

*Clear-water tributaries of the Colorado River in the Grand Canyon,
Arizona: stream ecology and the potential impacts of managed flow*

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ABSTRACT

Heightened attention to the sediment budget for the Colorado River system in Grand Canyon Arizona, and the importance of the turbid tributaries for delivering sediment has resulted in the clear-water tributaries being overlooked by scientists and managers alike. Existing research suggests that clear-water tributaries are remnant ecosystems, offering unique biotic communities and natural flow patterns. These highly productive environments provide important spawning, rearing and foraging habitat for native fishes. Additionally, clear water tributaries provide both fish and birds with refuge from high flows and turbid conditions in the Colorado River. Current flow management in the Grand Canyon including beach building managed floods and daily flow oscillations targeting the trout population and invasive vegetation has created intense disturbance in the Colorado mainstem. This unprecedented level of disturbance in the mainstem has the potential to disrupt tributary ecology and increase pressures on native fishes. Among the most likely and potentially devastating of these pressures is the colonization of tributaries by predatory non-native species. Through focused conservation and management tributaries could play an important role in the protection of the Grand Canyon's native fishes.

INTRODUCTION

More than 490 ephemeral and 40 perennial tributaries join the Colorado River in the 425 km stretch between Glen Canyon Dam and Lake Mead. Of the perennial tributaries in the Grand Canyon, only a small number including the Paria River, the Little Colorado River and Kanab Creek drain large watersheds and deliver large quantities of sediment to the Colorado River mainstem (Oberlin et al. 1999, Hoknetcht 1981, Andrews 1991, Webb et al. 1991). In recent years, a decline in sandbars and resulting loss of crucial backwater habitat has focused a great deal of attention on the sediment budget for the Lower Colorado system. Since the 1963 closure of Glen Canyon Dam, and consequent reduction in sediment transport from upstream, mainstem turbidity in the Colorado has been largely determined by tributary derived suspended sediment

contributions (Stevens et al. 1997). The primary sediment delivering tributaries, the Paria River and the Little Colorado River, divide the Colorado into three distinct turbidity zones that have a significant impact on mainstem benthic ecology and aquatic communities (Stevens et al. 1997). These turbid tributaries are also important spawning habitat for some of the Colorado's native fishes (Valdez et al., 2001; Minckley, 1991) including the endangered humpback chub that spawn almost exclusively in the Little Colorado River (Meretsky et al 2000).

The focus on sediment budget for the Colorado system in the Grand Canyon, and the importance of the turbid tributaries for delivering sediment has resulted in clear-water tributaries receiving little attention. The emphasis on sediment delivery from turbid tributaries has only continued to grow since the 1996 introduction of a flow regime that includes managed floods for the purpose of habitat construction and sediment mobilization. This paper presents a review of the literature on the ecology of clear-water tributaries in the Grand Canyon, in the context of the current managed flow regime on the Colorado River. I hypothesize that changes to the main channel can cause a shift in the ecology and biota of clear-water tributaries. Current trends point towards the potential for major changes through increased colonization of clear-water tributaries by non-native predatory species, increased predation on juvenile native fishes, increased interspecific competition for spawning habitat, and the potential for an altered benthic community. In this paper, I will begin with an overview of some of the biota and major ecological functions the tributaries have and continue to support. I will then discuss recent changes to the Colorado River mainstem, and hypothesize about how the increased disturbance resulting from current flow management might impact tributaries and their biotic communities. I conclude this discussion with a summary of these hypotheses, as well as some management recommendations towards the preservation of tributary habitat, biota, and ecological processes.

TRIBUTARY ECOLOGY

Many of the major perennial tributaries to the Colorado River in the Grand Canyon including Bright Angel Creek, Shinumo Creek, Tapeats Creek, Dear Creek, Vasey's Paradise and Nankoweap Creek (Fig. 1) are spring fed, with relatively small watersheds and generally clear waters. Diamond Creek and Havasu Creek (Fig. 1), though more susceptible to the influence of runoff and flooding from large drainage areas, are also spring fed and clear. On a whole, the clear water tributaries are some of the most productive aquatic habitats of the Grand Canyon

(Oberlin et al. 1999). Perennial, but often not as impacted by flooding and runoff due to limited drainage size, these streams provide stable habitat with only limited disruption from increased sediment loads and major shifts in discharge. Oberlin et al. (1999) indicate that primary productivity and detritus, the major food resource for macroinvertebrates are higher overall in clear-water tributaries and highest in those originating inside the Grand Canyon. Additionally, phytoplankton species richness also increases in clear-water tributaries (Crayton and Sommerfield 1979, Oberlin et al. 1999) bolstering primary productivity and food quality in these environments.

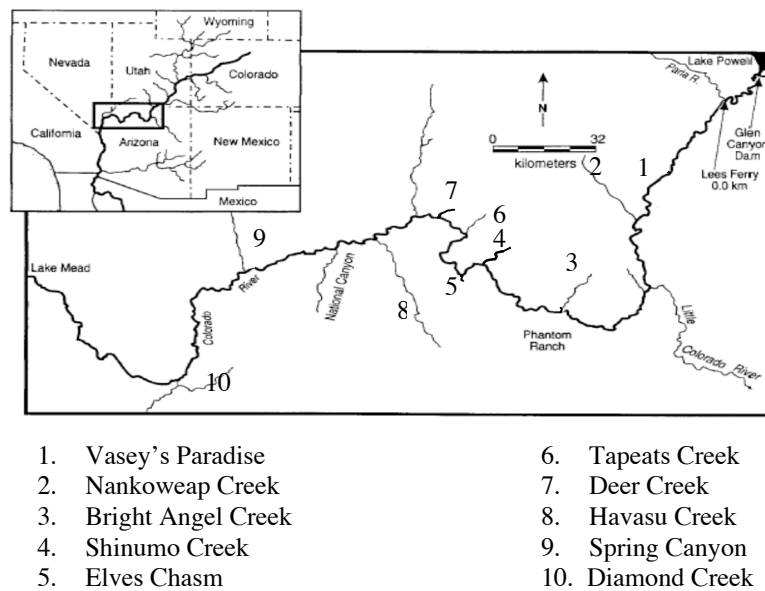


Figure 1. Ten major clear-water tributaries of the Colorado River in Grand Canyon, AZ.

Invertebrates

As a function of the low turbidity and productive waters, the Colorado River's clear-water tributaries support a large invertebrate community. Oberlin et al. (1999) found that macroinvertebrate biomass was higher in the clear, spring fed tributaries than in the larger more turbid tributaries originating outside of the Grand Canyon (Fig. 2). These differences also held true for species richness and were consistent across seasonal shifts (Oberlin et al. 1999). Invertebrate biomass was found to be most strongly correlated with drainage size and stream source (Oberlin et al. 1999), a relationship reflected in the larger drainages of Diamond Creek

and Havasu Creek having lower invertebrate biomass than some of the smaller clear water tributaries (Oberlin et al. 1999).

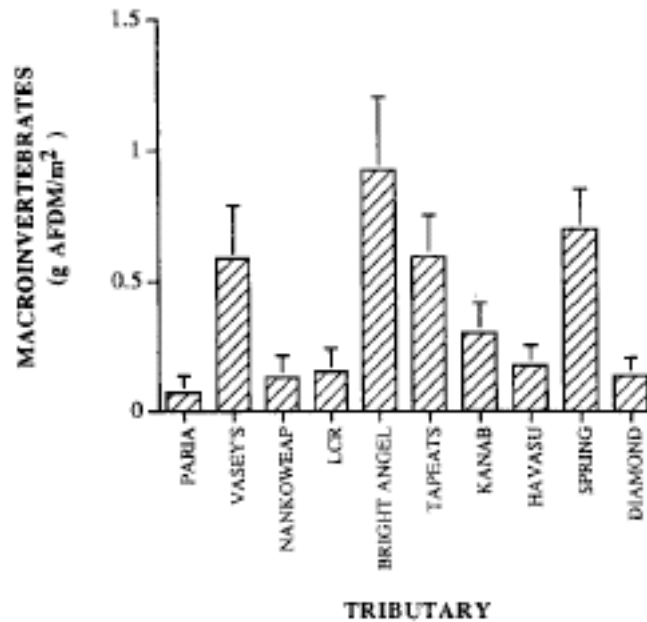


Figure 2. Mean annual ash free dry mass (g AFDM/ m²) for macroinvertebrates in 10 tributaries from 1991 collection trips. Error bars represent +/- 1 SE. . (Oberlin et al. 1999)

Fish foraging habitat

As a result of their stable conditions and rich invertebrate communities the Grand Canyon's clear-water tributaries provide excellent foraging habitat for fish. Eight species of native fish were found in the Grand Canyon in the early 19th century. Although none of these are extinct from the Colorado River Basin, the Colorado pikeminnow (*Ptychocheilus lucius*), bonytail (*Gila elegans*), roundtail chub (*Gila robusta*) and razorback sucker (*Xyrauchen texanus*) have been extirpated from Grand Canyon (Minckley 1991, Campos 2005, this volume). The endangered humpback chub (*Gila Cypha*) (Fig. 4), flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*Catostomous discobolous*) (Fig. 3) and speckled dace (*Rhinichthys osculus*) all retain reproducing populations in the Canyon (Valdez et al. 2001, Minckley 1991, Campos 2005, this volume). Prior to the string of non-native fish introductions beginning in the late 1800s (Wilson 2005, this volume), the Colorado pikeminnow was the only primarily piscivorous predator in Grand Canyon. As a result, benthic invertebrates have evolved as an especially

important source of food for the native fishes of the Grand Canyon. Available data suggests that invertebrates made up some portion of the diet of all native fishes in the Colorado - with the possible exception of the mostly herbivorous bluehead sucker - and the main component of the diet for the humpback chub, and the speckled dace (Minckley 1991, Minckley et al. 1986, Miller 1959).

Fish rearing habitat

Another key ecological function of the clear-water tributaries is to provide slow water rearing habitat for juvenile fish. Prior to the Glen Canyon Dam closure, rearing conditions in tributaries were improved by seasonal high flows from spring snowmelt that pushed tributary water back forming large pools at the mouth and in the lower reaches (Webb et al. 1999). Accounts from high water trips in the 1950s recall water backed up into Rider Canyon, South Canyon, Nankoweap Creek, the Little Colorado River, Shinumo Creek, Kanab Creek and Havasu Creek with fish sometimes observed in the high water pools (Webb et al. 2002). Rearing habitat in tributaries has become especially important since the closure of Glen Canyon Dam. Lack of sediment has teamed with the altered flow regime from the dam and triggered the progressive erosion of sandbars. This erosion in turn has resulted in the loss of much of the mainstem lentic backwater habitat (Schmidt et al. 1998). Tributaries may therefore provide the most viable alternative for juvenile native fishes seeking warmer slower waters and confronted with diminished mainstem habitat.



Figure 3. The mostly herbivorous bluehead sucker (*Catostomous discobolous*), makes its home in some of the Grand Canyon's clear-water tributaries. (Leibfreed et al. 2003)

Fish spawning habitat

Clear water tributaries also provide crucial spawning habitat for native fishes. Flannelmouth suckers, and the largely extirpated razorback sucker have both been observed spawning in Havasu Creek, and aggregations of flannelmouth suckers have been linked with flows in Havasu Creek though not with those in the Colorado (Douglas and Douglas, 2000). Bluehead suckers have been found during sampling in Bright Angel Creek and speckled dace are known to spawn in clean gravel substrates at several tributary mouths (Minckley 1991). In related research, Johnson and Hines (1999) showed that young razorback suckers preferred clear water to varying degrees of turbidity. Clear water tributary spawning appears less important for the endangered humpback chub that currently spawn predominantly in the turbid waters of the Little Colorado River (Merettsky et al. 2000, Valdez and Ryel 1997). It has been suggested that the reason for this is that the Little Colorado River is providing habitat most closely resembling the main channel in the Canyon prior to the closure of Glen Canyon Dam that caused a drop in turbidity and water temperature in the Colorado mainstem (Douglas and Marsh 1996, Kading and Zimmerman 1983). Though not directly dependant on the clear-water tributaries, the spawning practices of the humpback chub reflect the way in which shifts in the mainstem environment can dramatically increase the importance of tributary habitat.



Figure 4. The endangered humpback chub (*Gila Cypha*) spawns exclusively in the Little Colorado River. (Leibfreed et al. 2003)

There are a variety of different characteristics common to the Colorado's clear water tributaries that may interact to create habitat preferences such as those exhibited by the flannelmouth sucker and razorback sucker. Many of these tributaries have always differed from the mainstem of the Colorado in terms of their hydrology and dominant geomorphic processes. Just as increased suspended sediments have been associated with reduced spawning, feeding, growth and recruitment (Johnson and Hines 1999, Johnston and Wildish 1982, Sigler et al. 1984, Barrett et al. 1992, Miner and Stein 1993, Waters 1995), decreased suspended sediments and turbidity can mean better foraging conditions for juvenile fish and may enhance site based mate selection during adult spawning. Additionally, since the closure of Glen Canyon Dam, tributary waters have been significantly warmer than that of the Colorado River (Fig. 5). As a result, tributaries now provide fish of multiple life phases with crucial thermal refugia. Robinson and Childs (2001) found growth to be positively correlated with water temperature for flannelmouth suckers, speckled dace, humpback chub, and bluehead suckers and suggest that fish that migrate into the Colorado river as larvae will likely experience greater mortality than those that migrate after growth and rearing in tributaries.

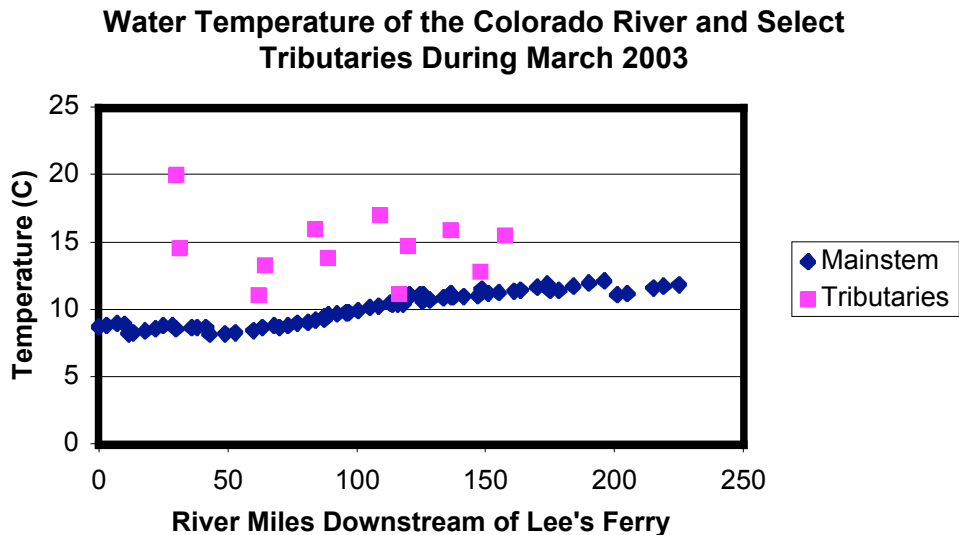


Figure 5. Colorado River vs. tributary water temperature - collected March 2003. (Hammersmark 2003)

Bird habitat

The productive refuges provided by the clear water tributaries may also be important habitat for members of the Grand Canyon's expanding waterbird population. The American dippers present in the Canyon require clear water for foraging, and breed only along the tributaries (Stevens et al. 1997). Research indicates that bald eagles forage primarily in tributary creeks during medium to high flows and exclusively in creeks at flows greater than 568 cms (Brown et al. 1998). The same study attributes this pattern to the added difficulty in foraging created by the increased depth, turbidity and velocity of the higher flows (Brown et al. 1998). Similarly, the patterns of distribution and abundance of several waterbird species in the Grand Canyon have been tied to decreasing water clarity as well as standing biomass of benthic alga, and invertebrates (Stevens et al. 1997). Though the specific role and impacts of waterbirds on the ecology of the tributaries is not clear from the existing research, waterbird use of the tributaries does appear to be closely related to turbidity and disturbance in the mainstem.

The available research clearly points to the importance of the stable, warmer, less turbid, highly productive habitat provided by the Canyon's clear-water tributaries for several species at multiple trophic levels. This is especially true for those tributaries originating from springs inside the Canyon with smaller drainages such as Bright Angel Creek and Nankoweap Creek, but is also the case, for larger less stable systems such as Havasu Creek and Diamond Creek. Given the richness and critical ecosystem functions within the clear-water tributaries and the important breeding, foraging and rearing habitat they provide to mainstem biota, it is easy to imagine that changes in the mainstem environment might, through altering the behavior of that biota, have a pronounced impact on tributary ecology.

MAINSTEM DISTURBANCE AND ECOLOGIC CHANGE

Since the closure of Glen Canyon Dam and the resulting release of colder, hypolimnetic waters from Lake Powell, tributaries have provided thermal refugia for native fishes and non-native fishes alike. The current managed flow regime in the Grand Canyon, is nominally focused on habitat restoration and species conservation. However, the extreme degree of disturbance it is causing may be having the opposite affect, destabilizing the Colorado River to the greatest extent in history. Though smaller than historic floods, large-scale beach building releases, and

oscillation in flow such as those designed for trout “perturbation” which fluctuate daily from 5-20 kcfs from January to march (Korman et al. 2003) are creating an environment of almost estuarine extremity. Disturbance of this magnitude increases pressure on mainstem biota creating the potential for a heightened dependency on clear-water tributary refugia. Increased use of tributaries paired with a shift in the timing and duration of the use could impact tributary ecosystems in a number of ways.

Increased Colonization

One of the potential effects of the current managed flow with especially significant implications for tributary ecology is increased colonization of the tributaries by residents of the Colorado River mainstem.

Invasive fish

In addition to its native fishes the Grand Canyon portion of the Lower Colorado is also home to a variety of invasive alien species including rainbow trout (Fig. 6), brown trout (Fig. 7), common carp, channel catfish, fathead minnows and plains killifish (Valdez et al. 2001, Wilson 2005, this volume). Invasive species populations have grown steadily over time and are regarded as the ultimate factor in the extirpation of the lower Colorado’s native fishes (Minckley 1991, Campos 2005, this volume). As such the increased predation and competition pressure they place on tributary spawning and rearing grounds is an important, if little researched, consideration in the ecology of these habitats.

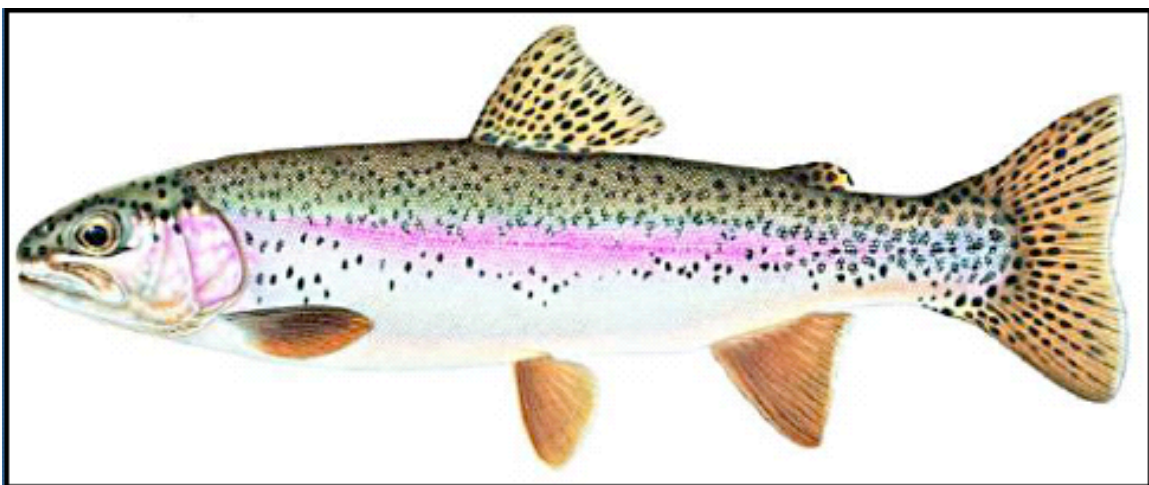


Figure 6. Rainbow trout, already present in Bright Angel Creek may soon become established in other tributaries. (Leibfreed et al. 2003)

Colonization by non-natives has already occurred in many of the tributaries, but the impact of this is only beginning to be investigated. Anecdotal accounts dating back as early as the 1920s recall catfish in multiple tributaries including Havasu Creek and Tapeats Creek and later accounts chronicle carp being sighted and taken from tributaries as well (Webb et al. 2002). Given the existing presence of non-native species in tributaries, it's easy to envision competition and predation levels increasing dramatically, were significant mainstem disturbance to render that habitat uninhabitable or less desirable.

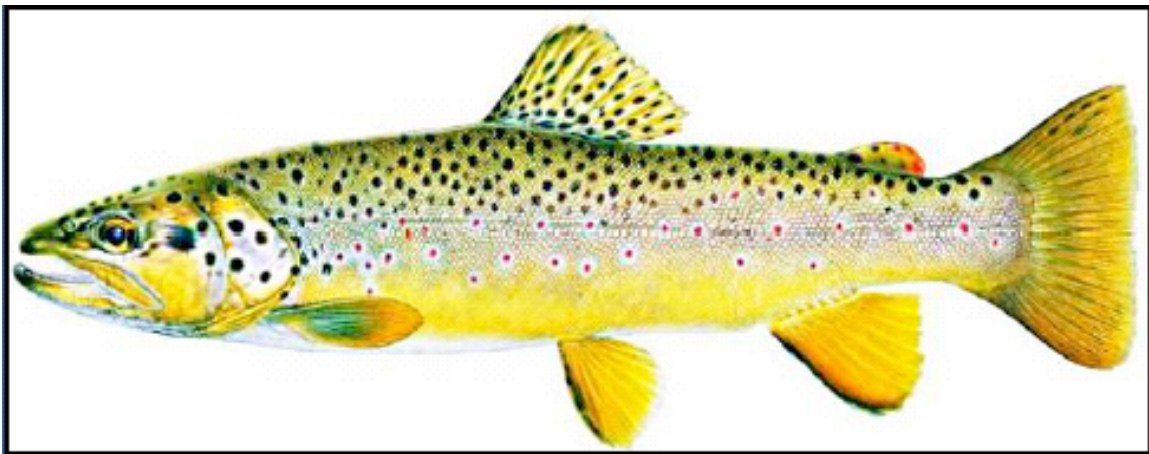


Figure 7. The highly predatory brown trout are already established in Bright Angel Creek. (Leibfreed et al. 2003)

Colonization of tributary spawning habitat by non-native species is already a topic of concern. Temperature tolerances for several non-native species present in the Colorado River mainstem (Haden 1992, Wilson 2005, this issue) fall within the range supported by many of the clear water tributaries (Fig. 8). Rainbow trout and brown trout, prized by anglers and flourishing in the Lees Ferry tailwater are already common in some downstream tributaries (Valdez et al. 2001) and established and spawning in Bright Angel Creek (Leibfreed et al. 2003). The consequent threat to the native fishes in Bright Angel Creek, which include the flannelmouth sucker, bluehead sucker, speckled dace and humpback chub, have prompted efforts on the part of the park to control the spread of the invasive trout (Leibfreed et al. 2003). Though current flow

oscillations targeting introduced brown and rainbow trout may be successful at preventing spawning upstream (Epstein 2005, this volume), they may also have the effect of displacing smaller trout downstream thereby increasing the chances of populations taking root in lower spring fed tributaries. Findings from assessment of the effects of the beach and bar building flood of 1996 suggest that young rainbow trout were displaced downstream by this large event (Valdez 2001). Historically, the gradual increase in temperature and high turbidity below the Little Colorado River confluence with the mainstem is thought to have slowed trout downstream habitat expansion. However, if washed down by high flows, trout may find their way into productive, clear-water tributaries downstream. Potential for this seems especially high in Tapeats Creek and Kanab Creek both of which have temperature, pH, and dissolved oxygen levels similar to Bright Angel Creek (Oberlin et al. 1999) (Fig. 8). Anecdotal evidence suggests that trout have been present in Tapeats Creek for several decades (Webb et al. 2002). With the impact of two additional large events since the 1996 flood, winter daily flow oscillations, and more large events planned for the future, the potential for downstream habitat expansion by brown and rainbow trout seems only to be increasing.

Tributary	Temperature	pH	Dissolved oxygen	Specific conductance
Paria River	16.5 (4.6)	8.1 (0.1)	8.9 (1.0)	0.78 (0.08)
	7.1–35.5	7.8–8.5	6.7–12.2	0.53–0.99
Vasey's Paradise	14.4 (1.9)	8.3 (0.1)	8.0 (1.4)	0.34 (0.02)
	7.4–18.2	8.1–8.5	8.3–10.4	0.28–0.36
Nankoweap Creek	15.5 (4.2)	8.5 (0.1)	9.6 (0.9)	0.61 (0.02)
	1.0–28.4	8.2–8.9	7.6–12.4	0.55–0.69
Little Colorado River	16.4 (2.6)	7.8 (0.1)	9.1 (0.4)	2.5 (0.72)
	9.4–24.2	7.3–8.1	7.5–10.3	0.33–4.49
Bright Angel Creek	13.3 (2.8)	8.4 (0.1)	10.0 (0.5)	0.33 (0.03)
	6.2–25.4	8.0–8.6	8.2–11.4	0.22–0.40
Tapeats Creek	14.6 (2.3)	8.3 (0.1)	10.4 (0.2)	0.31 (0.02)
	9.7–15.6	7.9–8.6	9.8–10.9	0.23–0.33
Kanab Creek	13.9 (2.6)	8.1 (0.1)	10.6 (0.5)	1.27 (0.11)
	7.8–22.8	7.7–8.3	9.2–12.0	0.9–1.80
Havasu Creek	15.4 (1.8)	8.2 (0.1)	9.9 (0.2)	0.73 (0.01)
	10.9–21.5	8.0–8.4	9.2–10.3	0.70–0.75
Spring Canyon	23.9 (1.3)	7.3 (0.3)	7.2 (0.5)	0.62 (0.03)
	20.2–28.0	6.3–7.9	5.6–8.8	0.48–0.68
Diamond Creek	15.8 (4.1)	8.3 (0.1)	9.1 (1.1)	0.74 (0.05)
	11.2–24.2	8.0–8.6	8.4–11.0	0.63–0.89

Figure 8. Annual mean values and ranges for water temperature (°C), pH, and dissolved oxygen (mg/l) and specific conductance (mS) for 10 major tributaries of the Colorado River through the Grand Canyon during 1991. (Oberlin et al. 1999)

Introduced invertebrates

Pressure on clear-water tributary ecosystems due to colonization from the mainstem could also pose a problem at the benthic level. The current status of the aquatic foodbase in the Colorado River reflects the high level of disturbance caused by the current flow regime (Purdy 2005, this volume). Assessment of the 1996 test flood impacts on the benthos revealed extensive scour and entrainment of primary and secondary producers (Shannon 2001). Downstream displacement of benthos could affect both benthic ecology and primary productivity in tributaries. The likelihood of extensive tributary colonization by the introduced amphipod *Gammarus lacustris* could increase if high flows scour these invertebrates from their interstitial dwellings and displace them downstream. Competition with *G. lacustris* over habitat is thought to be a factor limiting the distribution of the net building Caddisfly *Ceratopsyche oslari* (Haden et al. 1999). If introduced to tributaries, competition with *G. lacustris* could impact distribution, abundance and foodweb dynamics among the invertebrate population. Competition between benthic invertebrates also has the potential for indirect effects at multiple trophic levels. Research on streamside avian feeding patterns found that multiple canyon dwelling species diets included insects of aquatic origin and that yellow warbler diets were composed of 45% aquatic midges (Yard et al. 2004). Thus, a change in tributary species composition and abundance could limit food availability for insectivorous birds. Similarly, competition with shredding aquatic insects, largely absent from the mainstem but present in the tributaries could increase the amount of leaf pack and the invertebrate communities associated with them (Pomeroy et al. 2000). In addition, given the historic lack of riparian vegetation on the mainstem, allochthonous input to tributaries, may be an important carbon source for both the tributaries and the mainstem. Carbon processed by shredding aquatic insects, found mainly in the tributaries, may provide important fine particulate organic matter for collectors and grazers downstream (Vannote 1980). In this way, loss or displacement of shredding aquatic insects in tributaries could have repercussions for invertebrates in the mainstem as well.

Piscivorous birds

Use of the tributaries as foraging habitat for piscivorous birds may also prove a developing threat to native fishes. Bald eagles, and other predatory waterbirds including ospreys forage in the canyon (Stevens et al. 1997). Waterbird assemblages are known to respond

strongly to dam induced habitat changes and serve as indicators of ecosystem change (Stevens et al. 1997). As such, shifts towards increased use of the tributaries like that observed in bald eagles (Brown et al. 1998) may signal a larger scale pattern of increased tributary foraging during high flows.

Frequency and timing of flow

The frequency, and timing of high flows might magnify some of the potential pressures on the spawning success of native fishes. Prior to the closure of Glen Canyon Dam, seasonal flow increases in the mainstem may have increased use of the tributaries by both aquatic and avian predators avoiding the elevated velocity and turbidity. By contrast, periods of medium to low flow may have allowed for natural spawning and rearing windows in tributaries, when predatory pressure was relatively low. Under current conditions, continuous disturbance in the mainstem from elevated or changing flows may encourage mainstem predators to linger in tributaries or even become established there. This in turn could impact native fishes that have adapted the timing of their spawning or rearing phases to coincide with a seasonal decline in predatory presence in tributaries.

In contrast with the now highly disturbed mainstem, tributary high flows and disturbance remains seasonal and continues to provide opportunities for native fish to leverage adaptations to seasonal flow. This is illustrated by the late summer spawning of flannelmouth and razorback suckers in Havasu Creek (Douglas and Douglas 2000). This late season spawning is viewed as an adaptive strategy to protect populations from catastrophic events (Douglas & Douglas 2000, Minckley 1991). Given that late summer is often the time when larger tributaries like Havasu Creek historically experienced an increase in flow and turbidity from thunderstorms, there may also be a component of this adaptive strategy that is reliant on high flows. Research shows that though razorback suckers prefer clear water, predation on them increases as turbidity decreases (Johnson and Hines 1999). Given this and that the largely extirpated razorback suckers are believed to be primarily spring spawners (Minckley 1991), it may be that the hybridized razorback suckers discovered spawning in Havasu Creek in late fall have survived as the result of an adaptive strategy that leverages high flows. Perhaps this small group of razorbacks has lowered the rate of predation of newly hatched juveniles through timing of their emergence with increased turbidity and higher water. The potential significance of a seasonally timed adaptive

strategy is also reflected in flannelmouth suckers having maintained a healthy population in the Grand Canyon where other sucker populations have declined (Campos 2005, this volume). Though this explanation for the success of the suckers is speculative, what is clear is that a complex web of ecological processes and adaptations are founded on a dynamic flow pattern and seasonal high flows, that are no longer present and that have been replaced by a new more regimented pattern of disturbance without the same recovery potential.

CONCLUSION

The goal of these speculations on potential shifts in the ecology of the clear-water tributaries is to illuminate the rich and delicate nature of these systems and the importance of the habitat they provide for both their own biotic communities, and mainstem biota. Although research focused specifically on the Grand Canyon's clear-water tributaries has been limited in the past, the findings are sufficient to demonstrate the integral role these habitats play in Grand Canyon ecology. Together with disturbance regime in the main channel, the stable, productive, refuge the tributaries provide serves as a platform upon which species adaptations and life history traits are constructed and balanced. Under current flow management, drastically increased mainstem disturbance is significantly increasing the likelihood of widespread colonization of tributaries by invasive and predatory fish species. Similarly, increased frequency of high flows in the mainstem may significantly increase foraging in tributaries by piscivorous birds. At the same time, the relatively undisturbed habitat in tributaries and their natural flow pattern make them crucial spawning and rearing habitat for native fishes adapted to seasonal high flows. With all of these converging pressures, tributary habitat in the Grand Canyon may be both more significant and more in peril than it has ever been.

Recommendations for Management

A great deal of opportunity exists for research and management towards preservation of tributary habitat and ecology. Above all, basic research and monitoring of the tributaries is necessary to map the existing biotic communities and assess the extent and impact of colonization by non-natives. In tributaries where invasive species are becoming established, population management or removal of those species through efforts like those already initiated to remove brown trout from Bright Angel Creek could be implemented (Leibfreed et al. 2003).

Minckley et al (2003) propose a conservation plan for native fishes involving construction of streamside hatchery facilities. If properly managed, tributary habitat could, in a similar fashion, be used to provide a rearing ground for native species with a natural food source, where pressures on young could be minimized until they have achieved a size that significantly decreases the threat of predation. Management of this kind could likely be implemented in smaller tributaries at only a fraction of the cost associated with the construction and maintenance of the streamside hatcheries proposed by Minckley et al. (2003).

In the mainstem flow management that closely couples flow level with season, climate and hydrologic activity in the larger basin would likely benefit tributaries. Specifically, this approach would decrease overall mainstem disturbance and lower the related likelihood of non-natives becoming established there. At the same time, seasonally timed flows micromanaged to create a disturbance regime in the mainstem that more closely mimics that which existed before the dam, in terms of timing, frequency and duration of flows would allow native species a greater opportunity to leverage adaptations based on seasonal disturbance patterns. Under any managed flow regime, the tenuous state of the unique tributary habitats and the essential ecological processes they support necessitate additional tributary targeted research and extensive ecological monitoring. Through coordinated adaptive management and research, the uniquely undisturbed habitats of the Grand Canyon's clear-water tributaries can be conserved and so leveraged towards the larger effort to protect and restore the ecology of the Grand Canyon.

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