Salt Lake City, Utah.

Vinson, M. R. 2001. Long-term dynamics of an invertebrate assemblage downstream of a large dam. Ecological Applications 11:711–731.

Ward, D. L., O. E. Maughan, S. A. Bonar, and W. J. Matter. 2002. Effects of temperature, fish length, and exercise on swimming performance of age-0 flannelmouth sucker. Transactions of the American Fisheries Society 131:492–497.

Ware, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. Journal of the Fisheries Research Board of Canada 29:1193–1201.

Wesp, H. M., and A. C. Gibb. 2003. Do endangered razorback suckers have poor larval escape performance relative to introduced rainbow trout? Transactions of the American Fisheries Society 132: 1166–1178.

Submitted 7 July 2006. Accepted 16 November 2006. Associate Editor was Gary Garrett.