EFFECTS OF POOL FORMATION AND FLASH FLOODING ON RELATIVE ABUNDANCE OF YOUNG-OF-YEAR FLANNELMOUTH SUCKERS IN THE PARIA RIVER, ARIZONA

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ABSTRACT

Flannelmouth sucker, *Catostomus latipinnis*, a fish endemic to the Colorado River basin in the western United States, appears to experience poor recruitment to adult size in the Colorado River, downstream of Glen Canyon Dam. Lack or impermanence of rearing areas for young-of-year (YOY) fish is hypothesized to be the problem. Knowing the importance of tributary mouths as rearing areas in other river systems, we studied use of the mouth of the Paria River, a tributary of the Colorado River, by YOY flannelmouth suckers, and the availability of rearing area in the mouth at different flow levels in the Colorado River in 1996 and 1997. We also examined the relationship between flash floods in the Paria River and catch-per-unit-effort (CPUE) of YOY in the Paria River between 1991 and 1996.

Maximum mean daily discharge in the Paria River was inversely correlated with CPUE of YOY flannelmouth suckers (Spearman Rho = -0.9856, p = 0.0003) during their critical rearing period (15 March-30 June). Thus, it appears that YOY flannelmouth suckers rear longer in the Paria River in years when flash flooding is minimal.

Recruitment of YOY flannelmouth suckers at the Paria River may also be improved by enhancing pool formation during spring and summer rearing seasons. YOY flannelmouth sucker was captured in a pool created by high Colorado River flows ($\geq 336 \text{ m}^3/\text{s}$) that inundated the mouth of the Paria River during spring and summer, 1996. In 1997, high flows (about 550–750 m³/s) in the Colorado River during winter and spring initially inundated the Paria River and formed a pool in the mouth. However, these high flows eventually caused 0.5–1.0 m of suspended sediment from the incoming Paria River to deposit in the mouth. Thus, despite higher flows than 1996, the slackwater area formed only occasionally in 1997. Differences in pool formation between 1996 and 1997 demonstrate that pool formation cannot be inferred solely from Colorado River flows. Copyright © 2001 John Wiley & Sons, Ltd.

KEY WORDS: Colorado River; dam management; flannelmouth sucker; rearing habitat; recruitment; tributary mouths; young-ofyear

INTRODUCTION

Historically, flannelmouth sucker, *Catostomus latipinnis*, occurred in the mainstem Colorado River and large tributaries throughout the Colorado River basin (Minckley and Holden, 1980). More recently, its range has been reduced in the lower Colorado River basin. In Arizona, flannelmouth sucker has been extirpated from the lower Salt, San Pedro and Gila Rivers (Minckley, 1973; Fradkin, 1984). In the upper Colorado River basin, the flannelmouth sucker still occurs throughout its known historic range (Tyus *et*

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al., 1982); however, hybridization with white sucker, *C. commersoni*, threatens its survival and genetic purity (Prewitt, 1977). Reduction in range in the lower basin, and hybridization in the upper basin prompted this species to be categorized as a 'species of concern' in 1991 (US Fish and Wildlife Service, 1996).

Surveys conducted over the last 5 decades have shown that flannelmouth suckers have remained relatively common or abundant in the Colorado River, Grand Canyon, as compared with previous surveys at similar locations (Carothers and Minckley, 1981; Valdez and Ryel, 1995). However, there is concern about recruitment of flannelmouth suckers to age 1, and ultimately to spawning size, especially in the 125 km below Glen Canyon Dam. In this section of river, a relatively small number of young-of-year (YOY; < 90 mm total length (TL)) and sub-adults (90–360 mm TL) have been captured in the Paria River, or in downstream backwaters of the mainstem Colorado River, despite extensive sampling (Maddux *et al.*, 1987; Valdez and Ryel, 1995; AGFD, 1996; Weiss *et al.*, 1998). In addition, mean length of spawning adults in 1992 and 1993 increased significantly compared with mean length of fish spawning in 1981 (Weiss *et al.*, 1998), indicating low recruitment of fish to age 1, or spawning size.

Cold summer water temperatures from hypolimnetic releases from Glen Canyon Dam and, hence, the lack of warm rearing areas, is likely the major factor limiting survival of YOY, and ultimately recruitment of flannelmouth suckers in the Colorado River in Grand Canyon. Before closure of Glen Canyon Dam, Colorado River temperatures were about $18^{\circ}-26^{\circ}$ C in May and June (Valdez and Ryel, 1995), the period corresponding to YOY flannelmouth suckers drifting out of tributaries into the mainstem Colorado River. Under current operational flows of Glen Canyon Dam, temperatures in the Colorado River, Glen Canyon, are about $7^{\circ}-11^{\circ}$ C (McKinney *et al.*, 1999). Cold water temperatures ($7^{\circ}-14^{\circ}$ C versus $\leq 20^{\circ}$ C) limit or slow growth, cause cold coma/shock, and reduce swimming performance of larval and juvenile native Colorado River fishes (Berry and Pimentel, 1985; Berry, 1988; Lupher and Clarkson, 1993; Childs and Clarkson, 1996; Clarkson and Childs, 2000). Larval flannelmouth suckers exhibit much slower growth at 10°C than at 20°C. For example, 7-day old flannelmouth sucker reared in 10°C water were only about 20 mm long at 90 days, while those reared in 20°C were about 40 mm at 90 days (Clarkson and Childs, 2000).

Backwaters or return current channels (as described in Rubin *et al.*, 1990; Schmidt and Graf, 1990) and nearshore slackwater areas presently provide rearing areas for YOY fish in the Colorado River through Grand Canyon (Valdez and Ryel, 1995; AGFD, 1996). Return current channels and nearshore areas are characterized by low velocities and, depending on season and discharge from Glen Canyon Dam, warmer temperatures than the mainstem Colorado River. However, availability of these areas changes with fluctuating flows on a daily and weekly basis, causing only a portion of drifting YOY to have access to these potential rearing areas (Valdez and Ryel, 1995; AGFD, 1996).

Tributary mouths also provide rearing areas for YOY fishes (Brown and Coon, 1994; Galat *et al.*, 1997). In the Colorado River, Grand Canyon, high discharge can create large pools in the mouths of tributaries. An experimental flood conducted by the Bureau of Reclamation in 1996 (1274 m³/s) created a pool > 600 m long in the mouth of the Little Colorado River (LCR) (T. Hoffnagle, personal observation). If high mainstem flows occur at the right time, they could provide warmer temperatures for larval and juvenile native fishes, including the endangered humpback chub, *Gila cypha*. Clarkson *et al.* (1994) suggested that spring flows from Glen Canyon Dam be increased to a sustained maximum so that tributary mouths would be impounded and transport of YOY native fishes to the mainstem Colorado River would be reduced.

Knowing the important role that tributary mouths may play in recruitment of YOY fishes, we examined presence and persistence of YOY flannelmouth sucker in the Paria River, a tributary of the Colorado River. Our specific objectives were to: (1) determine if and how long YOY rear in the mouth of the Paria River, (2) determine growth rates of YOY flannelmouth suckers rearing in the mouth of the Paria River, (3) document changes in available habitat as a result of changes in Colorado River flow, and (4) examine the relationship between flash flooding and presence of YOY in the Paria River during the rearing season between 1991 and 1996.

STUDY AREA

The study area encompassed the lower 6 km of the Paria River and its confluence with the Colorado River. The study site is located in central northern Arizona in Glen Canyon National Recreation Area, about 25 km downstream from Glen Canyon Dam (Figure 1). The Paria River is a perennial spring-fed stream in its lower 16 km, but intermittent in the 72 km above that point. It drains an area of 3730 km² and its headwaters are located in the Pink Cliffs of Bryce Canyon National Park in southern Utah. Mean instantaneous discharge for the Paria River is 0.77 ± 3 m³/s, but the river is prone to flash floods and has a mean annual flood discharge of 88 m³/s (Topping, 1997). The lower 16 km of the Paria River are generally surrounded by an open floodplain with alluvial deposits and sparse vegetation. At base flow, the Paria River carries fine sediments and, thus, is nearly always turbid. Flash floods, which occur largely in late summer/early fall from thunderstorms, and in late winter from the passage of frontal systems, cause the river to carry large amounts of sediment (up to 780000 mg/L) into the Colorado River (Graf *et al.*, 1991). The stream throughout the lower 16 km is uniformly shallow (< 0.3 m deep), and occupies a channel ≤ 20 m wide at base flow.

The Colorado River drains an area approximately 626780 km² from seven states, about one-twelfth of the US. It is one of the world's largest desert rivers, and one of the most hydrologically modified (Andrews, 1991). Glen Canyon dam has significantly altered the temperature regime, seasonal hydrologic cycle, and sediment load of the river (Valdez and Ryel, 1995). Water immediately below the dam is now perennially clear and constantly between 8° and 12°C, whereas historically it was turbid and ranged seasonally from 2° to 26°C. Seasonal variations in flow have been considerably dampened, but daily flows can fluctuate between 142 and 849 m³/s and have a maximum daily change of 227 m³/s (US Department of Interior, 1995) as a result of power generation. As a result of dam operation, there are no longer high spring flows that likely flooded tributary mouths weeks at a time (Topping, 1997); however, there are daily variations in flow that result in inundation and dewatering of shallow nearshore areas and backwaters.

METHODS

Abundance and growth of YOY flannelmouth suckers

We sampled for larval and juvenile flannelmouth suckers using drift nets, larval light traps, dip-nets and seines. We seined (4.6 m long \times 1.5 m deep, 6.4-mm mesh) at least once monthly from March 1996 to

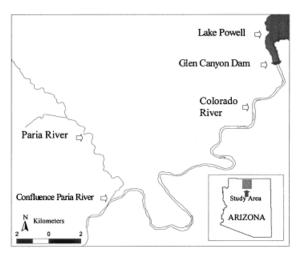


Figure 1. Location of the confluence of the Paria and Colorado Rivers, Arizona, in relation to Glen Canyon Dam

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April 1997. On each sampling date, one haul was completed at each of 9 sites in the lower 6 km of the Paria River, and between five and seven hauls at the confluence (mouth) of the Paria and Colorado Rivers (Figure 2). We calculated catch-per-unit-effort (CPUE) (fish/100 m²) for each sample site and ran a repeated measures analysis of variance (RM ANOVA) on the CPUE data for the five dates when YOY were present and all nine upriver Paria sites, as well as the confluence area, were sampled. This analysis tested for significant differences between upriver and confluence sites. In May and June 1997, we seined at established transects in the mouth of the Paria River, and dipnetted in the Paria River proper. All fish were measured (TL) to the nearest millimeter. We regressed fish length on dates for YOY caught in the summer of 1996 to determine growth rate (mm/day).

Habitat conditions in the mouth of the Paria River

Observations were made on the effect of Colorado River discharge on presence or absence of a pool in the mouth of the Paria River during sampling trips between May 1996 and June 1997. Discharge data for the Colorado River were collected from the United States Geological Survey (USGS) gaging station (# 09380000) at Lees Ferry, Arizona, and Paria River discharge data from the gaging station (# 09382000) located 2.0 km up the Paria River. Seven transects, 10–20 m apart, were established in the impounded mouth of the Paria River in June 1996. Depth (m) was measured at 1-m intervals along transects on 9 and 10 June, 15 and 17 July 1996, and 13 May and 14 June 1997. Position and elevation of the end points of transects were located with electronic survey instruments, using industry standard data collection and reduction software. Elevations of the points along transects were calculated using the elevations of endpoints and depth measurements taken along transect lines. For comparative purposes, streambed elevation in June 1996 was contrasted with elevation in June 1997.

Relationship between flash floods in the Paria River and recruitment of YOY

We hypothesized that an absence of flash floods in the Paria River during the critical rearing period of YOY flannelmouth sucker would allow their presence, and possibly, survival in the mouth. This critical

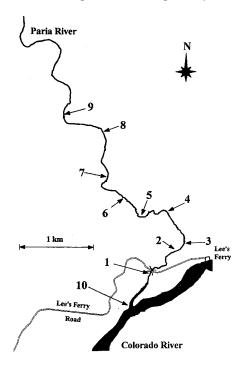


Figure 2. Study area and sampling sites in the Paria River and the confluence of the Paria and Colorado Rivers, Arizona

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rearing time for YOY flannelmouth suckers was estimated from previous research. Spawning season for flannelmouth suckers in the Paria River is suggested to be 15 March-15 April (Thieme, 1997; Weiss *et al.*, 1998). Robinson *et al.* (1998) found that YOY flannelmouth suckers were present in the LCR (a tributary of the Colorado River located ~ 100 km downstream of the Paria River) throughout June. Therefore, the critical rearing period was defined as 15 March-30 June.

Maximum daily flow in the Paria River between 15 March-30 June 1991–1996 was derived from data collected from the USGS gaging station. Observed CPUE (fish/100 m²) data from 1991–1996 were collected from various sources (Table 1). All researchers sampled for YOY fish by seining in the Paria River and at the confluence, at the same designated sampling sites (Figure 2, Table 1), and when the Paria River discharge was at base flow. Weiss (1993) used a straight seine (4.6 m long \times 1.5 m deep, 3.2-mm mesh) similar to that used in this study, while AGFD (1996) used a bag seine (5 m long \times 2 m deep (2 m \times 2 m \times 2 m bag), with 3.2-mm mesh on the wings and 1.6-mm mesh in the bag). Data from 1997 were not included because of ineffective sampling in that year. The maximum flow level obtained between 15 March and 30 June was then correlated with mean CPUE for each year using Spearman's correlation coefficient.

RESULTS

Abundance and growth of YOY flannelmouth suckers

1996. YOY were caught from May to September 1996. The majority (86%) of 576 YOY was captured in the impounded mouth of the Paria River. CPUE of YOY flannelmouth suckers was significantly higher in the mouth than at sampling sites upstream in the Paria River (RM ANOVA, Wilks' Lamda = 211.34, df = 1.7; $p \le 0.002$, Figure 3). Between mid-June and mid-July 1996, CPUE of YOY in the mouth dropped dramatically, and only two YOY flannelmouth suckers (89 and 94 mm TL) were captured in the Paria River above the mouth after 15 July. YOY grew about 0.52 mm/day (Figure 4, $R^2 = 0.78$, F = 1002.1, df = 2, p < 0.0001).

1997. Two flannelmouth suckers (85 and 88 mm TL), presumably from the 1996 year-class, were caught on 22 February 1997. On 13 May 1997, two YOY suckers were captured in the mouth. In addition, 17 were captured by dipnetting, and nine were counted in nearshore slackwater areas in the Paria River above the confluence. These fish were small (16.9 mm, S.E. = 3.14, n = 19) and identified to family Catostomidae. No YOY were captured in June of 1997; however sampling was ineffective because of the amount of silt in the mouth of the Paria River.

Habitat conditions in the mouth of the Paria River

A slackwater area, created when Colorado River flows inundated the mouth of the Paria River, was consistently present during the spring and early summer (mid-July) of 1996. During this period, the inundated area fluctuated between 20 m and > 200 m long as a result of daily flow fluctuations in the

Year	Researcher	Sampling period	Maximum flow level (m ³ /s)	CPUE YOY (fish/100m ²)	Total effort (m ²)
91	AGFD (1996)	May–June	79	1.7	2096
92	Weiss (1993)	March-June	1790	0.002	18 099
93	Weiss (1993)	March-June	607	0	6180
94	AGFD (1996)	May–June	40	14.5	5132
95	AGFD (1996)	June	426	0.4	1664
96	Thieme (1997)	March-June	57	4.1	3965

Table 1. Sampling period for YOY flannelmouth suckers and maximum flow in the Paria River within their critical rearing period (15 March-30 June) in 1991–1996

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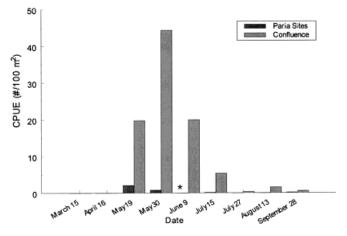


Figure 3. CPUE (number of YOY flannelmouth sucker/100 m²) at sampling sites in the Paria River and the confluence of the Paria and Colorado Rivers, Arizona, 1996. * Designates no sampling in the Paria above the confluence

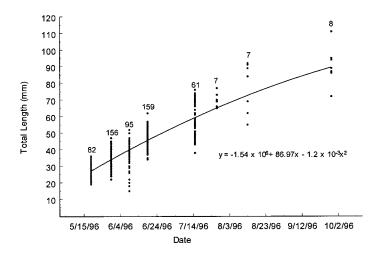


Figure 4. TL (mm) of YOY flannelmouth sucker at the Paria River, Arizona, from May to September 1996. Numbers above each sampling period are number of fish

Colorado River, and possibly sediment accumulation in the mouth of the Paria River. On 19 May, the impounded mouth comprised several small, connected pools up to 1 m deep. On 30 May, 9, 10 and 19 June, the mouth was inundated and one large slackwater pool, which had little or no velocity, was formed. In July, the impounded area represented conditions similar to those observed on 19 May. Flows in the Colorado River were never below 336 m³/s between 9 April and 15 July, whereas flows in the Paria River were consistently low from 1 April to 10 July (mean daily flow for this period: 0.16 m³/s, S.E. = 0.008, n = 100 days). In 1996, flows from the Colorado River did not completely inundate a gravel bar that extended from the mouth of the Paria River into the mainstem perpendicular to Colorado River flow. Instead, Colorado River water ran around this bar and backed water up into the Paria River.

Colorado River flows were steady and high $(566-736 \text{ m}^3/\text{s})$ from February to June 1997 (Figure 5). These flows inundated the gravel bar and caused the area between transects 1–3 to become part of the Colorado River proper. Therefore, comparisons between 1996 and 1997 could only be made for transects 4–7. On 13 May 1997, despite higher flows in the Colorado River (566 m³/s) than on 14 June 1996 (515 m³/s), virtually no pool was formed in the mouth of the Paria River. However, on 14 June 1997, Colorado River flows had increased by 170 m³/s to 737 m³/s, and a pool was formed in the mouth of the Paria River.

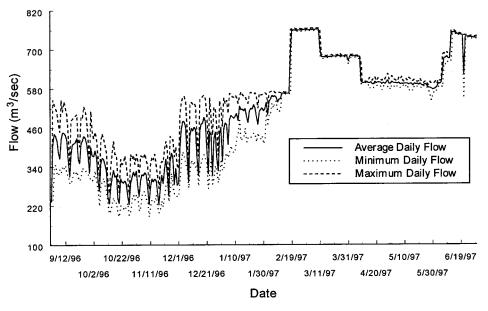


Figure 5. Colorado River hydrograph, 1 September 1996-30 June 1997, Lee's Ferry, Arizona

Bed elevation of the Paria River rose 0.5-1.0 m between June 1996 and June 1997 as a result of sediment deposition (Figure 6). A major spate (about 45.3 m³/s) occurred in the Paria River in January 1997, but flow levels decreased after January and never exceeded 5.95 m³/s through June 1997.

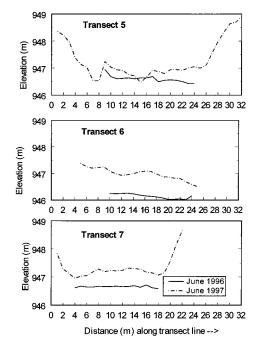


Figure 6. Elevation of the streambed in the mouth of the Paria River, Arizona, in June 1996 and 1997

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Relationship between flash floods in the Paria River and recruitment of YOY

Maximum flood level and CPUE of YOY were inversely related (Spearman Rho = -0.9856, p = 0.0003). There was low abundance of YOY in the Paria River in all years (1992, 1993 and 1995) when there were flash floods during the critical rearing period (15 March-30 June) for YOY flannelmouth suckers (Table 1). Conversely, CPUE was higher (1.7–14.1 fish/100 m²) in 1991, 1994 and 1996, when flow in the Paria River never exceeded 2.2 m³/s during the critical rearing period for YOY.

DISCUSSION

Abundance and growth of YOY flannelmouth suckers

YOY flannelmouth suckers were captured in a slackwater pool present in the mouth of the Paria River from mid-May to mid-July 1996. In mid-July, CPUE of YOY flannelmouth sucker declined following a flash flood in the Paria River on 10 July that possibly displaced YOY out of the mouth and into the mainstem Colorado River. Alternatively, fish may have descended into the mainstem voluntarily; YOY flannelmouth suckers commonly move from the tributaries into the mainstem at this time of year in the upper Colorado River (Paul Holden, BIO/WEST, Inc., Logan, Utah, personal communication).

Our growth curve corresponds closely to that presented by Clarkson and Childs (2000) for YOY flannelmouth suckers grown at 20°C. In their study, YOY flannelmouth sucker grew about 20 mm in a 20-day period from 25 mm at 41 days to 45-mm at 60 days,. Similarly, YOY in 1996 grew, on average, from 25 to 45 mm between 19 May and 19 June, about 20 mm in 30 days. The temperature ranged between 16° and 32°C in the mouth of the Paria River when YOY where caught there. The lower growth rate in the wild may be a result of limited food availability or fluctuations in temperature in the mouth of the Paria River.

It is unclear at what size YOY flannelmouth suckers can survive the thermal transition into the mainstem Colorado River. Clarkson and Childs (2000) found that 7–8-day old flannelmouth suckers enter cold coma for 5–10 s when transferred from 20° to 10°C water. Older YOY (14–15 and 42–43-day olds) did not experience cold coma, but all appeared to swim lethargically. Valdez and Ryel (1995) suggest that YOY humpback chub must be a minimum of 52 mm TL (average 74 mm TL) to survive the transition from the warm LCR to the cold mainstem Colorado River. On 19 June 1996, YOY flannelmouth suckers averaged 47 mm long (S.D. = 5.02, n = 160), suggesting that the end of June is an appropriate end date for the critical rearing period, as YOY flannelmouth suckers are probably able to successfully move into the mainstem Colorado River at this time. Regardless of the exact size, YOY flannelmouth suckers that are moved prematurely out of the Paria River into the cold Colorado River may experience low survival as a result of reduced growth (Clarkson and Childs, 2000), or increased predation as a result of cold shock (Berry, 1988; Lupher and Clarkson, 1993). Cold shock and its side effects (e.g. increased predation) appear to most seriously affect larvae and early juvenile, as opposed to older YOY, native Colorado River fishes. Thus, the presence of a warm rearing area is likely most vital during the larval and early juvenile stages of YOY flannelmouth sucker.

The Paria River, above the lowermost portion near its confluence with the Colorado River, appears to be an unsuitable rearing area for YOY flannelmouth suckers, possibly owing to uniformly shallow depths and lack of submerged vegetation or other structure. YOY fishes have been shown to use impounded tributary mouths as rearing areas in other river systems (Brown and Coon, 1994; Galat *et al.*, 1997; Ponton and Vauchel, 1998). In addition, flooding of tributary mouths and floodplains along rivers appears to be synchronized with drift of some larval fishes (Ponton and Vauchel, 1998).

Recruitment of YOY flannelmouth suckers in the reach of the Colorado River in western Grand Canyon, although still below recruitment levels in the upper basin (Richard Valdez, SWCA, Logan, Utah, personal communication), appears to be much higher than in the vicinity of the Paria River. Twenty-four percent of the catch between river kilometer (rkm) 265 and rkm 460 in 1995 were YOY flannelmouth sucker compared with 0% of the catch in the 70 km below the Paria River (Hualapai Department of

Natural Resources (HDNR), 1995; AGFD, 1996). Higher catch in western Grand Canyon most likely reflects warmer mainstem temperatures ($\sim 14^{\circ}-16^{\circ}$ C) encountered there from May to June (Valdez and Ryel, 1995).

Habitat conditions in the mouth of the Paria River

Steady high flows from February to June 1997 in the Colorado River and no flushing flows from the Paria River apparently caused suspended sediment transported by the Paria River to be deposited in the pool area at the mouth, eventually filling in this area. When Colorado River flows first increased in February 1997, the mouth of the Paria River was inundated, creating a pool about 150–200 m long and up to 1 m deep. However, by May of 1997, this pool was completely filled with sediment, causing the elevation of the streambed to rise.

Pool formation in the mouth of the Paria River depends on flow levels in the Paria and Colorado Rivers, as well as antecedent flows and their effects on sediment deposition in the mouth of the Paria River. Pool formation is dependent on both bed elevation of the Paria River at the mouth, and the magnitude of flows in the Colorado River. Elevation of the bed in the mouth of the Paria River changes as flooding events in the Paria River transport, scour and deposit sediment. Reduction in Colorado River flows may allow sediment to be more easily transported out of the mouth of the Paria River during flash floods. If prolonged high flows in the Colorado River act as a dam, impounding the mouth of the Paria River, sediment from the Paria River drainage is deposited, eventually filling any pool previously created until such time as spates in the Paria River flush sediments out.

Before closure of Glen Canyon Dam in 1963, there was seasonal inundation of the Paria River by high spring and summer Colorado River flows (Topping, 1997). In addition, the Colorado River was heavily sediment-laden during spring run-off, so that sediment, not only from the Paria River, but also from the Colorado River, was being deposited in the mouth. This aggradation would often be followed by flash floods in the Paria River during summer monsoons or winter cold fronts that scoured sediment out of the mouth of the Paria River into the main Colorado River (Topping, 1997). Spring flows in the Colorado River, before the dam, impounded the Paria River as far as 2.0 km up the Paria River. Although large spring floods in the Colorado River (i.e. $> 2265 \text{ m}^3/\text{s}$) were common before closure of Glen Canyon Dam, this flow level has been exceeded only in 1984 and 1985 since closure of the dam. (Topping, 1997). Thus, at present, tributary mouths are less likely to be impounded; thereby reducing rearing areas for larval and juvenile fish derived from tributary (or mainstem) spawning events.

Relationship between flash floods in the Paria River and recruitment of YOY

The fact that few, if any, YOY were captured at the Paria River in years when there were substantial spates from the Paria in the spring supports the idea that YOY do not rear in the Paria River in years when there are flushing flows during their critical rearing period. In 1996, when a pool formed in the mouth, there was not a substantial spate in the Paria River. Thus, it is unclear if a pool would be able to retain larvae and juveniles that a flash flood would otherwise move into the Colorado River. Further investigation could possibly provide more insight to the magnitude of flood that would displace YOY into the mainstem and the ability of a pool in the mouth to prevent such displacement.

CPUE was highest in 1994 and 1996 (14.5 and 4.1 fish/100 m², respectively). In 1996, in addition to no occurrence of flash floods in the Paria River, there was a pool formed in the confluence. Closer examination of data and field notes from 1994 (AGFD, unpublished data) suggested that a pool was also present in the mouth of the Paria River on 15 June when CPUE of YOY was highest. We infer the presence of a pool based on depth at the mouth on this day (0.36 m), compared with an average depth of 0.09 m in the Paria River above the confluence. In addition, the sampling location was 0.32 km up the Paria River, not at the traditional 0.0 km confluence. These observations strongly suggest that the Paria River was inundated, despite a mean daily flow in the Colorado River of only 323 m³/s. Evidence of survival of YOY from the 1994 year-class comes from the capture of 18 sub-adults in 1996, 78% of which were presumably from the 1994 year-class, based on their size (151–215 mm) and month captured. Prior

to this study, the last recorded sub-adult in the vicinity of the Paria River was captured in October 1984 (Weiss, 1993; Valdez and Ryel, 1995; AGFD, 1996). Thus, it appears that pool formation in the mouth combined with no flash flooding in the Paria River likely facilitated successful rearing of YOY spawned in the Paria River in 1994 and 1996.

Management implications

Flow regimes in rivers worldwide have been altered as the result of dam operations, creating changes downstream that have affected native biota. Several authors have documented that changes in flow regimes have caused a loss of nursery habitat for YOY fish species owing to temperature changes, fluctuating flows, and lack of seasonal flooding of adjacent floodplains (Burt and Mundie, 1986; Bain *et al.*, 1988; Scheidinger and Bain, 1995). Higher base flows since impoundment in both the Colorado River and the River Great Ouse have caused habitat quality of shorelines to decrease for YOY fish species (Garner, 1997; Converse *et al.*, 1998) owing to increased velocities and depths along shorelines. In the Sinnamary River, French Guiana, Ponton and Vauchel (1998) documented that before the Petit Saut Dam was in place, high flows during the rainy season inundated the mouth of a tributary and adjacent floodplains. After impoundment, velocities were significantly higher in the tributary mouth, floodplains adjacent to the tributary were not inundated and species richness and abundance of fishes decreased in the tributary mouth. Our findings also suggest that changes in flow regime in the Colorado River below Glen Canyon dam have affected seasonal flooding of the mouth of the Paria River and, hence, availability of one of the few remaining types of rearing areas for YOY flannelmouth sucker.

This study has shown that if conditions are optimal (i.e. no flash floods combined with pool formation), then YOY will rear in the mouth of the Paria River. Managers have no control over flash flooding, thus the focus must be on pool formation. However, one specific flow level in the Colorado River will not always cause pool formation, given the dynamic nature of the confluence of the Colorado and Paria rivers. Our results show that a high flow during the critical rearing period (when sediment input is likely low), combined with a lower flow during parts of the year when sediment input is typically high (generally as a result of summer monsoons and winter cold fronts) would be the best strategy. If a management goal is survival of YOY spawned in the Paria River, then an attempt should be made to further define the necessary combination of conditions that would create a pool. The criteria would be specific flow levels in the Colorado River, matched with a bed elevation in the mouth of the Paria. An alternative to attempting to define conditions necessary for pool formation would be to provide an artificial pool adjacent to or in the mouth of the Paria River (Larry Stevens, Grand Canyon Wildlands Council, Flagstaff, Arizona, personal communication). Although we lack control over the frequency of flash flooding, analysis of the long-term data set of flash flooding in the Paria River during the critical rearing period of YOY could provide management goals for the frequency with which successful rearing at the Paria River would be expected to occur. Although it is possible that flash flooding alone is the determining factor in survival of YOY flannelmouth suckers at the Paria River, the present data suggest the presence of a pool enhances YOY survival in this tributary mouth. We encourage continued monitoring of the Paria River to further explore the interplay between these two factors.

An alternative to providing spring and early summer rearing areas in the mouths of impounded tributaries would be to use a multi-level intake structure to warm Colorado River water released from Glen Canyon dam during the spring and summer (Valdez, 1990). In sections of the Colorado River, where spring/summer water temperatures are higher than in Glen Canyon ($14^{\circ}-16^{\circ}$ C versus $8^{\circ}-12^{\circ}$ C), YOY flannelmouth sucker do not rely solely on impounded tributary mouths to rear, but rear throughout the mainstem in available warm, slackwater areas (AGFD, 1996). Under conditions provided by the multi-level intake structure, larval and early juvenile flannelmouth sucker drifting out of the Paria River would no longer encounter ~ 10°C Colorado River water, in which their survival and growth is limited. In the lower reaches of Grand Canyon, where temperatures are higher (~ $14^{\circ}-16^{\circ}$ C, May–June), YOY flannelmouth suckers appear to be surviving better under the conditions provided by present dam operations (HDNR, 1995; AGFD, 1996). However, releasing warmer water from Glen Canyon Dam

during the spring and summer could potentially negatively affect native fishes in the Colorado River via interactions with non-native fishes presently far more abundant in central and western Grand Canyon. With warming temperatures, non-native fishes that may compete with or prey upon native fishes could potentially extend their range upstream to Glen Canyon Dam (Clarkson *et al.*, 1994). In addition, parasites found in endangered fishes in the warmer LCR could potentially expand their range into the mainstem Colorado River and other tributaries (Brouder and Hoffnagle, 1997; Hoffnagle *et al.*, 2000).

CONCLUSIONS

We found a strong year-class of YOY flannelmouth sucker in 1996, probably because of no occurrence of flash floods in the Paria River, coupled with the creation of an impounded rearing area in the mouth of the Paria River during the critical rearing period. We also captured 14 sub-adults, presumably from the 1994 year-class. In 1994, there were no flash floods during the critical rearing period, and a pool apparently formed at the mouth of the Paria River. Results of this study suggest that virtually no recruitment occurs when there are flash floods in the Paria River during the rearing period for YOY flannelmouth suckers, and that recruitment may be enhanced by pool formation at the tributary mouth.

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