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Source: *Copeia*, Vol. 2000, No. 1 (Feb. 1, 2000), pp. 238-244
Published by: American Society of Ichthyologists and Herpetologists
Stable URL: http://www.jstor.org/stable/1448256

Copeia, 2000(1), pp. 238–244

Late Season Reproduction by Big-River Catostomidae in Grand Canyon (Arizona)

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To estimate residency and population sizes, endemic fishes were marked and released during October 1998 at confluence of Colorado River and Havasu Creek (Grand Canyon National Park, Coconino County, Arizona). Ripe *Catostomus* (*Pantosteus*) discobolus females and newly hatched fry confirmed late season (i.e., early October) spawning by this species. Reproduction by other catostomids was inferred through physical examination of adult *C. latipinnis* and by capture of a possible *Xyrauchen texanus* larva. The latter is an endangered species not considered a constituent member of the endemic Grand Canyon fish community; its potential presence in Grand Canyon will influence adaptive management of endemic and introduced fishes. Results of ANCOVAs (with fishing effort as covariate) indicated numbers of aggregating *C. latipinnis* were significantly associated with flows in Havasu Creek but not those in the mainstem Colorado River. The ecology of big-river endemic fishes in Grand Canyon is clearly linked to tributary outflows, and environmental cues which elicit spawning of native fishes are discussed.

MOST freshwater fish species exhibit seasonal reproduction that peaks in spring or early summer (Matthews, 1998:426, and references therein). However, late summer or autumnal reproduction is often mentioned when life histories of western North American fishes are discussed (Koster, 1957:46; Moyle, 1976:215; Constantz, 1981:table 6). Individuals that spawn late are believed to be those who, for a variety of reasons, did not do so during the normal reproductive period. Thus, late season spawning is viewed as an adaptive strategy in western fishes, similar to that of adult longevity (Smith, 1981; Minckley, 1991; Douglas, 1993). Both may offer an evolutionary mechanism by which catastrophic environmental events that impact early life-history stages are counterbalanced. Yet, data that corroborate late season reproduction are scanty for these fishes, which in turn suggests only anectodal support for this adaptationist argument.

To our knowledge, late season reproduction remains unverified in the literature for large-river endemic fishes of western North America. Environmental cues that may elicit it are equally ill-defined. In this study, we assay endemic big-river fishes for evidence of late season spawning in the Colorado River at its confluence with Havasu Creek [Grand Canyon National Park (GCNP); Coconino County, Arizona]. We also test the hypothesis that densities of fishes were significandy related to flow characteristics of both river and creek.

MATERIALS AND METHODS

The Colorado River was accessed 0900 Sunday 27 September 1998 at Lee's Ferry [river km (= rkm) 0] and Havasu Creek (rkm 252.4) at 1400 Thursday 1 October (less than 100 hours in-transit; see Fig. 1B). River flows [daily maximums and minimums in cubic meters per minute (m^3min)] at Phantom Ranch (i.e., confluence of Bright Angel Creek and Colorado River: rkm = 87.8; Fig. 1B) were obtained from U.S. Geological Service (USGS; Tucson, AZ). A time differential of 12 hours is required for water to move from Phantom Ranch to Havasu Creek (Stevens, 1998:table 6). Thus, flows at confluence of Havasu Creek during our sampling were projected from those recorded at Phantom Ranch.

Havasu Creek is the second largest tributary in Grand Canyon, draining 7822 km^2 of the Coconino Plateau along the western edge of the south rim (Melis et al., 1996; see Fig. 1). It is perennial from 19 km upstream and has dams, pools, and waterfalls that, much like the Little Colorado River (LCR: rkm 99; Fig. 1B), result from travertine deposition over evolutionary time (Douglas and Marsh, 1996). However, access to Havasu Creek from the river is obstructed above 400 m by a series of natural travertine falls. Flows for Havasu Creek during the study period were again provided by USGS.

From 3–20 October inclusively, a 15.3 m × 1.8 m × 2.5 cm (inner mesh) × 30 cm (outer mesh) trammel net was fished within the alcove at confluence of creek and river (Fig. 1C). Fishing effort varied from 1.5–3.0 h/evening (average 2.07), and total effort was 39.25 net hours for the 18 days (Table 1). Captured fishes were identified, measured (TL to nearest mm) and sex determined. Big-river endemics greater

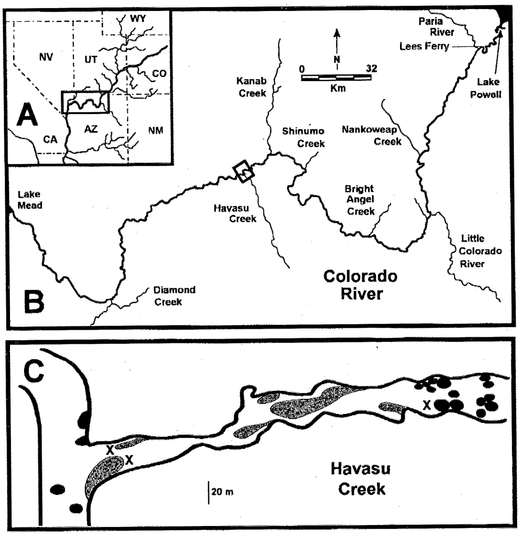

Fig. 1. Map of the Colorado River Basin in western North America. (A) Box circumscribing Grand Canyon; (B) Colorado River and its tributaries in Grand Canyon National Park (Coconino and Mohave Counties, AZ), with box circumscribing Havasu Creek confluence; (C) confluence of Havasu Creek with the Colorado River, Grand Canyon National Park (Coconino County, AZ). Black circles are rocks; stippled areas are gravel bars; "X" indicates those sites where catostomid fry were observed and sampled.

than 150 mm TL (= adults) were injected with passive integrated transponder (PIT) tags (Prentice et al., 1990) and released at capture point. For computational purposes, individual fishes tagged previously by other researchers were considered as tagged during the present study (as per Douglas and Marsh, 1996, 1998).

Cormack-Jolly-Seber (CJS) open population estimates were produced for *C. latipinnis* using POPAN-5 for Windows (A. N. Arnason, L. Baniuk, C. J. Schwarz, and G. Boyer, Dept. Computer Sci., Univ. Manitoba, Canada, 1998, unpubl.). Data for captures, flows, fishing effort, and population estimates were normalized and variances stabilized using Box-Cox-Bartlett transformations (procedure VERNORM of the R-Package vers. 3, P. Legendre and A. Vaudor, Univ. de Montreal, Canada, unpubl., 1991). The relationship between daily population estimates, total captures, and daily flows (both Colorado River and Havasu Creek) was examined using ANCOVA [Proc GLM; Statistical Analysis System (SAS), Cary, NC, unpubl., 1986], with fishing effort as covariate. Prerequisites and rationale for ANCOVA are discussed in Douglas and Marsh (1996).

Results

Maximum September flows for the Colorado River at Phantom Ranch averaged 30,582

Table 1. Daily Flow Data, Total Captures, Population Estimates, and Fishing Effort Recorded at Confluence of Colorado River and Havasu Creek, October 1998. DAY = day of month; CO CFS = Colorado River flows (cubic feet/sec.); CO M^3M = Colorado River flows (cubic meter/min.); H CFS = Havasu Creek flows (cubic feet/sec.); H M^3M = Havasu Creek flows (cubic meter/min.); FMS = *Catostomus latipinnis* catch; TOTAL= total catch; POP = population estimate for *Catostomus latipinnis*; EFFORT = fishing effort (in hours).

Day	CO CFS	C0 M^3M	H CFS	H M^3M	FMS	TOTAL	POP	EFFORT
03	15600	26504.4	58	98.5	52	51	—	3
04	14900	25315.1	58	98.5	5	2	242	1.5
05	13000	22087	58	98.5	5	3	18	1.5
06	15600	26504.4	58	98.5	8	6	32	1.25
07	15600	26504.4	58	98.5	8	7	98	2
08	15700	26674.3	59	100.24	6	4	64	2
09	15600	26504.4	59	100.24	4	4	27	2
10	15600	26504.4	59	100.24	8	7	9	2
11	14900	25315.1	59	100.24	4	3	3	2
12	13100	22256.9	59	100.24	4	1	0	1.5
13	15600	26504.4	60	101.94	7	5	0	2.5
14	15600	26504.4	60	101.94	1	0	—	2
15	15700	26674.3	60	101.94	4	3	0	2.5
16	15600	26504.4	60	101.94	1	1	0	2
17	15600	26504.4	60	101.94	4	2	0	2.5
18	14400	24465.6	60	101.94	4	3	0	2.5
19	12900	21917.1	60	101.94	1	0	—	2.5
20	15500	26334.5	61	103.6	1	4	0	2.5

m^{3}min (23,616–36,698), whereas minimum flows were 25,462 m^{3}min (22,767–29,563). For October, maximum flows averaged 26,192 m^{3}min (21,917–30,922), whereas minimum flows were 20,701 m^{3}min (18,349–25,145). Flows in Havasu Creek averaged 97 m^{3}min (95–109) in September and 102 m^{3}min (97–109) in October. Daily flows are in Table 1. Temperatures (14 Oct. at 1300) were recorded as follows: air (27 C); Havasu Creek (18.5 C); eddy at creek/mainstem interface (17 C); mainstem Colorado River (16 C).

Total captures were: 102 *C. latipinnis* [377–540 mm TL (mean = 460)]; 16 *C. discobolus* [65–344 mm TL (mean = 209)]; 11 *Oncorhynchus mykiss* [200–270 mm TL (mean = 229) with five (45%) exhibiting parr marks]; one *Salmo trutta* (285 mm TL); one *Gila cypha* (130 mm TL). Daily capture data are presented in Table 1.

Of 102 adult *C. latipinnis* captured, 82 (80%) were untagged, and 20 were recaptures. Eight (36%) of the latter were tagged during the current study; 14 were tagged previously. Individual *C. latipinnis* were often caught in close proximity to one another at or near the lead line (i.e., three individuals within 0.5 m at bottom of net). Many exhibited abraded anal fins; 70% were tuberculate. More fish were caught earlier in the sampling period than later. Population estimates for *C. latipinnis* are provided in Table 1. However, two (of 18) sampling periods were not estimated due to lack of captures.

Neither daily flows in the Colorado River ($P > 0.86$) nor fishing effort ($P > 0.87$) were significantly related to *C. latipinnis* population estimates. Havasu Creek flows were significantly related to *C. latipinnis* population estimates ($F = 12.94$, $P < 0.005$), whereas fishing effort was not ($P > 0.08$). In the latter analysis, interaction between fishing effort and Havasu Creek flows was also nonsignificant ($P > 0.45$). Nonsignificant ANCOVAs also resulted from comparing total captures of fishes to riverine flows ($P > 0.82$) and creek flows ($P > 0.31$).

On 7 and 11 October 1998, female *C. discobolus* expressed ova upon capture. On 9 October, unidentified fry were observed along the northwest wall of Havasu Creek alcove (Fig. 1C). Seven were preserved in 10% formaldehyde solution for later identification. Numerous additional larvae were subsequently noted (but not sampled) in various areas of the alcove during the remainder of the study (Fig. 1C). Six of seven (LFL 54438–54440, 54442–54444) were identified as *C. discobolus* (K. Bestgen and D. Snyder, Larval Fish Laboratory, Colorado State University, pers. comm.). The remaining individual larva (LFL 54441) had sparse pigmentation on head, dorsal, ventral, and lateral surfaces, no lateral pigmentation, little yolk for its size, and a relatively well-developed gut. This specimen was classified as *X. texanus*(?).

Discussion

Late season reproduction is often inferred from capture of tuberculate and/or ripe adults. For example, eight tuberculate (one ripe) male *C. discobolus* (158–278mm TL) were captured 13–22 September 1993 at confluence of Colorado and Little Colorado Rivers (Fig. 1B; M. E. Douglas and P. C. Marsh, unpubl.). Additionally, 18 tuberculate (12 ripe) male *C. latipinnis* (379–498mm TL) were taken at confluence of these rivers 12–21 October 1993. Two of the latter (and a single female) were either razorback sucker (*X. texanus*) or hybrids between it and *C. latipinnis* (Douglas and Marsh, 1998). Late season reproduction was inferred from both examples.

Presence of tubercules is a characteristic insufficient for diagnosis of incipient or ongoing reproduction. Minckley et al. (1991:319) noted male *X. texanus* in Lake Mohave (AZ) possessed tubercles in all months of the year except July through September. Expression of milt by males is also deemed a poor indicator of ongoing or recent spawning, whereas presence of females with expressible ova is a positive indicator (various agency reports cited in Minckley, 1996:57).

A more direct method of documenting late season reproduction is presence of recently hatched fry or young larvae. Branson et al. (1960) captured such as evidence of late season (i.e., Aug.) spawning by *C. bernardini* (or a similar form) in the Rio Magdalena (Sonora, Mexico). Likewise, presence of larvae was used by Moyle (1976:215) as evidence of mid-August reproduction by *C. occidentalis* in the Russian River (California). Other western fishes also exhibit extended reproductive periods. Minckley (1996) evaluated hatching dates for *G. cypha* larvae over a 10-year period (1980–1990) in the Colorado River of Grand Canyon. Reproduction occurred primarily March through early summer but also as early as February and as late as October.

At Havasu Creek, both capture data and inference indicated two catostomid species engaged in autumnal reproduction during 1998. Female *C. discobolus* were captured running ripe and *C. discobolus* fry were subsequently collected within the alcove. The contention that other catostomids were involved in late season reproduction is supported by identification of a captured larva as *X. texanus*(?). The questionable status of this larva is actually a much stronger endorsement than it appears. In previous studies, larvae initially identified as *X. texanus*(?) by the CSU Larval Fish Laboratory were subsequently verified as such through analysis of mtDNA (K. Bestgen, pers. comm.). Thus, the identification of the larva in this study reflects a conservative but rigorous approach. It also sparks considerable interest in that *X. texanus* is not considered a constituent member of the indigenous Grand Canyon fish community (Douglas and Marsh, 1998).

There is also a possibility that the larva is a hybrid between *X. texanus* and *C. latipinnis*. Indeed, such hybrids have been recorded in the Marble Canyon area (reviewed in Douglas and Marsh, 1998:920–921). This aggregation averages 30 adults, is predominantly male, and frequents the LCR in spring, approximately 2.2 rkm above its confluence (see Fig. 1B). However, presence of either adult *X. texanus* or hybrid/backcrossed *X. texanus/C. latipinnis* at Havasu Creek remains speculative. In addition, larval morphologies of hybrid catostomids, particularly those in the Colorado River system, are relatively unknown (K. Bestgen, pers. comm.). Thus, an analysis of cytoplasmic or nuclear DNA would be needed to correctly identify a larva as either hybrid or backcrossed. Such an analysis could also be used to test the hypothesis of concurrent late season reproduction by catostomids at Havasu Creek alcove.

Reproduction by more than one catostomid species at Havasu Creek also has inferential support. In the lower Paria River (rkm 25; Fig. 1B), Weiss et al. (1998:424) observed small groups of male *C. latipinnis* (i.e., 2–4 individuals per group) congregating in spring directly over (or immediately peripheral to) gravel spawning sites. Of all observed matings, 59% involved but two males, each adjacent and posterolateral to a single female. An additional 12% involved but three males. As oviposition began, females would often move forward approximately one meter while on the gravel bed as males pressed tightly to her, cupping their anal fins directly toward her vent. Oviposited eggs were avidly predated upon by *O. mykiss* and *S. trutta*, both of which were caught in this study concomitant with *C. latipinnis*. Additionally, both sexes of *C. latipinnis* exhibited tuberculation and abraded anal fins; all were caught tightly clustered in duos and trios at the bottom of the net. These observations suggest spawning activities by *C. latipinnis* on the gravel beds of Havasu Creek outflow.

Environmental cues that elicit spawning are unclear. Historically, mainstem flows are believed instrumental in prompting aggregations of riverine fishes at tributary mouths (Minckley, 1996) and may in fact be influential in cueing their reproduction. Several upper basin endemic fish species incorporate flow pulses into their reproducive cycle. *Ptychocheilus lucius* migrates on the ascending limb of the spring hydrograph (Tyus, 1990; Osmundson and Burnham, 1998) yet spawns on the descending limb (Tyus, 1991), as does *G. cypha* (Karp and Tyus, 1990; also agency reports cited in Minckley, 1996:55). However, *X. texanus* spawns on the ascending hydrograph (Tyus, 1987; Tyus and Karp, 1990; Modde and Irving, 1998). Spawning may be a response to rearranged gravel or other substrates on bars and stream bottoms. Elevated flows would shift substrates and purge interstitial spaces of accumulated detritus and silt, thus promoting microcurrents within the gravel necessary for successful incubation of eggs (as per Osmundson and Burnham, 1998:967). Weiss et al. (1998) noted that fertilized eggs of *C. latipinnis* in the Paria River fell within interstitial spaces of gravel spawning bars.

In the lower basin Colorado River, the descending hydrograph could also be a natural cue for late season reproduction. Here, streams are often characterized by late summer floods induced by monsoon rains. John (1963, 1964) observed both spring and late summer reproduction by *Rhinichthys osculus* inhabiting intermittent streams of the Chiricahua Mountains (Arizona). He argued spring reproduction was stimulated by an apparent combination of rising temperatures, increasing day lengths, and flowing waters from snowmelt. However, late season reproduction was cued solely by flowing waters from monsoon rains (see also Minckley, 1973: 131–132). Over the last century, flooding in Havasu Creek has occurred most frequently in summer; indeed some of these were catastrophic (Melis et al., 1996). Minckley (1996) examined the hypothesis that *G. cypha* spawns on a descending hydrograph in the LCR. To do so, he back-calculated dates of hatching from larvae collected over a 12-year period (1977–1981 and 1984–1990). As with the mainstem, estimated spawning in the LCR ran from early February through October. Yet no consistent relationship was observed when calculated spawning dates were superimposed onto LCR flow records (Minckley, 1996:fig. 10). Although timing of flow events has been linked with successful reproduction in some upper basin endemic fishes, no apparent relationship has been established for onset of reproduction in *G. cypha* from the lower basin.

Similarly, on a typical year in the Paria River

(Fig. 1B), *C. latipinnis* will spawn and larvae emerge on a descending (or at best stable) hydrograph, whereas in Bright Angel Creek (rkm 165; Fig. 1B) the same is accomplished on an ascending hydrograph (Weiss et al., 1998). Spawning in *C. latipinnis* thus appears temporally synchronous within two Grand Canyon tributaries separated by 140 rkm. Yet, these tributaries exhibit dissimilar temperature profiles and asynchronous hydrographs. This suggests either additional factors other than temperature and discharge are important as reproductive cues or that temperature and discharge are much less important than originally thought.

Reproductive activities and the cues that elicit them are often difficult to ascertain for endemic big-river fishes. Longer term studies (like those of Douglas and Marsh, 1996, 1998) are clearly of greater value in answering these questions if for no other reason than to accommodate the recognized longevity of these fishes (Douglas and Marsh, 1998:920 and references therein). In this sense, the current study was not of sufficient duration to formulate broad generalizations with regard to fish aggregations and flow characteristics. However, the significant relationship between population estimates of *C. latipinnis* and flows in Havasu Creek, and the concomitant lack of significance between these estimates and riverine flows, is an important starting point for future work. Similar results (as well as data regarding onset of reproduction) may reside within agency-generated annual and final reports which are unpublished (i.e., "gray") and thus unavailable to the larger scientific community. Minckley (1996:03), for example, stated that 80% of data reported for *G. cypha* were in gray literature.

The analytical approach in the current study is exemplary in that population estimates and overall catches were cast as hypotheses against which mainstem and tributary flows were tested. To date, most studies comparing fish densities and flow regimes have instead been posthoc. In actuality, this may have more to do with process than philosophy. Many rivers in western North America are now regulated, and a natural hydrograph is no longer apparent. The spring hydrograph that historically provided numerous cues to indigenous fishes (as above; also Modde et al., 1996) has been absent in Grand Canyon for 20+ years. Now, flood events are temporally erratic and on a much reduced scale. Ascending and descending hydrographs occur daily. How these changes affect big-river endemic fishes, who have coadapted their behaviors over evolutionary time to a predictive seasonal hydrograph, is more than a moot question. Effects may be more subtle than originally thought. Chart and Bergerson (1992) indicated movements and breeding migrations of *C. latipinnis* in the upper basin White River did not change appreciably in spite of dam construction. Spawning movements of *C. latipinnis* still occur into the LCR (Douglas and Marsh, 1998), the Paria River, Bright Angel Creek (Weiss et al., 1998), and Havasu Creek (this study). Yet, spawning persistence does not always equate to spawning success. *Xyrauchen texanus* continues to spawn and produce abundant larvae in Lake Mohave (a lower basin Colorado River reservoir), yet juveniles are virtually unknown in this system and recruitment is undetected (Minckley et al., 1991; reviewed in Dowling et al., 1996). Before a behavioral baseline can be established within the context of an altered ecosystem, spawning aggregations of big-river endemic fishes must be monitored consistently and over longer durations. A similar argument was made by Douglas and Marsh (1996:25) regarding reproductive response of *G. cypha* to dam-induced conditions in the mainstem Colorado River.

Population estimates for *C. latipinnis* in this study were eightfold to 10-fold less than those for a comparable period six to eight years earlier at the LCR (Douglas and Marsh, 1998:appendix 1). Some discrepancy is explained by the five-year duration of the LCR study, which permitted a larger pool of tagged fish to accumulate. In the present study, only 7.8% ($n = 8$) of tagged *C. latipinnis* were recaptured, which may be attributable to a chronic lack of long-term monitoring at Havasu Creek. Densities at Havasu Creek may also be damped when compared to other tributaries. Although it is the second largest tributary in Grand Canyon, Havasu Creek watershed is 6% of that recorded for the LCR. Its confluence is thus narrower and more canyon-bound (Fig. 1C), which in turn restricts access by fishes at low-to-moderate mainstem flows.

Results of this study underscore the premise that long-term monitoring of big river endemic fishes in Grand Canyon should focus primarily at tributary confluences (Douglas and Marsh, 1998; Weiss et al., 1998). Adult fishes are more easily sampled in these areas, as are early life-history stages and coexisting predators. However, the research philosophy underpinning conservation and management of endemic fishes in Grand Canyon is driven by operation of Glen Canyon Dam. Tributaries do not fit within this conceptual picture and thus their influence on native fish population dynamics and recruitment will remain underemphasized.

ACKNOWLEDGMENTS

Research herein was conducted under U.S. Fish and Wildlife Endangered Species permit PRT-797129 to Arizona State University, Arizona Game and Fish Department (AGFD) permit SP775718 to MED, Grand Canyon National Park/Glen Canyon National Recreation Area permit 1996-0206-01 to MRD/MED, and Arizona State University Institutional Animal Care and Use Committee (IACUC) permit 98-456R to MRD/MED. Travel on the Colorado River in Grand Canyon was conducted under auspices of a Grand Canyon National Park (GCNP) River Use Permit. We particularly thank J. Behan (Grand CN Monitoring and Research Center), L. Niemi [Canyon Supply and Inflatables (CS&I)], W. Persons (AGFD), and R. Winfree (GCNP) for numerous considerations, without which our research could never have been initiated. N. Niemi (CS&I) was an able and stout-hearted guide, while S. Francisco (USGS) facilitated retrieval of flow data. Larval fishes were identified by K. Bestgen and D. Snyder (CSU Larval Fish Laboratory). Manuscript critiques were provided by H. Tyus and an anonymous reviewer. The rafting community (private, commercial, and research) offered good cheer and many helpful assists on the river. We recognize their numerous contributions and thank them all.

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