

Population and Survival Estimates of *Catostomus latipinnis* in Northern Grand Canyon, with Distribution and Abundance of Hybrids with *Xyrauchen texanus*

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Population sizes, movements, and potential hybridization were examined for two indigenous Colorado River fishes, *Catostomus latipinnis* (flannelmouth sucker) and *Xyrauchen texanus* (razorback sucker) in the Little Colorado River (LCR) of Grand Canyon National Park and the Navajo Nation (Coconino County, AZ). *Catostomus latipinnis* is a "species of concern," and *X. texanus* is federally listed as endangered. Within Grand Canyon, both occur in greatest abundance in the LCR and its confluence with the mainstem Colorado River. During a 50-trip period (1 July 1991-27 June 1995), 2619 unique individuals (> 150 mm TL) were evaluated, consisting of 2578 *C. latipinnis* and 41 putative *X. texanus/C. latipinnis* hybrids. Cormack-Jolly-Seber estimates (adjusted for effort) were calculated by trip for *C. latipinnis* and ranged from 1591-5214 (average 2507). Seasonal estimates indicated peak movements in spring and autumn (especially the former). During 1991-1993, survival estimates of *C. latipinnis* were stable over all adult size classes (defined by overall body size) but decreased within larger size classes during 1994. Population estimates remained stable during the four years of the study. It is unknown whether *C. latipinnis* is at carrying capacity within Grand Canyon. A population estimate of putative *X. texanus/C. latipinnis* hybrids ranged from 8-136 (average 30) for 26 (of 48) trips. *Xyrauchen texanus* is a transitory member of Grand Canyon's indigenous fish community, moving through the canyon to more viable habitat up- or downriver. This aspect of its life history is now curtailed by Glen Canyon Dam, at the northern terminus of Grand Canyon.

THE Colorado River basin comprises nearly 650,000 km² of the most arid terrain in western North America. It is composed of several divisions (Minckley et al., 1986): the Colorado and Green Rivers (and tributaries) form a distinct zoogeographic segment in the upper basin because they terminated in closed basins prior to Pliocene. A "contemporary middle segment" straddles both upper and lower basins of the Colorado River [demarcated at Lee's Ferry by the Colorado River Compact of 1922 (Martin, 1989:25)]; it is composed of the White, Virgin, and Little Colorado Rivers (and parts of the Bill Williams drainage). The lowermost segment consists of the Gila River and the remaining portion of the Colorado River. Major changes have occurred in these segments as a result of dam construction and chronic dewatering for agriculture and urban development (Fradkin, 1984). The 2400 km of riverine habitat formerly occupied by large-river fishes has been fragmented into 965 km (Miller, 1982). A corollary to this urbanization and agricultural development is a significant reduction of fish biodiversity in southwestern United States (fig. 1c of Dobson et al., 1997).

Minckley et al. (1986:580) grouped endemic

Colorado River fishes into three major categories. His "big-river forms" range throughout the system in larger streams and are composed of seven species: four cyprinids (*Gila robusta*, *G. cypha*, *G. elegans*, *Ptychocheilus lucius*) and three catostomids [*Catostomus latipinnis*, *C. (Pantosteus) discobolus*, *Xyrauchen texanus*]. The first of the cyprinids and the first two catostomids are "species of concern" (U.S. Fish and Wildlife Service, 1996); the remainder are endangered (U.S. Fish and Wildlife Service, 1994). *Catostomus latipinnis* and *X. texanus* are the subject of this report.

Catostomus latipinnis was historically distributed in all moderate-to-large rivers throughout the Colorado River basin (Minckley and Holden, 1980). Today, it is essentially extirpated from the lower basin; reintroduction has been attempted by Arizona Game and Fish Department below Lake Mead (W. L. Minckley, pers. comm.), but *C. latipinnis* does poorly in impoundments (Minckley, 1973).

The ecology of *C. latipinnis* is relatively unknown (McAda and Wydoski, 1985). It typically inhabits pools and deeper runs of rivers and often enters mouths of small tributaries (Minckley and Holden, 1980). In the Yampa River, ripe

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adults congregate at upstream ends of cobble bars to spawn (McAda and Wydowski, 1985). Postreproductive adults remain in flatwater or eddies near margins of strong currents, generally in water at least 1 m deep. Young often congregate downstream or on riffles and along shoreline of flatwater reaches. Chart and Bergersen (1992) suggested adult movements are size-related, with larger individuals more sedentary than those 300–400 mm TL. They also suggested that adult *C. latipinnis* occupy a definable home range. Individuals are considered adult at 300–400 mm TL (Minckley and Holden, 1980); maximum size recorded in this study was 661 mm TL.

Xyrauchen texanus was also historically distributed throughout the Colorado basin. It was common in the lower basin (Kimsey, 1957) and in reservoirs created by main-channel dams. It was uncommon and declining in the upper basin by 1950 [Hubbs and Miller, 1953; Vanicek, 1967 (citing early 1960s agency reports)]. Holden (1973) collected *X. texanus* only from middle and lower sections of the upper basin and again noted its scarcity. It was also recorded as sparse within Grand Canyon and areas immediately north. Smith (1959) called *X. texanus* "... rare, or possibly just difficult to collect in Glen Canyon, since extensive collecting turned up only two immature (i.e., YOY) specimens" (Glen Canyon, immediately upriver from Grand Canyon, is now inundated by Lake Powell). Many researchers (Minckley et al., 1991:310; this study) contend *X. texanus* was never abundant in Grand Canyon, regardless of its current conservation status.

Genetic variability within remnant Colorado River populations of *X. texanus* is distributed in a north-south cline (Dowling et al., 1996a) similar to that recorded for abundance. More northern populations (i.e., upper Green and Yampa Rivers, upper Colorado River) exhibited reduced variability, whereas the most extant southern population (i.e., Lake Mohave, AZ) was highest. Geographically intermediate populations (i.e., Lakes Mead and Powell) were themselves intermediate in haplotype diversities (with Powell populations greater than Mead). Over evolutionary time, this species was panmictic throughout its range.

Hybrids between *C. latipinnis* and *X. texanus* occur in small numbers and have long been recognized. Jordan's (1891) description of *X. uncomphgre* was based on a *C. latipinnis* × *X. texanus* hybrid. Hubbs and Miller (1953) examined eight putative hybrids (two from upper Colorado and six from upper Green Rivers) and noted morphological intermediacy in lateral-

line scale count, and a much abbreviated but distinct nuchal keel. Hybrid intermediacy was also reported by Vanicek (1967:45), who subsequently collected 16 putative hybrids from the Green River following closure of Flaming Gorge Dam (Vanicek et al., 1970). Holden (1973) collected 40 putative hybrids and 53 *X. texanus* throughout the upper basin, usually associated with one another in quiet backwater areas. Hybrids in upper Green and lower Yampa Rivers were attributed by Tyus and Karp (1990) to an abundance of *C. latipinnis*, a paucity of *X. texanus*, and a temporal/spatial overlap in their spawning. Smith (1992b) listed hybrids of these two species as occurring broadly across drainages.

The present study was a four-year, localized study with three goals: to estimate population numbers and survival probabilities of *C. latipinnis* and *X. texanus* within the Little Colorado River (LCR) area of Grand Canyon; to evaluate their seasonal and yearly movement patterns within that area; and to determine relative abundance and distribution of potential hybrids.

MATERIALS AND METHODS

Study area and data collection.—Our study was confined to the LCR and its confluence with the mainstem Colorado River, 99 river km (RKM) below Glen Canyon Dam. The study area, in both Grand Canyon National Park (GCNP) and the Navajo Nation (Coconino County, AZ), is described and mapped in Douglas and Marsh (1996).

Base camps were established in the LCR gorge at 0.6, 3.1, and 10.8 RKM upstream from the confluence. Biologists worked at each camp during 49 six- to 14-day trips at approximately monthly intervals from July 1991 to June 1995 (Appendix). Fishes were captured with hoop and trammel nets (the latter primarily at confluence; net dimensions provided in Douglas and Marsh, 1996). Effort was recorded as number of net-hours fished. All captured fishes were identified, measured (TL to nearest mm), weighed (nearest g), and sex determined. Big-river endemics greater than 150 mm TL (= adults) were injected with passive integrated transponder (PIT) tags (Prentice et al., 1990) and released near points of capture.

Capture matrices.—Adults were classified as newly tagged fish, recaptured fish, or those with old tags. The first group represented fish PIT-tagged by Arizona State University (ASU) personnel at time of capture. The second group

contained fish captured by ASU personnel but already PIT-tagged; PIT-tag implanted by any of several agencies or research groups, including ASU. The third contained fish tagged previously by other researchers with either a Carlin or floy-tag, and subsequently PIT-tagged by ASU personnel; old tags were removed and retained. For purposes of this report, fishes in all three capture groups start their capture histories when first handled by ASU personnel. Therefore, fish previously PIT-tagged by other groups or agencies ("recaptured") were considered "tagged" by ASU personnel at recapture.

All three categories were merged and sorted for a given species by PIT-tag number. Individuals then were condensed into a capture-history (CH) matrix (Burnham et al., 1987), where each individual (i.e., each unique PIT-tag) comprised a single row and each of the 49 sampling periods a column. If an individual was captured (or recaptured) during a given sampling period, that respective column was scored "1," otherwise "0." Thus, an individual's capture and all subsequent recaptures were represented as a row vector in the CH-matrix.

The CH-matrix was sorted two different ways for analysis. Capture histories were first compiled by season and year (where winter = Dec., Jan., Feb.; spring = March, April, May; summer = June, July, Aug.; and autumn = Sept., Oct., and Nov.). In all, 16 seasons were represented (four each over four years). Individual *C. latipinnis* (≥ 150 mm TL) were also compiled into nine 50 mm (TL) size classes.

Population estimates.—Cormack-Jolly-Seber (CJS) population estimates were generated by trip ($n = 49$), season ($n = 16$; $n = 4$), and year ($n = 4$). Trips were occasionally combined due to lack of recaptures. These were grouped with the trip immediately preceding or following so as to maintain continuity by season; trips that were grouped received the same estimate. For *X. texanus* and hybrids, CJS estimates were generated for 26 of 49 trips, due to zero sample sizes for the remaining periods (Appendix). For *C. latipinnis*, only four trips lacked recaptures.

Sampling effort and population estimates were transformed to common logarithms. ANCOVA was used to test for significant differences among and between seasons, and between years, with effort as covariate. Because of the manner in which trips were partitioned into seasons, and the staggered initiation and completion of the project (i.e., July 1991–June 1995), only years 1992, 1993, and 1994 could be tested in pairwise comparisons. The rationale and prerequisites for ANCOVA were discussed

in Douglas and Marsh (1996). Population estimates, standard deviations, and 95% confidence limits were generated for the entire LCR rather than by river reach (as defined in Douglas and Marsh, 1996). Open estimates (via POPAN-4 for Windows, A. N. Arnason, L. Baniuk, C. J. Schwarz, and G. Boyer, Dept. Computer Sci., Univ. Manitoba, Canada, 1995, unpubl.) were used exclusively, in that demographic closure was precluded due to the temporal span over which sampling was conducted.

Annual survival probabilities (adjusted for effort) were calculated by size class for *C. latipinnis*, again using POPAN-4. Probabilities could not be calculated for 1995 in that capture/recapture data from 1996 were required. Survival probabilities were not calculated for *X. texanus* and hybrids due to low sample sizes.

Hybrid identification.—The presence of a nuchal razor was used as a criterion for designating an individual as hybrid. Of the 41 individuals so identified, 12 were examined genetically via restriction endonuclease analysis of mtDNA (Dowling et al., 1996a:545). Nine of these were also assayed electrophoretically at five diagnosable loci scorable from muscle tissue (D. G. Buth, pers. comm.).

RESULTS

Catostomus latipinnis.—We captured and PIT-tagged 2179 *C. latipinnis*, recaptured 1550, and replaced carlin/floy tags with PIT-tags on another 10. These 3739 individuals were collapsed into a CH-matrix of 2578 entries (where each unique PIT-tag was represented but once). Individuals often were recaptured several times during the study (maximum = 12). Cormack-Jolly-Seber population estimates (adjusted for effort over all 49 trips; Appendix) indicated greatest abundance in early summer 1994 [5214 individuals, trips 36 (± 587) and 37 (± 575)]. Smallest estimates occurred in winter 1992/spring 1993 (1591 individuals, trips 20 (± 260) and 21 (± 265); Fig. 1).

Captures varied by season (Appendix; Table 1), by size class (Table 2), and by effort [total effort = 401,367 net-hours; trip mean = 8191 net-hours (± 500)]. Interaction between population estimates and sampling effort was not significant across seasons. A standard ANCOVA indicated population size of *C. latipinnis* varied significantly over the 16 seasons [$F = 2.44$; $df = 16$; $P < 0.01$; Proc. GLM ANCOVA, Statistical Analysis Systems (SAS, vers. 6.08), Cary, NC, 1989, unpubl.; Fig. 2].

Pairwise linear contrasts of population esti-

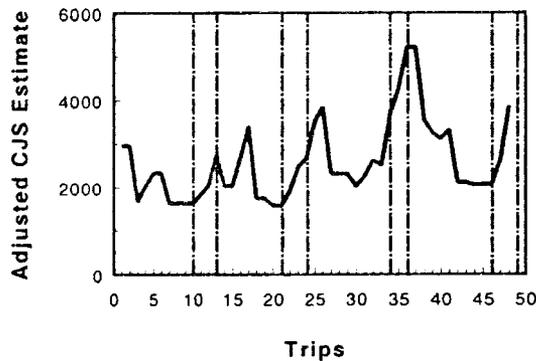


Fig. 1. Cormack-Jolly-Seber population estimates (adjusted for effort) for adult (> 150 mm TL) *Catostomus latipinnis* by sampling trip in the Little Colorado River (Navajo Nation, Coconino County, AZ). Trip 49 not plotted due to close of project. Vertical lines bracket March–April–May (i.e., spring) of 1992, 1993, 1994, and 1995.

TABLE 1. INDIVIDUAL *Catostomus latipinnis* GROUPED BY SEASON. Winter = December, January, February; spring = March, April, May; summer = June, July, August; and autumn = September, October, and November. Year refers to year-of-capture.

Number	Season/year	<i>C. latipinnis</i>
01	Summer 1991	236
02	Autumn 1991	166
03	Winter 1991	65
	Total 1991	467
04	Spring 1992	75
05	Summer 1992	125
06	Autumn 1992	171
07	Winter 1992	1
	Total 1992	372
08	Spring 1993	131
09	Summer 1993	250
10	Autumn 1993	73
11	Winter 1993	139
	Total 1993	593
12	Spring 1994	255
13	Summer 1994	323
14	Autumn 1994	218
15	Winter 1994	102
	Total 1994	898
16	Spring 1995	248
	Total 1995	248
	Total	2578

TABLE 2. INDIVIDUAL *Catostomus latipinnis* GROUPED FROM RESPECTIVE CAPTURE-HISTORY MATRICES BY SIZE CLASS.

Size class	Total length	<i>C. latipinnis</i>
1	150–200	258
2	201–250	271
3	251–300	251
4	301–350	184
5	351–400	345
6	401–450	417
7	451–500	403
8	501–550	314
9	551–600+	135
	Total	2578

mates over four seasons revealed two of six comparisons were significant: summer versus autumn ($F = 4.41$; $P < 0.04$) and autumn versus spring ($F = 4.86$; $P < 0.03$). However, there were no significant differences among years with regard to overall population size.

Survival probabilities.—During 1991–1993, survival rates for *C. latipinnis* were relatively uniform over size classes 1–4 (Fig. 3). Steep decreases occurred in size classes 2 (201–250 mm TL) and 4 (301–350 mm TL), whereas a steep increase was noted in size-class 3 (251–300 mm TL). A generally positive trend occurred from size-classes 5 through 9 (351–600+ mm TL). However, survival in 1994 was lowest of the study for size-classes 4 and 6–8.

Xyrauchen texanus/Catostomus latipinnis hybrids.—Forty-one *X. texanus/C. latipinnis* hybrids were

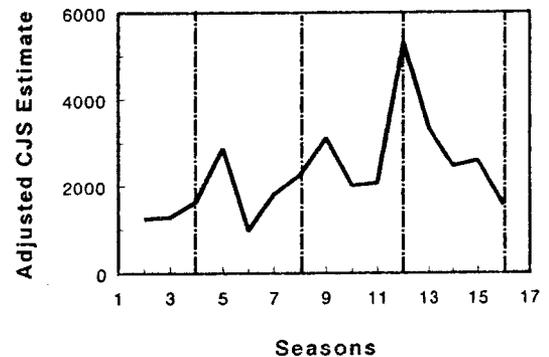


Fig. 2. Cormack-Jolly-Seber population estimates (adjusted for effort) for adult (> 150 mm TL) *Catostomus latipinnis* by season ($n = 1-16$) in the Little Colorado River (Navajo Nation, Coconino County, AZ). Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

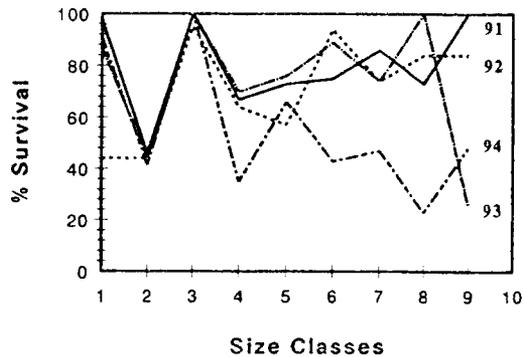


Fig. 3. Yearly survival probability by size-class for adult *Catostomus latipinnis* (> 150 mm TL) in the Little Colorado River (Navajo Nation, Coconino County, AZ). Probability values are for years 1991–1994.

reported, based upon morphological identification at different capture dates. The 41 individuals were recaptured a total of 60 times: a single individual was recaptured seven times; two individuals were recaptured five times; five individuals four times; eight three times; eight two times; and 17 but once. Additionally, 85% (35/41) were male, and 12% (5/41) were female (one individual was not sexed). This suggests males may be more vagile or more numerous than females. Also, males were expressing gametes in 46% (38/82) of captures, whereas 79% (65/82) were tuberculate. Twenty-four individuals had multiple (i.e., > 1) captures and, thus, at least two chances for sex determination. Only two contradictions were noted out of 76 opportunities (3%).

Mitochondrial DNA was evaluated in 12 of 41 putative hybrids. Seven of these (58%) had *X. texanus* mtDNA (T. E. Dowling, pers. comm.). Five of the seven were electrophoretically identified as hybrids, whereas two were not evaluated (D. G. Buth, pers. comm.). Of five individuals with *C. latipinnis* mtDNA phenotypes, three were of hybrid origin, one was pure *C. latipinnis*, and one was electrophoretically unscorable. Thus, in synopsis, nine (of 12) individuals with morphologies suggesting hybrid origin were evaluated electrophoretically and with RFLP analysis of mtDNA. Eight of the nine (89%) were of hybrid origin, whereas one was pure *C. latipinnis*. None of the eight was an F_1 hybrid. Instead, they were backcrossed to *C. latipinnis* in varying degrees (ranging from 60–90%). The one individual judged 60% *C. latipinnis* appeared to be an $F_1 \times F_1$ hybrid (D. G. Buth, pers. comm.).

Population estimates for *X. texanus/C. latipinnis* hybrids over 26 of 49 trips (Appendix) were unadjusted for effort and consistently small

(08–136; mean = 30). Captures varied across seasons: 46% (43/94) occurred in spring; 32% (30/94) in autumn; 12% (11/94) in summer; and 10% (10/94) in winter. Clearly, the fish were more vulnerable to capture in spring and autumn, presumably due to greater movement or use of shallower habitats.

Captures were occasionally numerous. Six tuberculate males were captured with *C. latipinnis* in November 1991, 3.1 km above the LCR confluence. None was expressing gametes; an individual captured at the confluence two days earlier was. Eight tuberculate males were similarly captured with *C. latipinnis* in April 1992, 3.01 km above the confluence (one was expressing gametes). Likewise, 11 tuberculate males were captured with *C. latipinnis* April 1995, 2.98 km above the confluence. All were expressing gametes. Overall, 56% (53/94) of captures occurred approximately 3 km (or greater) above the confluence (one occurred almost 11 km above). Average capture distance above confluence was 2.2 km.

DISCUSSION

Catostomids are primarily benthic, and the basal stock is a deep-bodied fish of large, low-gradient rivers. A major adaptive event in the radiation of this family was gradual diversification of mountain suckers (Smith and Koehn, 1971; Smith, 1992a). The two study species of this report are members of the subfamily Catostomini and are part of an indigenous but declining Colorado River fish community.

Catostomus latipinnis.—In Marble and Grand Canyons, Carothers and Minckley [S. W. Carothers and C. O. Minckley, U.S. Bureau of Reclamation, Final Rpt., 1981, unpubl. (hereafter USBR, 1981, unpubl.)] caught ripe *C. latipinnis* from March–May (= spring) at the mouth of the Paria River and other low-gradient streams. Postreproductive adults remained in these habitats through summer but returned to mainstem in winter when temperature equilibrated between tributary and mainstem (Suttkus and Clemmer, 1979). Our results concur with and extend these observations. In the LCR, greatest numbers of *C. latipinnis* occurred either in midsummer (1993, 1994) or early autumn (1992). Populations gradually increased in number before peaking significantly in late spring and then declining significantly into autumn/winter. A smaller population peak often occurred in late summer/early autumn as an apparent reproductive response to late summer rains.

Our consistent annual population estimates

are particularly encouraging for a species of concern. However, these results may be misleading; the adult population may appear numerically steady because adults are long-lived, rather than because of extensive recruitment. This was the situation with *X. texanus* in Lake Mohave, Arizona, where adult numbers were steady for more than a decade (Minckley, 1983; Minckley et al., 1991; Dowling et al., 1996b). Despite abundant seasonal reproduction, a chronic lack of recruitment (Horn, 1996) will inexorably reduce the Lake Mohave *X. texanus* population to extinction unless effective intervention occurs (as per Dowling et al., 1996b:125–126).

Longevity is a recognized and effective adaptive strategy for catostomids in western North American rivers (Smith, 1981; Douglas, 1993). It provides a mechanism by which vagaries of the environment are counterbalanced over evolutionary time. Adults may miss numerous sequential spawning seasons due to a variety of physiological or environmental reasons (e.g., lack of accrued fat resources; shortage of suitable breeding habitat due to flow characteristics; restricted access to tributaries; etc.). If reproduction does occur, prolonged drought and concomitant low-water may restrict development of backwater nursery habitat. Other factors known to decimate a year class (Horn, 1996) are extreme predation, exogenous nutrient depletion, and entrainment of larvae within current. The species maintains itself because probability of achieving an eventual abundant year class is enhanced due to adult longevity.

This adaptation can also foster benign neglect by managers because potential for swift recovery in these long-lived fishes is deemed great. But adult senescence can be rapid and drastic (as noted in Lake Mohave *X. texanus*). Thus, it is important not only to establish a baseline for adult longevity but also to define survival rates according to age. Studies that attempt to determine age of individual catostomids often have conflicting results, and suitability of biological materials used in these analyses is questioned. McAda (1977) and McAda and Wydoski (1985) used scales to ascertain an age of eight or nine years for upper basin *C. latipinnis*. Other researchers (Usher et al., 1980; Minckley, 1983; McCarthy and Minckley, 1987) argued that the regenerative capability of scales make them inappropriate media from which to determine maximum age. In addition, scale annuli are often unreadable after the first few years of life, a condition which adds to unreliability of (and elevated variance in) this medium. Usher et al. (1980) and Carothers and C. O. Minckley (USBR, 1981, unpubl.) used opercular bones to

estimate a maximum age of 10 years for *C. latipinnis* in Marble/Grand Canyons. Minckley (1991) suggested these were underestimated. His otolith data (unpubl., 1991) estimated Green River *C. latipinnis* (TL = 530 mm) at 30 years, whereas Scopettone (1988) judged five individuals (TL = 530–590 mm) from the same area at > 17 years of age.

Given inherent limitations of scales and opercular bones to age big-river endemic fishes, we grouped individuals for analysis by overall body length. This offers a simple and repeatable mechanism, even though cut points are recognizably arbitrary. With this approach, we noted reductions in survivability among the largest size classes (i.e., 301–600+ mm TL). Yet, during this period, population estimates showed an overall increase. Predation is an improbable cause for a reduction in survivability because the decline occurred in larger fish. Alternative hypotheses that appear more viable include natural variability in long-term movement patterns of large adults and senescence. Neither was testable within the temporal framework of our study.

Xyrauchen texanus and hybrids with *Catostomus latipinnis*.—The first record of *X. texanus* in Grand Canyon was by an angler in 1944 at Bright Angel Creek (RM 87.8; National Park Service files; cited in S. W. Carothers and C. O. Minckley, USBR, 1981, unpubl.). A single specimen was caught in 1963 somewhere in the region from Paria River confluence (RM 1) to Lee's Ferry (RM 0) [AZ Game and Fish records, cited in Carothers and Minckley, USBR, 1981, (unpubl.); Minckley et al., 1991; SWCA Inc., Grand Canyon Data Integration Project, Final Rpt., U.S. Bureau of Reclamation, 1997]. In 1978, a gravid female was captured (and two others observed) in the Paria River 100 m above its confluence with the mainstem (Minckley and Carothers, 1980). The last reported capture (specimen photographed and released) was above Bass Rapids (RM 107.7) in 1986 (cited in Carothers and Brown, 1991:330). Extensive electrofishing by Carothers and Minckley (USBR, 1981, unpubl.) in 1977–1979 never resulted in a mainstem capture of *X. texanus*. Similarly, Valdez and Ryel [Life History and Ecology of the Humpback Chub (*Gila cypha*) in the Colorado River, Grand Canyon, AZ, Final Rpt., U.S. Bureau of Reclamation, 1995, unpubl. (hereafter USBR, 1995, unpubl.)] failed to capture *X. texanus* during extensive fieldwork from 1990–1995.

A putative hybrid *X. texanus/C. latipinnis* was collected at the mouth of the Paria River by G.

H. Clemmer (unpubl. field notes, 1976, 1980; Special Coll., Hayden Library, Arizona State University). Similarly, R. D. Suttkus, G. H. Clemmer, C. Jones, and C. R. Shoop [GCNP survey of fishes, mammals, and herpetofauna, 1976, unpubl. (hereafter GCNP survey, 1976, unpubl.)] collected three hybrids (but no *X. texanus*) in the Grand Canyon. Valdez and Ryel (USBR, 1995, unpubl.) captured five hybrid *X. texanus/C. latipinnis* (332–631 mm TL) during intensive mainstem sampling (four near the LCR confluence). These results suggest *X. texanus* (and putative hybrids) are rare in the Grand Canyon region. The low numbers of putative hybrids we report herein are in agreement.

If *X. texanus* is a constituent member of the indigenous big-river fish community, then why is it so rare in the Grand Canyon region? Suttkus et al. (GCNP survey, 1976, unpubl.) concluded *X. texanus* had been displaced in Grand Canyon. They believed hypolimnetic releases from Glen Canyon Dam were too cold for main-channel *X. texanus* spawning and that the dam prevented upstream movement to other spawning areas. They also suggested *X. texanus* does not utilize as breeding habitat the numerous smaller tributaries in Grand Canyon. These researchers argued that, during the period when Lake Powell was filling (i.e., 1958–1963), main-channel water temperatures remained suitable for spawning, and *X. texanus* hybridized with *C. latipinnis*. Today, spawning conditions are completely unfavorable for *X. texanus*, and it is being genetically swamped by the latter.

We agree with Suttkus et al. that *X. texanus* and hybrids now have low population numbers in the Grand Canyon and that hybridization has occurred historically between *X. texanus* and *C. latipinnis*. However, it is unknown whether putative hybrids captured in Grand Canyon were spawned there. These individuals may have been produced either downstream in Lake Mead or upstream in (now-inundated) Glen Canyon and are now blocked from extensive upstream movement (as per Suttkus et al.). *Xyrauchen texanus* is migratory and capable of long movements (Tyus and Karp, 1990), which is often a characteristic of large-river desert fishes (Smith, 1981; Tyus, 1990).

We do not believe *X. texanus* was once more abundant within Grand Canyon. Skeletal remains of indigenous fish species (*Gila cypha*, *G. elegans*, *Ptychocheilus lucius*, *C. latipinnis*, and *C. discobolus*) found in 4000-year-old deposits of Stanton's Cave (GCNP, RKM 50.7) did not include *X. texanus* (Miller and Smith, 1984). Today, these species (less the extirpated *G. elegans*

and *P. lucius*) persist and comprise the indigenous big-river fish community of the Grand Canyon. This, as well as other anecdotal evidence (see above), suggest it was not a historic resident of Grand Canyon but instead a transient. *Xyrauchen texanus* may have used Grand Canyon as a corridor to move up- or downriver to more satisfactory habitat [i.e., wider, slower-flowing, noncanyon reaches of river (as per Tyus, 1987:112; Minckley, 1991)].

Buth et al. (1987) used allozymes to examine potential for hybridization in *C. latipinnis* and *X. texanus* collected throughout the Colorado River basin. Overall, the propensity was 0–3% toward *X. texanus* and 0–5% toward *C. latipinnis*. Of 41 putative hybrids morphologically identified in this study, nine (22%) were examined electrophoretically and with RFLP analysis of mtDNA. Eight of these were backcrossed. This suggests two points: our morphological identification of putative hybrids was reasonable [in that 89% (8/9) of this small sample were correctly identified]; and a very small hybrid subpopulation exists within the Marble Canyon reach of Grand Canyon. The hybrid subpopulation averages 30 in number, is predominantly male, and frequents the LCR in spring, on average 2.2 km above the confluence.

To avoid ambiguity, comments (above) pertaining to efficacy of morphological evaluation in identification of hybrid individuals should be expanded. A different picture appears when capture records for the seven individuals with *Xyrauchen* mtDNA are examined. These seven were recaptured a total of 13 times. When their field determination at time of capture is contrasted against their genetic background, it becomes clear that field personnel had difficulty in consistently recognizing hybrid individuals. The seven were listed as *C. latipinnis* 53% (i.e., 8/15) of the time, as *C. latipinnis* hybrid 40% (6/15) of the time, and as *X. texanus* 7% (1/15) of the time. There are several reasons for these discrepancies. When field biologists weigh, measure, and tag large numbers of bulky fishes, detail is often sacrificed for expediency. Individual researchers also vary in their abilities to consistently recognize key phenotypic characteristics (i.e., "the art of seeing well"; Douglas et al., 1989). These aspects are compounded when phenotypic characteristics are muted by several generations of backcrossing (as herein). Thus, given the above, variance in field designation to species is to be expected. Nevertheless, on occasion, anecdotal phenotypic information is recorded which aids in diagnosis. For example, individual "7F7D1B780C" was captured seven times; it was designated as *C. latipinnis* in 43%

(3/7) of the captures, whereas 43% of the time it was called *X. texanus* hybrid. Once it was designated as *X. texanus*. During the data collection process, biologists noted on two different occasions that it possessed "a definite keel" or "a small, distinct keel." Similarly, individual "7F7F33064D" was captured four times. It was designated as *C. latipinnis* in 75% (3/4) of its captures. Yet, in its final capture, it was designated as *X. texanus* hybrid with "a small but definite keel." From the above, one point is clear. The ability in this study to recapture (and thus reexamine) potential hybrids was a great aid in their eventual diagnosis.

Results from our study underscore the paucity of baseline data for these species in Grand Canyon (as per Miller, 1946). Two areas of additional research are recommended. The first is a Grand Canyon-wide genetic study to estimate patterns of variability and divergence among endemic fishes. This is especially necessary for *C. latipinnis*, which may encompass several forms within Grand Canyon [Minckley, 1973; unpubl. (cited in Minckley, 1991:159); Minckley and Holden, 1980]. Genetic research is also required to ascertain extent of hybridization and backcrossing between *C. latipinnis* and *X. texanus*.

Long-term monitoring of these (and other) big-river fishes is also required. Research should focus at confluences of major tributaries (Paria and Little Colorado Rivers; Bright Angel, Shinumo, Tapeats, Kanab, and Havasu Creeks). Our data show *X. texanus/C. latipinnis* hybrids move extensively into and from the LCR. Monitoring of other low-gradient tributaries (Paria River and Kanab Creek, for example) may discover similar aggregations. *Catostomus latipinnis* also has a demonstrated propensity to congregate at (and enter into) a variety of tributary outflows, and it is there it can be most parsimoniously monitored.

Like *X. texanus*, *C. latipinnis* is also capable of long-range movements (S. Weiss, M. Douglas, B. Persons, and R. Valdez, unpubl.). Sampling should thus be extensive enough to statistically verify these movements within Grand Canyon yet possess sufficient resolution that local (or tributary) year classes can be adequately monitored. Knowledge of the latter is particularly important as benchmarks for recruitment and onset of senescence. In this way, *C. latipinnis* can be adaptively managed and protected within Grand Canyon before it is pushed into endangerment.

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APPENDIX. COMPUTATIONAL STATISTICS FROM CJS ANALYSIS OF ADULT *Catostomus latipinnis* AND *Xyrauchen texanus*/HYBRIDS. No. = numerical designation for trip; Date (from/to) = sampling periods; Season = sampling season (V = spring, S = summer, A = autumn, W = winter); Effort = sampling effort in net-hours; NH(I) = CJS population estimate at time (i), adjusted for effort; SE NH(I) = standard error of nh(i) (not calculated for *X. texanus*/hybrids).

No.	Date (from/to)	Season	Effort	<i>C. latipinnis</i>		<i>X. texanus</i>
				NH(I)	SE NH(I)	NH (I)
01	01 July–14 July 1991	S	7630	2952	430	—
02	21 July–03 Aug. 1991	S	10,146	2951	430	—
03	11 Aug.–23 Aug. 1991	S	12,172	1679	402	08
04	13 Sep.–25 Sep. 1991	A	5188	2015	500	20
05	15 Oct.–24 Oct. 1991	A	5622	2325	488	17
06	07 Nov.–16 Nov. 1991	A	5282	2325	541	22
07	09 Dec.–16 Dec. 1991	W	6375	1642	313	—
08	08 Jan.–15 Jan. 1992	W	7133	1642	288	—
09	11 Feb.–19 Feb. 1992	W	5607	1642 ^a	330	—
10	05 Mar.–13 Mar. 1992	V	6412	1642 ^a	330	—
11	26 Mar.–03 Apr. 1992	V	9554	1832	271	102
12	20 Apr.–29 Apr. 1992	V	6326	2054	366	22
13	18 May–27 May 1992	V	7990	2736	376	—
14	15 June–24 June 1992	S	8194	2037	304	—
15	14 July–23 July 1992	S	7591	2037	318	—
16	10 Aug.–19 Aug. 1992	S	4862	2697	708	24
17	14 Sep.–23 Sep. 1992	A	7570	3415	453	21
18	12 Oct.–22 Oct. 1992	A	7607	1750 ^a	341	—
19	09 Nov.–18 Nov. 1992	A	4527	1750 ^a	341	—
20	10 Feb.–17 Feb. 1993	W ^b	8162	1591	260	—
21	02 Mar.–10 Mar. 1993	V	7846	1591	265	15
22	22 Mar.–31 Mar. 1993	V	8962	1915	276	15
23	12 Apr.–21 Apr. 1993	V	8809	2467	328	29
24	10 May–19 May 1993	V	7052	2674	396	28
25	08 June–16 June 1993	S	7561	3513	459	45
26	12 July–21 July 1993	S	7735	3841	481	—
27	10 Aug.–18 Aug. 1993	S	6718	2307 ^a	340	136
28	13 Sep.–22 Sep. 1993	A	8602	2307 ^a	340	26
29	12 Oct.–21 Oct. 1993	A	8199	2307	342	33
30	08 Nov.–17 Nov. 1993	A	9005	2027	283	16
31	06 Dec.–15 Dec. 1993	W	8322	2260	316	24
32	11 Jan.–20 Jan. 1994	W	8517	2615	344	33
33	10 Feb.–19 Feb. 1994	W	7672	2516	357	33
34	15 Mar.–24 Mar. 1994	V	9661	3683	444	—
35	12 Apr.–21 Apr. 1994	V	8913	4269	473	—
36	10 May–19 May 1994	V	7920	5214	587	—
37	14 June–23 June 1994	S	8143	5214	575	19
38	12 July–21 July 1994	S	8634	3553	420	—
39	09 Aug.–18 Aug. 1994	S	9162	3248	390	15
40	13 Sep.–22 Sep. 1994	V	9048	3121	380	—
41	11 Oct.–20 Oct. 1994	V	9158	3322	399	—
42	01 Nov.–10 Nov. 1994	V	7442	2115	326	15
43	06 Dec.–15 Dec. 1994	W	10,152	2115	314	15
44	10 Jan.–19 Jan. 1995	W	11,150	2064	377	29
45	07 Feb.–16 Feb. 1995	W	9180	2072 ^a	352	15
46	28 Feb.–09 Mar. 1995	V	12,285	2072 ^a	352	—
47	21 Mar.–30 Mar. 1995	V	12,182	2625	616	—
48	11 Apr.–20 Apr. 1995	V	9292	3862	471	—
49	26 Apr.–25 May 1995	V	10,095	594	146	—
50	13 June–27 June 1995	S	*	*	*	—

* Not calculated.

^a Combined with previous trip.

^b Dec. 1992/Jan. 1993 not sampled due to inclement weather.