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FINAL REPORT:

Ecology and Conservation Biology of Humpback Chub

(Gila cypha) in the Little Colorado River

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The present study formed one component of the Bureau of Reclamation's Glen Canyon Environmental Studies (GCES; reviewed by Wegner, 1991), in which Phase II (see Patten, 1991) was authorized to specifically ascertain if flow releases from the dam could be modified to minimize impacts on natural and cultural resources downstream.

This report represents five years of research on four indigenous big-river fishes of the Grand Canyon ecosystem: *Xyrauchen texanus*, *Catostomus latipinnis*, *C. (Pantosteus) discobolus* (family Catostomidae), and *Gila cypha* (family Cyprinidae). The first and last species are currently listed as "endangered," while the second is being evaluated for candidacy and the third is believed secure. This study focused on distributions, abundances, and survivability of these fishes within the Little Colorado River and its confluence with the mainstream Colorado River, 99 river-kilometers downstream from the dam. As is often the case with scientific investigations, more questions are asked than answers provided. In addition, more questions are engendered by application of the scientific method. However, data herein provide necessary baseline evidence for long-term management of these fishes, and will (hopefully) serve as springboard to more extensive investigations of the entire indigenous fish community in the Canyon [to include smaller adult forms (such as speckled dace, *Rhinichthys osculus*) as well]. This is as it should be.

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SECTION 1:

POPULATION ESTIMATES/ POPULATION MOVEMENTS OF *GILA CYPHA*,
AN ENDANGERED CYPRINID FISH IN THE GRAND
CANYON REGION OF ARIZONA

[COPEIA 1996(1):15-28]

ABSTRACT

Gila cypha (the humpback chub) is a unique but endangered cyprinid fish endemic to the Colorado River system in western North America. Its distribution within the system is patchy; occurrence is restricted primarily to narrow, canyon-bound reaches of these rivers. Greatest abundance is achieved at the confluence of the Colorado and Little Colorado rivers (= LCR) in northern Grand Canyon (Coconino Co., AZ). This study defines the nature and extent of *G. cypha*'s movements within the LCR, and tests the hypothesis that its duration of stay within that river is restricted to the reproductive period.

During 1991/92, adult *G. cypha* were captured and tagged during 19 6--14 day sampling periods in three separate reaches of the LCR. From these data, population estimates were derived for each reach on a monthly basis, by month for the entire LCR, and over the entire study period. Results indicate an upriver migration by some individuals in early spring, followed by a slow, protracted post-reproductive movement downstream. Localized stasis by adults in the LCR, particularly summer through winter, is also strongly supported by the data. Movements by *G. cypha* in the LCR thus appears to be an amalgam of two processes: Upriver movement in spring coupled with localized movements by overwintering adults. The latter suggests a possible alteration in life-history strategy for the species, and is discussed in the context of Glen Canyon Dam, built in 1963 to impound Lake Powell at the northern extent of Grand Canyon.

"The Colorado is probably the most utilized, controlled, and fought over river in the world. It flows through lands of incomparable beauty and includes nearly seven percent of the nation's contiguous land mass, including parts of seven states. From the time of early settlers to the present, the waters of the Colorado River have been the key to development of the arid region" (Crawford and Peterson, 1974:vi).

Waters of the Colorado River basin are not only economically important, but also contain the most distinctive ichthyofauna in North America, with species-level endemism approaching 75% (Minckley, 1991) (93% if undescribed forms and subspecies are included, as in Carlson and Muth, 1989). The parallel importance of economic potential and ichthyofaunal diversity has initiated a classic and ongoing confrontation between development and conservation (see Wydowski and Hamill, 1991).

From the conservation viewpoint, at risk is a unique and endemic ichthyofauna of ancient origin, extending as far back as the Miocene (Miller, 1959, 1961; Minckley et al., 1986). These fishes possess remarkable adaptations to survive in a turbulent environment. Foremost are a suite of morphological and anatomical modifications which may act in concert to minimize the river's impact upon the phenotype of the fish while optimizing the abilities of the fish to negotiate boulder-strewn, high velocity rapids. While alternative hypotheses may explain the evolution of these phenotypes, morphological trends across numerous, unrelated taxa speak for commonality in other than phylogeny, and the selective arena of the river seems reasonable (Minckley, 1991:128). The majority of these fishes are endangered (or candidates for such listing; see Minckley and Douglas, 1991), due to numerous recent habitat modifications by modern humans.

The specialized morphologies of the mainstream Colorado River fish fauna reach their culmination in the phenotype of humpback chub (*Gila cypha*; Fig. 1--1), the most remarkably specialized minnow in western North America and one of the most bizarre in the world (Miller, 1964; Minckley, 1991; Douglas, 1993; and references therein). It is known only from the Colorado River and its major, swift-flowing tributaries (Holden and Minckley, 1980); it occurs only sporadically and is seldom locally abundant, particularly when compared to other indigenous fishes. *Gila cypha* has been recorded from: (a) the gorge sections of the Green and Yampa rivers in Utah and Colorado (Green River Wilderness Area and Dinosaur National Monument, respectively); (b) the Colorado River in Utah above Lake Powell (Canyonlands National Park); and (c) the Colorado River above its junction with the Green River [between confluences of the Dolores (in eastern Utah) and Gunnison rivers (in western Colorado; Fig. 1--2a)]. *Gila cypha* was also within other canyon-bound reaches of the Colorado River, as documented from archaeological remains (Miller, 1955; Miller and Smith, 1984; Sigler and Miller, 1963).

Gila cypha was the last fish to be described from the mainstem Colorado River (Miller, 1946), the type specimen caught in 1932 by angling within Grand Canyon National Park (GCNP) [at Bright Angel Creek, now 141.3 river kilometers (RKM) below Glen Canyon Dam] (Carothers and Brown, 1991:95). The largest population of *G. cypha* is in the Marble Canyon section of GCNP, at the junction of the Little Colorado (LCR) and mainstem Colorado rivers, 99 RKM below Glen Canyon dam (Fig. 1--2b). While the life history of *G. cypha* is enigmatic (discussed in Douglas, 1993), the Grand Canyon population is least known of all. For example, *G. cypha* inhabiting the Colorado River at the LCR confluence were not even recognized as a reproducing population until 1975 (R. R. Miller, unpubl. field notes, Special Coll., Hayden Library, ASU). Even then their numbers were not considered substantial; the largest population of *G. cypha* at that time was believed to inhabit the Colorado River near Grand Junction (based upon 32 specimens captured in 1974; J. E. Johnson, Bur. Land Manag. Tech. Note 280, 1976, unpubl.).

This study was undertaken to estimate numbers of adult *G. cypha* within the LCR, define the nature and extent of their movements within that river (where reproduction occurs annually), and test the hypothesis that both local movements and residency are restricted to the reproductive period. Habitat use is then discussed in context of Glen Canyon Dam, constructed in 1963 (completed in 1968) to impound Lake Powell at the northern extent of Grand Canyon.

METHODS AND MATERIALS

The study river.---The LCR drains 141,155 km² of eastern and northern AZ and western NM, and flows 412 km from headwaters to confluence with the Colorado River (GCNP, Coconino Co., AZ; Figs. 2a, 2b). Unless in flood, the LCR is seasonally dry in much of its upper 390 km, a result of modern land-use practices and water impoundments initiated at the turn of the century (Miller, 1961). However, flow in the lower 21 km is perennial, from numerous groundwater springs which drain 72,520 km² of the Black Mesa north and east of Flagstaff, AZ. The largest of these (i.e., Blue Springs, at LCR RKM 21; Fig. 1--2b) has a discharge of 6.1-6.6 m³/sec (Johnson and Sanderson, 1968).

The LCR at base flow is saline (conductivity exceeds 5000 umhos/cm⁻¹) and travertine-forming. Carbonate precipitates onto surfaces and in the water column, the latter giving the river a distinct turquoise color. Carbonate deposition (a function of CO₂ degassing and photosynthetic activity of algae and cyanophyceans) produces an intricate and confusing water chemistry (Kubly and Cole, 1979). Travertine accumulations over geologic time define pools, runs, and rapids, and generate scalloped waterfalls and

cascades. Interspersed amongst this structure are broad sandbars and other depositional features more typical of erosive southwestern streams. These shift seasonally (and dramatically) according to duration and extent of flooding. Dominant riparian vegetation is a mixture of native [Catclaw acacia (*Acacia greggii*), Honey mesquite (*Prosopis glandulosa*), Coyote Willow (*Salix exigua*), Arrowweed (*Tessaria sericea*)], and nonnative species [Tamarisk (*Tamarix chinensis*), Camelthorn (*Alhagi camelorum*)] (Carothers and Brown, 1991; Johnson, 1991). Giant reed (*Phragmites australis*) and cattail (*Typha* spp.) occur patchily. The lower LCR passes through a narrow gorge that progressively widens and deepens as it drops towards Marble Canyon. A series of precipitous travertine falls at RKM 14.9 (Atomizer Falls, Fig. 1--2b) mark upstream distribution of *G. cypha*.

Base camps.---Three base camps were established in the LCR gorge: Near its confluence (RKM 0.55); at Powell Canyon (RKM 3.1); and at Salt Canyon (RKM 10.8). Biologists worked from each camp. Those at the confluence fished the lower 1.2 km of river, while those at Powell camp fished upriver from 1.3--7.0 km. Salt camp personnel fished from 8.0--14.9 km.

Data collection.---Fishes were captured during 19 6--14 day trips at approximately monthly intervals from July 1991 to December 1992. Hoop nets (0.76 or 1.2 m dia., 2.4 or 3.0 m length, four- or six-hoop, single- or double-throat) were deployed in all available habitat types of sufficient depth (i.e., > 0.4 m). Trammel nets (7.6 to 45.7 m length, 1.8 m depth, 1.3 to 3.8 cm inner and 30 cm outer meshes) were set routinely in the confluence. Fishing effort for a particular trip was recorded as number of net-hours per camp.

All captured fishes were identified, measured (TL to nearest mm) and weighed (nearest g). Native species were examined for tags, markings, secondary sexual characteristics, ripeness, and general health and condition. Those greater than 150 mm TL (= 'adults') were injected with passive integrated transponder (i.e., PIT) tags (see Prentice et al., 1990) and released near points of capture. Nonnative fishes were scanned for presence of PIT tags (a result of consuming tagged native fishes), then sacrificed and either dissected immediately or preserved for later study.

Analytical protocol.---One-way ANOVA (Proc GLM; SAS, 1985) was used to compare total fishing effort and captures of adult *G. cypha* by reach and year. To determine movements during 1992 (which represented a full year of sampling), adult chubs were grouped by reach and season (winter = December, January, February; spring = March, April, May; summer = June, July, August; and autumn = September, October, November). Numbers of *G. cypha* tagged/recaptured in a given reach during a given trip were

condensed into a capture history (i.e., CH) matrix (Burnham et al., 1987; Lebreton et al., 1991). Fifty-seven matrices were derived (three camps over 19 trips).

Closed population estimates.---Population estimates were generated from each CH-matrix under assumption that the three stream reaches contained closed populations. This was appropriate given the brief sampling period at each camp (see Otis et al., 1978), and because only adults were censused. Closure was tested by examining numbers of individuals tagged within one reach then recaptured within a second reach during the same trip. Nine different closed-population estimates were derived from each CH-matrix using an updated (30 Dec. 1991) version of the computer program CAPTURE (G. C. White, D. R. Anderson, K. P. Burnham, and D. L. Otis, Los Alamos Natl. Lab., 1982, unpubl.). Models and assumptions are explained in Otis et al. (1978), Pollock et al. (1990), and Nichols (1992). The single best-fitting population model, as indicated by goodness-of-fit tests and comparisons between competing models, was retained. In this first analysis, population estimates were made relative to one another by dividing each by length of reach (in km). ANCOVA (Proc GLM; SAS, 1985) then contrasted relative population estimates by reach, using fishing effort as a covariate.

In a second analysis, tag/recaptures were evaluated for the entire LCR (rather than by reach). Here, 19 CH-matrices were generated, one for each month of study. Again, the single best-fitting population model was retained. ANOVA was used to test the 19 estimates against those summed by reach for each month. The hypothesis under test is that monthly estimates are not significantly different from those summed by month over reaches.

Finally, a third analysis collapsed all tag/recaptures into a single CH-matrix (i.e., each column of the CH-matrix represented a single month). Here, five best-fitting estimates were retained. However, assumptions of closure may be violated in this analysis by movements of *G. cypha* into/from the mainstem Colorado River over the 19-month study interval, and by recruitment of juvenile chubs into the adult population. Thus, while this analysis is a logical culmination of population estimates (a) by reach, (b) by month summed over reach, and (c) solely by month, results are heuristic rather than practical.

RESULTS

Fishing effort and unadjusted population estimates.---Fishing effort differed significantly among reaches ($F=6.40$; $P < 0.0035$; Proc GLM; SAS, 1985), with effort at Salt Canyon greater than that at Confluence (Sidak's multiple range test; SAS, 1985). Efforts at Salt and Powell Canyon reaches were statistically similar, however. Population estimates (normalized by river km)

also differed significantly among reaches, with greatest overall values at Confluence ($F = 4.19$; $P < 0.01$; SAS, 1985).

Population estimates adjusted for fishing effort.---Differences in normalized population estimates could result from increased effort. To test our estimates with fishing effort fixed, we first evaluated two specifications: (a) that slopes of the between-camp regressions of population estimate vs effort were homogeneous (i.e., regression lines parallel; see Somers and Jackson, 1993), and (b) that interaction between fishing effort and population estimates was nonsignificant. Based upon a priori statistical contrasts, estimated populations in Confluence and Salt Canyon reaches were similar, but each was significantly larger than at Powell Canyon reach, irrespective of fishing effort (Table 1--1).

Population estimates for each reach and for the entire river.---Three-dimensional plots of adjusted population estimates by reach are presented in Figure 1--3. Powell Canyon exhibited lower estimates than either Confluence or Salt Canyon, particularly in 1991 (Fig. 1--3a). In 1992 (Fig. 1--3b), increased activity at confluence during early March was reflected in elevated estimates at Powell in late March-April, followed by elevated estimates at Salt Canyon April-through-June. Estimates at confluence again increased in April-June. Raw population estimates by reach per sampling period, and estimates normalized by river km, are in Appendix 1--1. Raw population estimates per sampling period for the entire LCR are presented in Appendix 1--2. This appendix also contains a second population estimate for the entire river, derived by summing estimates calculated over reaches for each sampling period (as recorded in Appendix 1--1). An ANOVA comparing these two estimates for the entire LCR (i.e., monthly vs summed by month over reaches) was nonsignificant ($F = 1.15$; $df = 1,36$; $P > 0.7$; Proc GLM, SAS, 1985). Both estimates are plotted in Figure 1--4. In 1991, highest estimates were recorded for early August (3157 vs 5390), while lowest were for December (745 vs 1285) (Fig. 1--4). In 1992, highest estimates were for April (5555 vs 5683), while lowest were for August (635 vs 408). A December sampling trip in 1992 was cancelled due to inclement weather. Both techniques indicated elevated population estimates from early March through June of 1992 (Fig. 1--4). Also, both techniques demonstrated an upswing in estimated population size in autumn of both years. The average estimate summed over reaches was larger (but not significantly so) than that calculated by month (2993 vs 2434; $N = 19$; Sidak's multiple range test; SAS, 1985).

Five best-fitting population estimates were retained from analysis of a CH-matrix for the entire 19 month study (Table 1--2). The highest criterion (0.61) was Pollock and Otto's estimator (M_{bh}), which assumes that capture probabilities vary by individual animal and by behavioral response to capture (i.e., behavior and

heterogeneity effects; Otis et al., 1978:40--50). The model with the second-highest criterion (i.e., the Null model; M_0) is also the simplest in that it presumes all members of the population are equally at risk of capture on every trapping occasion. Burnham's estimator (M_b) assumes capture probabilities vary with time and with behavioral effects (such as trap-happiness, trap-shyness). The last two models (Jackknife estimator M_h , and Chao's M_c) accept that capture probabilities vary by individual animal.

Movement by season within- and among reaches.---To determine extent of movement by *G. cypha* within the LCR, capture and subsequent recapture(s) for 1992 were compiled by reach and season (Table 1--3). Because these data reflect numbers of individuals tagged within each reach for a given season then subsequently recaptured, percentages for each reach and season total 100%. For *G. cypha* tagged at confluence during winter and subsequently recaptured, 49% (n = 47) were taken upstream in Powell or Salt reaches during winter/spring. Similarly, of those tagged at confluence during spring and subsequently recaptured, 51% (n = 96) were taken upstream during spring/summer. For Powell reach, 18% (n = 7) of recaptures initially tagged there during winter were taken in Salt reach during winter/spring, while 31% (n = 59) of recaptures tagged there in spring were taken at Salt during spring/summer. Overall, 21% of total movements in 1992 (ascertained by mark/recapture) was upstream.

Elevated population estimates at confluence in January/February of 1992 (Fig. 1--3b), followed by upstream movement, argue strongly for staging. Estimates at the confluence peaked in early March, then gradually decreased through June. A similar peak occurred within Powell Canyon reach in late March, extended into April, then decreased into June. Population size did not peak in Salt Canyon reach until April; estimates remained elevated through June. The last six months of 1992 were similar to that of 1991 (Fig. 1--3a, 1--3b), with estimated population sizes dwindling through late summer. However, estimates rose again in Autumn, 1991 but remained low during a similar period in 1992.

Evidence for downstream movement is less convincing (Table 1--3). Of *G. cypha* tagged in Powell reach during winter and subsequently recaptured, 21% (n = 8) were taken at confluence in the remainder of the year. Similarly, 16% (n = 30), and 15% (n = 15) of recaptures tagged at Powell in spring and summer, respectively, were taken at confluence in the remainder of the year. At Salt, 16% (n = 33) and 7% (n = 12) of recaptures tagged in spring and summer, respectively, were taken in the two lower reaches over the remaining seasons. Overall, 9% of recaptures in 1992 indicated downstream movement.

Table 1--3 primarily reflects population stasis by reach,

particularly summer through winter. At confluence, 17% (n = 33) of individuals tagged in spring were subsequently retaken there summer through winter, while 76% (n = 54) of chub tagged in summer were recaptured in that same reach summer through winter. Similarly, 77% (n = 10) of chub tagged at confluence in autumn were retaken there autumn/winter. At Powell, 23% (n = 45) of individuals tagged in spring were again recaptured there summer through winter, 78% (n = 80) of those tagged during summer were recaptured summer through winter. In addition, 91% (n = 20) of those tagged in autumn were recaptured in that same reach autumn/winter. A similar situation occurred at Salt, where 53% (n = 109) of individuals tagged during spring were recaptured there summer through winter, while 93% (n = 159) tagged during summer were recaptured summer through winter. In autumn, 89% (n = 24) tagged at Salt were recaptured there autumn/winter. Overall, 70% of recorded movements in 1992 was static (i.e., within-reach).

Evidence is minimal for movement of *G. cypha* between reaches during collecting periods (Table 1--4). In 1991, 13 out of 3272 fish were recaptured during the same trip in a reach upstream from their initial capture, while 23 of 3272 were recaptured downstream from their initial capture reach (i.e., N = 36; 0.01% of total; Table 1--4). In 1992, only 1 of 4030 fishes was recaptured during the same trip in a reach upstream from their initial capture, while none was recaptured in downstream reaches (i.e., N = 1; 0.0003% of total; Table 1--4).

DISCUSSION

The Colorado River as habitat.---During historic times, temperature and flow regimes of the Colorado River fluctuated greatly; seasonal flooding transported heavy sediment loads while low waters carried vast amounts of dissolved salts to the Sea of Cortez (Carlson and Muth, 1989). In flood, the Colorado was a wild, swift, turbulent river, the result of extreme flow, a channel constrained for most of its length by steep cliffs, and a 3700 m drop in altitude from headwaters to sea (Fradkin, 1984).

Dams and Impoundments.---Dam construction and chronic dewatering for agriculture and urban development precipitated major changes in the Colorado River ecosystem. Temperature and flow regimes as well as salt and sediment loads of the river are now greatly ameliorated. The 2400 km of riverine habitat suitable for large-river fishes has been reduced to 965 km (Miller, 1982).

Those sections of the Colorado River that were converted into lakes Mead and Mohave (following closure of Hoover and Davis dams in 1935 and 1954, respectively), clearly possessed the river's unique fish fauna, including *G. cypha* (Miller, 1955). These fishes [except for relictual bonytail chub (*Gila elegans*) and razorback sucker (*Xyrauchen texanus*)] are now extirpated (see

also Minckley, 1983). They were also eliminated from the Green River above the mouth of the Yampa River when Flaming Gorge Dam became operational in 1962 (Vanicek et al., 1970; Fig. 1--2a).

Glen Canyon Dam.---The operation of Glen Canyon Dam precipitated major changes in the Marble/Grand Canyon ecosystem of the Colorado River (Marzolf, 1991:33). Some occurred immediately upon closure of the dam in 1963 (e.g., decreased water temperatures; reduced sediment loads; diminished salinity; alteration of flow regimes). Others developed over a much longer time frame (e.g., geomorphic adjustment of channel; secondary succession of terrestrial vegetation; modification of aquatic species-composition) (Committee, 1991). All have severely impacted the natural ecosystem; some are irreversible.

Indigenous fishes inhabiting Glen, Marble and Grand canyons were impacted following closure of Glen Canyon Dam (Holden and Stalnaker, 1975; Suttkus and Clemmer, 1977; Minckley, 1991). Many (including *G. cypha*: Holden and Stalnaker, 1975; Anonymous, 1980) persisted in Lake Powell, but were unable to reproduce (Holden, 1973:4). Downstream from the dam, the fish community shifted from predominantly warm-water native and introduced fishes to one dominated by either cold-water fishes [i.e., rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*)] or those with broad temperature tolerances. Within GCNP, five of eight indigenous fishes still persist in low to moderate numbers. These are usually restricted to warmer habitats such as tributaries and backwaters. While terrestrial species in GCNP adapted to the post-dam Colorado River ecosystem (Carothers and Brown 1991:147; Johnson, 1991), indigenous fishes generally did not (Kaeding and Zimmerman, 1983:592).

The Little Colorado River as habitat.---Temperature and flow conditions in the LCR are similar to those of the pre-dam Colorado mainstem, and thus suit habitat requirements of indigenous fishes shaped over evolutionary time. Kaeding and Zimmerman (1983) argued that *G. cypha* persisted within the Canyon, whereas other endemics were eliminated, because a portion of its population spawned within the LCR. They also argued that, given post-dam temperature disparities between LCR and mainstem, significant reproductive success for *G. cypha* must occur within the LCR. Thus, selection should be strong for development of a spawning migration (Kaeding and Zimmerman, 1983). Critical though these observations are to the ecology and conservation of *G. cypha*, they have yet to be substantiated. While data presented herein do not address movements of *G. cypha* from the mainstem into the LCR, they do suggest that staging occurs at the confluence. Our data do demonstrate that adult *G. cypha* actively move up the LCR in spring (primarily to reproduce), and often remain within the LCR for long periods, possibly the entire year. These observations are based both on monthly population estimates by reach, and on seasonal recaptures of tagged *G. cypha*. Before

each of these results are discussed, however, it is important to review population models and their assumptions.

Open vs closed population models.---Modelling of capture history is defined by the idea of population closure. An open population is one in which study organisms enter and leave (via birth, death, immigration, emigration, or ontogeny). A closed population does not change composition during the course of the study (Nichols, 1992). While open populations are the norm in wildlife investigations, closed models approximate the short-duration realities of nature (Skalski and Robson, 1992). In fact, Pollock (1982) recommended as an ideal survey design a sequence of intense trapping sessions each followed by a longer period of cessation of trapping. Data from each session would be analyzed separately using closed models (as done herein). Survival rates derived from the time-duration between trapping sessions could then serve as input for open-population models (M. E. Douglas and P. C. Marsh, in prep.).

Three assumptions are crucial to closed-population studies: Closure is substantiated; organisms do not lose marks during the course of the experiment; and all marks are correctly recorded at each trapping occasion. The most critical is the first. Closure for the duration of a trapping session allows the resulting estimate to represent a "snapshot" of the population at a given point in space and time. In the present study, sampling each month was brief, and movements between reaches were negligible during sampling. Thus, closure both by reach/ month and by month for the entire LCR is indeed supported, and the resulting population estimates are robust.

Past and present population estimates in the LCR.---Population estimates for *G. cypha* in the LCR are presented in Table 1--5. Our May, 1992 estimate at the confluence was 1,320 adult *G. cypha*. This is a reduction of 27% and 54%, respectively, from estimates of 1,800 and 2,900 individuals in May of 1987 and 1988. An estimate for the entire 14.9 km length of the LCR during May of 1992 was 4,346 (summed estimate for the three reaches = 4,602). This contrasts with the estimate of 25,000 chub in 1989.

The best-fitting population estimate for our entire 19-month study (4,508 individuals) was obtained using Pollock and Otto's estimator (M_{bh}). This model is one of the most realistic and useful for a mark-recapture experiment, in that it allows for individual variance in behavioral response to capture (Otis et al., 1978). Its estimate is larger than two average estimates for the 19-month study [i.e., 2,992 (monthly summed over reaches) and 2,434 (monthly for LCR)]. Although results from a model utilizing 19-months of data should be superior to an average of those data, any such long-term estimate must be viewed skeptically, given the violations of demographic and temporal closure mentioned earlier.

Movements by G. cypha within the LCR.---Our results contrast with those of Kaeding and Zimmerman (1983), who found no consistent relationship between catch rate and river reach within the LCR [where 'river reaches' were 5 km increments, beginning at RKM 2 and ending at Blue Springs (RKM 21; Fig. 1--2b)]. In our analyses, river reaches were more extensive, and only encompassed those RKM within which *G. cypha* was active (i.e., 0--14.9).

The confluence has often been considered a staging area for *G. cypha* (R. R. Miller, GCNP report, 1975, unpubl.; R. D. Suttikus, G. H. Clemmer, C. Jones, and C. R. Shoop, GCNP report, 1976, unpubl.; C. O. Minckley, unpubl. field notes, 1977). Extent of *G. cypha*'s movement within the LCR was not clarified until September 1977, when three large individuals (278--295 mm TL) were captured 12.8 RKM above the confluence (C. O. Minckley, unpubl. field notes, 1977). From these data, and from AZGF monitoring efforts in spring 1987--1990 (C. O. Minckley, unpubl.), it was believed that *G. cypha* actively moved into the LCR in spring (i.e., April/May) to reproduce, then quickly returned to the mainstem. Greater numbers of *G. cypha* at the confluence during spring of 1992 support an hypothesis of staging prior to upstream movement. Downstream (i.e., postreproductive) movement also clearly occurred, but spanned a long period and was diffuse. Movements between LCR reaches during a given sampling period were negligible, suggesting temporal closure during periods of sampling. There was no evidence of explosive or extensive reproductive movements.

Our results indicate population stasis within reaches, particularly summer through winter, suggesting that *G. cypha* is more of a resident component of the LCR than previously imagined. These observations support similar data collected by Karp and Tyus (1990) in the Yampa River. There, *G. cypha* remained in or near specific eddies for extended periods, and even returned to the same eddy during the spawning season in different years. It could not be ascertained whether individual chub deposited eggs in the eddies or simply used them for staging, resting, or feeding.

Habitat use.---Data on habitat use by *G. cypha* are primarily anecdotal and observational. Adults characterize whitewater reaches, where they occupy deep, swirling eddies along canyon walls or concentrate in zones of turbulence near boulders and submerged rocks (Minckley 1991:150). Similarly, Kaeding et al. (1990) noted that commonality among *G. cypha* habitats is not great depth, but dynamic flow vectors that result from water moving rapidly among large, angular boulders and shoreline rock outcrops. Within other areas of the Colorado River, *G. cypha* often associates with large-scale riprap material from riverside railroad and highway construction (Kaeding et al., 1990).

Karp and Tyus (1990) argued that eddy habitat was crucial to

breeding requirements of *G. cypha* in the Yampa River. Interfaces between eddies and runs were similarly judged important in the Black Rocks area (below Grand Junction, CO) (R. A. Valdez and B. A. Nilson, Proc. Am. Fish. Soc., Bonneville Chapter, 1982, unpubl.). Adult *G. cypha* are primarily nocturnal (Fig. 1--5 of Valdez and Clemmer, 1982). During daylight hours in the LCR, they reside in deeper waters along cut banks with overhanging vegetation (primarily reeds), along sheer rock outcrops, or in deeper pools away from shore; they are active during crepuscular hours and in late evening (C. O. Minckley, pers. comm.; M. E. Douglas and P. C. Marsh, pers. obs.).

The greater numbers of *G. cypha* found in the Salt Canyon reach, when compared to Powell Canyon reach, sustain at least two alternative hypotheses. Increased habitat complexity in the Salt Canyon reach, with greater numbers of large travertine dams, eddy/run interfaces, and deep pools, may increase residency of *G. cypha* within this area. Alternatively, those *G. cypha* that move up the LCR may literally 'stack' within the upper reach, due either to a physical barrier at RKM 14.9, or a chemical one produced by high CO₂, or other chemical content.

Glen Canyon Dam and Gila cypha.---There is long-term residency by *G. cypha* within the LCR, particularly summer through winter. In fact, many adults apparently overwinter within the LCR, effectively using it as a warm-water refugium. Two hypotheses are presented to accommodate these data. One suggests residency is a pre-dam component of *G. cypha*'s life history. The other proposes that it is a post-dam alteration. It is unclear which can be rejected; both are untestable in their present form.

Long-term residency by adults may have always been an aspect of *G. cypha*'s life-history. We know, for example, that it spawned within the pre-dam LCR during spring (Kolb and Kolb, 1914:127; Carothers and Brown, 1991:93). However, its duration of stay was unknown. If residency has always been a component of *G. cypha*'s natural history, then our mark/recapture data simply define inherent behavior over evolutionary time.

An alternative hypothesis is that the altered thermal regime of the mainstem has forced *G. cypha* to adjust its life history. It now accommodates lower mainstem temperatures primarily through avoidance (i.e., by increasing residency within the LCR). This hypothesis is anecdotally supported by three facts: First, movements into/from the LCR are primarily accomplished by larger (and presumably older) *G. cypha* (R. A. Valdez, pers. comm.). *Gila cypha* attains great age (20+ years; Minckley, 1991:150); larger adults may thus represent mainstem-adapted individuals from pre-1968 cohorts (when Lake Powell filled). Secondly, larvae and juvenile *G. cypha* are often transported via flood into the mainstem, but adults less than 200 mm TL are seldom taken there

(R. A. Valdez, pers. comm.). Kaeding and Zimmerman (1983:585) similarly noted that individuals larger than 145 mm TL were never taken in the mainstream above the confluence, even though mature fish were present there. Third, hydrologic and thermal profiles of the LCR are consistent with the pre-dam Colorado River, but differ markedly from the post-dam river.

If *G. cypha* has altered its life history to accommodate dam-induced changes in the mainstem Colorado River, then its long-term persistence within the Grand Canyon is tied more intimately to the LCR than previously believed. The evolutionary effects of such a life-history alteration can only be speculated upon.

One potential saving factor (Committee, 1991:4) is that ecosystem components are linked to one another and to flow regimes imposed by the dam. Flows can therefore be manipulated to manage the river and protect the environment in GCNP. This offers the possibility that temperature, sediment load, and volume of discharge from the dam may eventually mimic a natural hydrograph, at least during parts of the year. This could, in turn, enhance long-term survival of *G. cypha* (but may conversely allow upriver movement of introduced fishes from Lake Mead; Minckley, 1991:146). In spite of such optimism, political and economic forces drive the system, even at the expense of cost efficiency (Leopold, 1991). These forces likewise impact indigenous fishes, and transform their conservation from the realm of science to that of politics.

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Appendix 1--1. Population estimates (= ESTIMATE) for *Gila cypha* in the Little Colorado River by reach and month, with standard deviation of the estimate (= S.D.), and 95% lower and upper confidence intervals (= L.CI; U.CI), and estimates relative to river km (= EST./RKM). TRIP=month/year; C=Confluence; P=Powell; S=Salt.

REACH	TRIP	ESTIMATE	S.D.	L.CI	U.CI	EST./RKM
C	07/91 ^d	0	0	0	0	0
P	07/91	643	218	356	1264	113
S	07/91	4007	1521	2001	8315	581
C	08/91 ^a	1034	366	552	2071	862
P	08/91 ^a	939	123	738	1239	165
S	08/91 ^a	3417	620	2430	4901	495
C	08/91 ^b	276	56	192	434	230
P	08/91 ^b	773	127	576	1084	136
S	08/91 ^b	1936	231	1552	2480	281
C	09/91	175	48	109	326	146
P	09/91	205	73	115	426	36
S	09/91	1142	176	862	1583	166
C	10/91	40	14	23	97	33
P	10/91	176	35	124	275	31
S	10/91	4761	2747	1722	13744	690
C	11/91 ^c	0	0	0	0	0
P	11/91	381	387	89	2042	67
S	11/91	1621	805	673	4134	235
C	12/91	68	15	48	108	57
P	12/91	339	322	85	5763	59
S	12/91	878	442	371	2283	127
C	01/92	509	506	119	2651	424
P	01/92	774	746	182	3872	136
S	01/92	1201	1199	263	6227	174
C	02/92	778	183	509	1249	648
P	02/92	880	470	368	3531	154
S	02/92	1323	1081	356	5467	192
C	03/92 ^a	1944	728	1067	6240	1620
P	03/92 ^a	1428	777	585	5720	251
S	03/92 ^{ac}	0	0	0	0	0
C	03/92 ^b	1173	440	602	2434	978
P	03/92 ^b	2585	773	1491	4642	454
S	03/92 ^b	1470	557	745	3067	213
C	04/92	653	118	471	964	544
P	04/92	2152	440	1486	3341	378
S	04/92	2878	508	2068	4091	417
C	05/92	1320	415	4738	944	1100
P	05/92	1050	703	362	6241	184
S	05/92	2232	880	1095	4769	323
C	06/92 ^c	670	103	507	931	558

P	06/92 ^c	1102	251	730	1741	193
S	06/92 ^c	3082	552	2200	4402	447
C	07/92	140	46	82	302	117
P	07/92	487	141	295	932	85
S	07/92	768	220	459	2791	111
C	08/92	48	29	20	261	40
P	08/92	68	25	40	150	12
S	08/92	292	31	240	362	42
C	09/92	124	80	50	417	103
P	09/92 ^c	0	0	0	0	0
S	09/92 ^c	0	0	0	0	0
C	10/92	397	379	100	1976	331
P	10/92	588	324	236	1658	103
S	10/92	758	49	670	862	110
C	11/92	376	188	167	987	313
P	11/92	545	312	213	1592	96
S	11/92	270	30	221	337	39
C	12/92	0	0	0	0	0
P	12/92	0	0	0	0	0
S	12/92	0	0	0	0	0

- ^a = Early month sampling
- ^b = Late month sampling
- ^c = In flood
- ^d = No net set at confluence
- ^e = No recaptures

Appendix 1--2. Population estimates for *Gila cypha* in the Little Colorado River by month (= TRIP), with standard deviation of the estimate (= S.D.), and 95% lower and upper confidence intervals (= L.CI; U.CI). $\Sigma(\text{Estimate})$ = monthly population estimates summed over the three reaches (data recorded in Appendix 1--1).

Trip	Estimate	S.D.	L.CI	U.CI	$\Sigma(\text{Estimate})$
07/91 ^d	2329	291	1842	2994	4650
08/91 ^a	3157	381	2516	4021	5390
08/91 ^b	2562	224	2172	3055	2985
09/91	1771	300	1296	2492	1522
10/91	2038	518	1276	3368	4977
11/91 ^d	1989	489	1264	3235	2002
12/91	745	210	453	1309	1285
01/92 ^c	2227	1251	839	6310	2484
02/92 ^c	1831	381	1246	2771	2981
03/92 ^{acd}	4380	1359	2459	8004	3372
03/92 ^{bc}	2555	674	1568	4294	5228
04/92 ^c	5555	671	4416	7067	5683
05/92 ^c	4363	1216	2594	7523	4602
06/92	4384	458	3573	5381	4854
07/92 ^c	1265	237	895	1888	1395
08/92 ^c	635	184	381	1222	408
09/92 ^{cc}	1950	1381	598	6908	124
10/92 ^c	1099	60	990	1224	1743
11/92 ^c	1417	408	839	2500	1191
12/92 ^c	0	0	0	0	0

^a = Early month sampling

^b = Late month sampling

^c = In flood

^d = Summation for two of three reaches only

^e = Summation for one of three reaches only

Table 1--1. Population estimates (number/river km) of adult *Gila cypha* (> 150 mm TL) in three reaches of the Little Colorado River (Confluence, Powell, Salt) from July, 1991 through December, 1992. Estimates were adjusted before analysis for length of reach (in km). Log₁₀ fishing effort was used as ANCOVA covariate. Diagonal elements represent average least squares population estimates (adjusted for log₁₀ fishing effort), and have been converted from log₁₀ values. Upper triangular cells represent F-values for pairwise a priori contrasts.

	CONFLUENCE	POWELL	SALT
CONFLUENCE	263	6.2 ²	0.2 ³
POWELL		110 ¹	4.3 ⁴
SALT			222

- ¹ F = 4.34; p < 0.019; df=3,48
- ² p < 0.016
- ³ p > 0.657
- ⁴ p < 0.044

Table 1--2. Population estimates generated under five different models (= MODEL) for adult *Gila cypha* within the Little Colorado River, from July 1991 through December 1992. Also provided are goodness-of-fit (= CRITERION), with standard deviation of the estimate (= S.D.), and 95% lower and upper confidence intervals (= LOWER CI; UPPER CI). Models are defined in text.

MODEL	CRITERION	ESTIMATE	S.D.	LOWER CI	UPPER CI
Pollock & Otto (M_{bh})	0.61	4508	120	4330	4811
Null Model (M_o)	0.49	6793	110	6585	7017
Burnham's (M_{tb})	0.48	8724	920	7242	10901
Jackknife (M_h)	0.42	10444	329	9833	11121
Chao's (M_n)	0.42	8039	210	7648	8472

Table 1--3. Adult *Gila cypha* tagged in 1992 within one reach (= TAG REACH) of the Little Colorado River during a given season (= TAG SEASON), then recaptured during the same or a subsequent season (= RCP. SEASON) within the same or a subsequent reach (= CONFLUENCE, POWELL, SALT).

TAG REACH	TAG SEASON	RCP. SEASON	CONFLUENCE	POWELL	SALT	TOTAL
Confluence	Winter	Winter	23 (23.6%)	7 (07.3%)	0 (00.0%)	30 (30.9%)
		Spring	11 (11.5%)	18 (18.8%)	22 (22.9%)	51 (53.2%)
		Summer	7 (07.3%)	4 (04.2%)	2 (02.1%)	13 (13.6%)
		Autumn	0 (00.0%)	0 (00.0%)	2 (02.1%)	2 (02.1%)
Confluence	Spring	Spring	56 (29.6%)	41 (21.7%)	20 (10.6%)	117 (61.9%)
		Summer	28 (14.8%)	14 (07.4%)	21 (11.1%)	63 (33.3%)
		Autumn	4 (02.1%)	3 (01.6%)	0 (00.0%)	7 (03.7%)
		Winter	1 (00.5%)	0 (00.0%)	1 (00.5%)	2 (01.0%)
Confluence	Summer	Summer	50 (70.4%)	5 (07.1%)	5 (07.1%)	60 (84.6%)
		Autumn	4 (05.6%)	4 (05.6%)	1 (01.4%)	9 (12.6%)
		Winter	0 (00.0%)	2 (02.8%)	0 (00.0%)	2 (02.8%)
Confluence	Autumn	Autumn	7 (53.5%)	1 (07.7%)	0 (00.0%)	7 (61.2%)
		Winter	3 (23.1%)	1 (07.7%)	1 (07.7%)	5 (38.5%)
Powell	Winter	Winter	2 (05.3%)	8 (21.1%)	1 (02.6%)	11 (29.0%)
		Spring	2 (05.3%)	12 (31.6%)	6 (15.8%)	20 (52.7%)
		Summer	4 (10.5%)	2 (05.3%)	0 (00.0%)	6 (15.8%)
		Autumn	0 (00.0%)	1 (02.6%)	0 (00.0%)	1 (02.6%)

Powell	Spring	Spring	4 (02.1%)	54 (28.0%)	37 (19.2%)	95 (49.3%)
	Summer	Summer	23 (11.9%)	37 (19.2%)	22 (11.4%)	82 (42.5%)
	Autumn	Autumn	2 (01.0%)	6 (03.1%)	4 (02.1%)	12 (06.2%)
	Winter	Winter	1 (00.5%)	2 (01.0%)	1 (00.5%)	4 (02.0%)

Powell	Summer	Summer	8 (07.8%)	59 (57.3%)	6 (05.8%)	73 (70.9%)
	Autumn	Autumn	5 (04.9%)	17 (16.5%)	1 (01.0%)	23 (22.4%)
	Winter	Winter	2 (01.9%)	4 (03.9%)	1 (01.0%)	7 (06.8%)

Powell	Autumn	Autumn	1 (04.5%)	16 (72.7%)	1 (04.5%)	17 (77.2%)
	Winter	Winter	0 (00.0%)	4 (18.2%)	0 (00.0%)	4 (18.2%)

Salt	Winter	Winter	0 (00.0%)	1 (01.7%)	9 (15.0%)	10 (16.7%)
	Spring	Spring	1 (01.7%)	0 (00.0%)	21 (35.0%)	22 (36.7%)
	Summer	Summer	0 (00.0%)	0 (00.0%)	21 (35.0%)	21 (35.0%)
	Autumn	Autumn	0 (00.0%)	1 (01.7%)	6 (10.0%)	7 (11.7%)

Salt	Spring	Spring	2 (01.0%)	1 (00.5%)	64 (31.1%)	67 (32.6%)
	Summer	Summer	11 (05.3%)	7 (03.4%)	81 (39.3%)	99 (48.0%)
	Autumn	Autumn	3 (01.5%)	0 (00.0%)	19 (09.2%)	22 (10.7%)
	Winter	Winter	4 (01.9%)	5 (02.4%)	9 (04.4%)	18 (08.7%)

Salt	Summer	Summer	3 (01.8%)	7 (04.1%)	92 (53.8%)	102 (59.7%)
	Autumn	Autumn	0 (00.0%)	0 (00.0%)	54 (31.6%)	54 (31.6%)
	Winter	Winter	1 (00.6%)	1 (00.6%)	13 (07.6%)	15 (08.6%)

Salt	Autumn	Autumn	1 (03.7%)	0 (00.0%)	16 (59.3%)	17 (63.0%)
	Winter	Winter	1 (03.7%)	1 (03.7%)	8 (29.6%)	10 (37.0%)

Table 1--4. Movement (as determined by tag/recapture) of individual *Gila cypha* between three reaches of the Little Colorado River during each of 18 different sampling trips of 1991/92. (Trip = month/year; N = Total Number; C = Confluence; P = Powell; S = Salt; Tot. UP = Total recaptured upstream; Tot. DN = Total recaptured downstream).

Trip	N	C-to-P	C-to-S	P-to-S	S-to-P	S-to-C	P-to-C	Tot.UP	Tot.DN
07/91	500	0	0	0	0	0	0	0	0
08/91 ^a	955	2	0	0	9	3	0	2	12
08/91 ^b	794	5	0	0	1	1	3	5	5
09/91	376	2	0	2	0	1	3	4	4
10/91	255	1	0	0	0	0	1	1	1
11/91	254	0	0	1	0	0	0	1	0
12/91	138	0	0	0	0	1	0	0	1
TOTAL	3272	10	0	3	10	6	7	13	23
01/92	125	0	0	0	0	0	0	0	0
02/92	299	1	0	0	0	0	0	1	0
03/92 ^a	292	0	0	0	0	0	0	0	0
03/92 ^b	275	0	0	0	0	0	0	0	0
04/92	933	0	0	0	0	0	0	0	0
05/92	341	0	0	0	0	0	0	0	0
06/92	841	0	0	0	0	0	0	0	0
07/92	258	0	0	0	0	0	0	0	0
08/92	115	0	0	0	0	0	0	0	0
09/92	90	0	0	0	0	0	0	0	0
10/92	278	0	0	0	0	0	0	0	0
11/92	183	0	0	0	0	0	0	0	0
TOTAL	4030	1	0	0	0	0	0	1	0

^a = Early month sampling
^b = Late month sampling

Table 1--5. Population estimates for adult Gila cypha in the Little Colorado River, based upon previous and current research (Confl. = confluence area; All = entire LCR).

YEAR	MONTH	AREA	METHOD	ESTIMATE	RESEARCHER(S)
1982	May	All	Multiple Census	7-8,000	Kaeding and Zimmerman ¹
1987	May	Confl.	-	5,783	C. O. Minckley ²
1987	May	Confl.	Multiple Census	1,800	Kubly ³
1988	May	Confl.	-	7,060	C. O. Minckley ²
1988	May	Confl.	Multiple Census	2,900	Kubly ³
1989	May	All	Multiple Census	25,000	Kubly ³
1992	May	Confl.	Multiple Census	1,320	Douglas and Marsh ⁴
1992	May	All	Multiple Census	4,346	Douglas and Marsh ⁴
1992	May	All	Multiple Census	4,602	Douglas and Marsh ⁵

¹L. R. Kaeding and M. A. Zimmerman, USFWS Final Report, 1982, unpubl. (Special Collections, Hayden Library, Arizona State University, Tempe).

²C. O. Minckley, AZ/NM Chapter, Amer. Fish. Soc. Proc., 1989, unpubl. (Special Collections, Hayden Library, Arizona State University, Tempe).

³D. M. Kubly, Bureau of Reclamation Draft Report, 1990, unpubl. (Special Collections, Hayden Library, Arizona State University, Tempe).

⁴Appendix 1--1.

⁵Appendix 1--2.

FIGURE LEGENDS

Figure 1--1: (Top) Adult female humpback chub (*Gila cypha*) captured by trammel net at confluence of Little Colorado and mainstream Colorado rivers (Grand Canyon National Park, Coconino Co., AZ); (bottom) adult male humpback chub (*Gila cypha*) captured by hoop net in Little Colorado River near Salt Trail Camp, 12.8 km above confluence (Navajo Indian Reservation, Coconino Co., AZ).

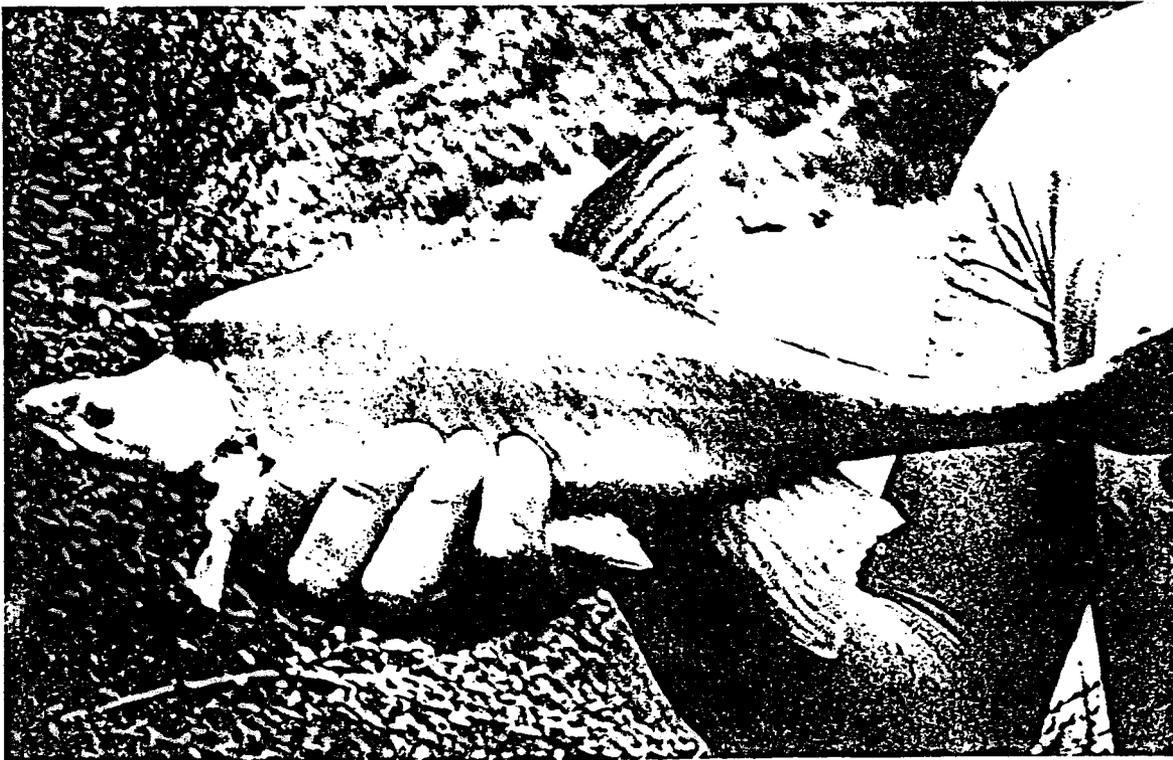
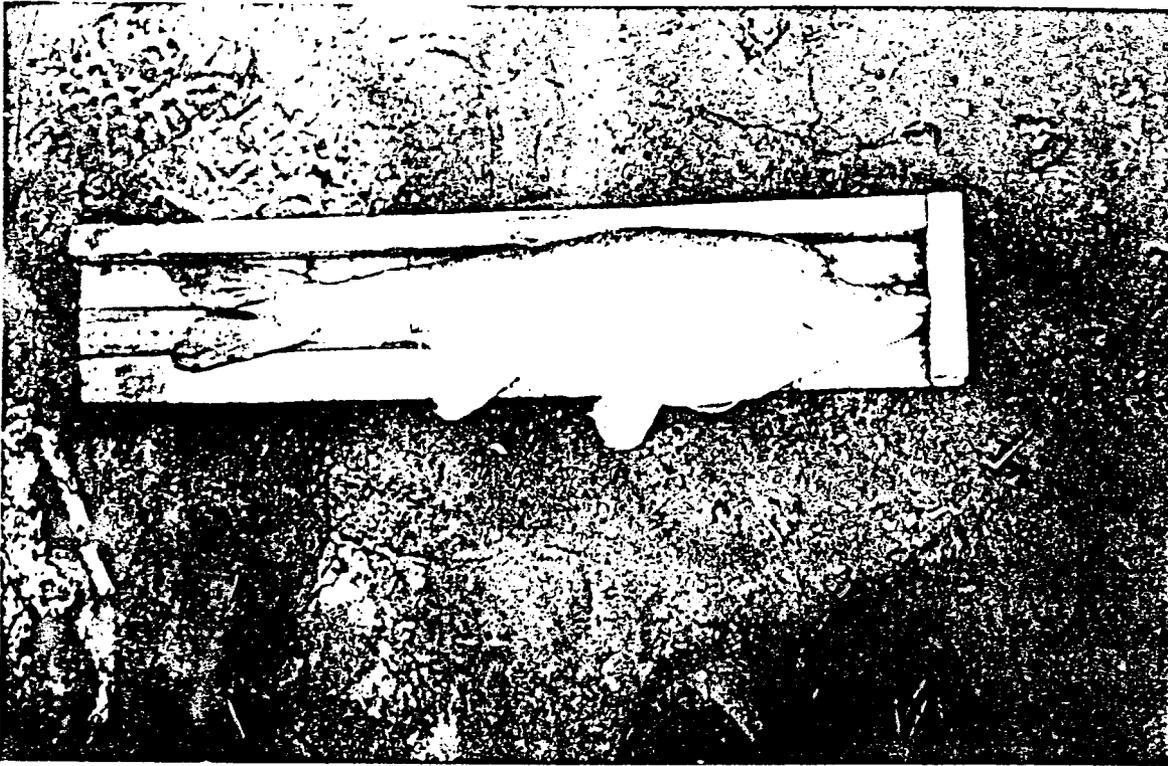
Figure 1--2a : Map of the Colorado River basin, depicting dams, reservoirs, and component rivers.

Figure 1--2b: Map of the lower Little Colorado River, from Blue Springs (21 km above confluence; Navajo Indian Reservation, Coconino Co., AZ) to its confluence with the Colorado River in Marble Canyon (Grand Canyon National Park, Coconino Co., AZ). Confluence is 99 km below Glen Canyon dam.

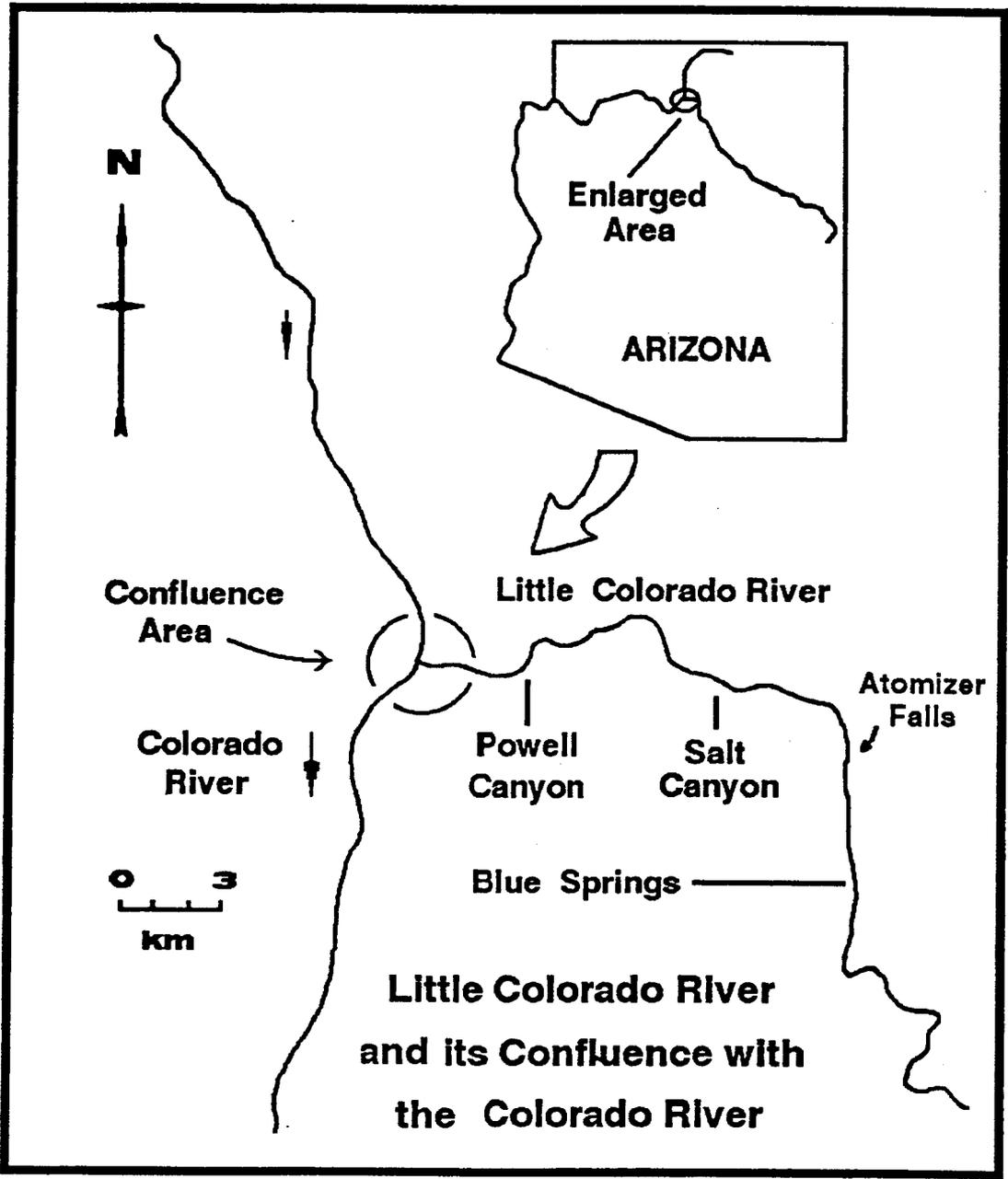
Figure 1--3a: Three-dimensional plot of population estimates by reach (where C = Confluence; P = Powell; and S = Salt) during July--December of 1991.

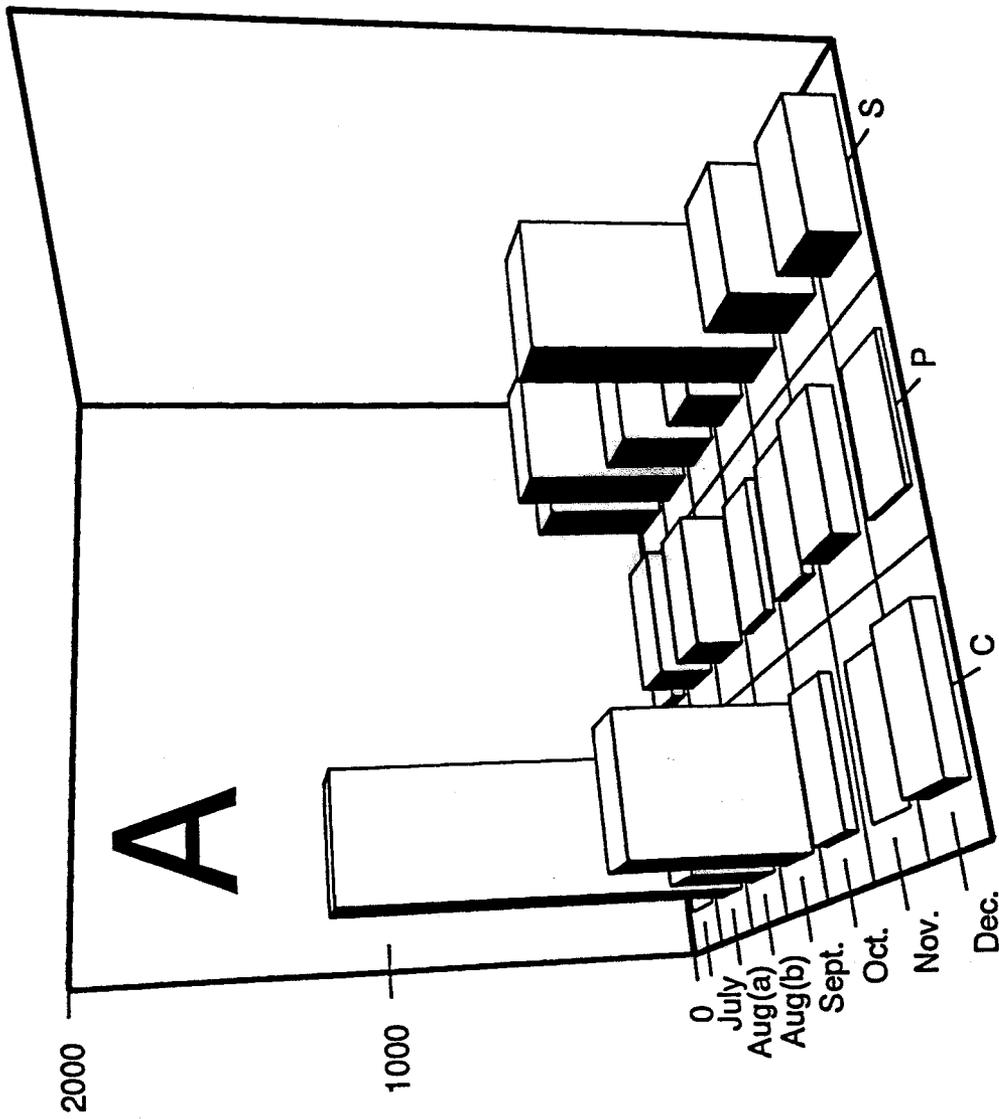
Figure 1--3b: Three-dimensional plot of population estimates by reach (where C = Confluence; P = Powell; and S = Salt) during January--November of 1992.

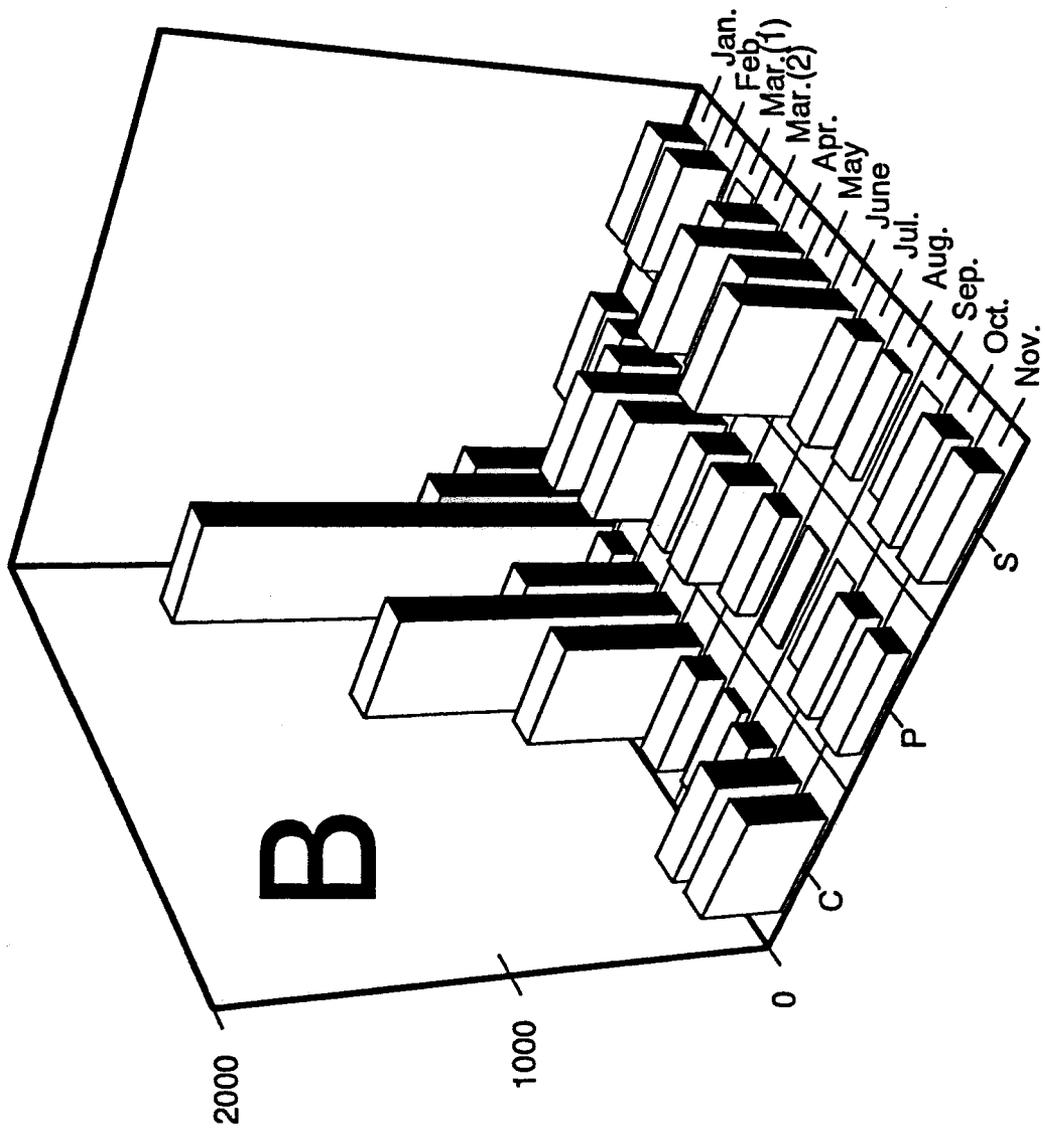
Figure 1--4: Bivariate plot of population estimates for 1991--92 by month (solid line) and by month summed over reach (dashed line).

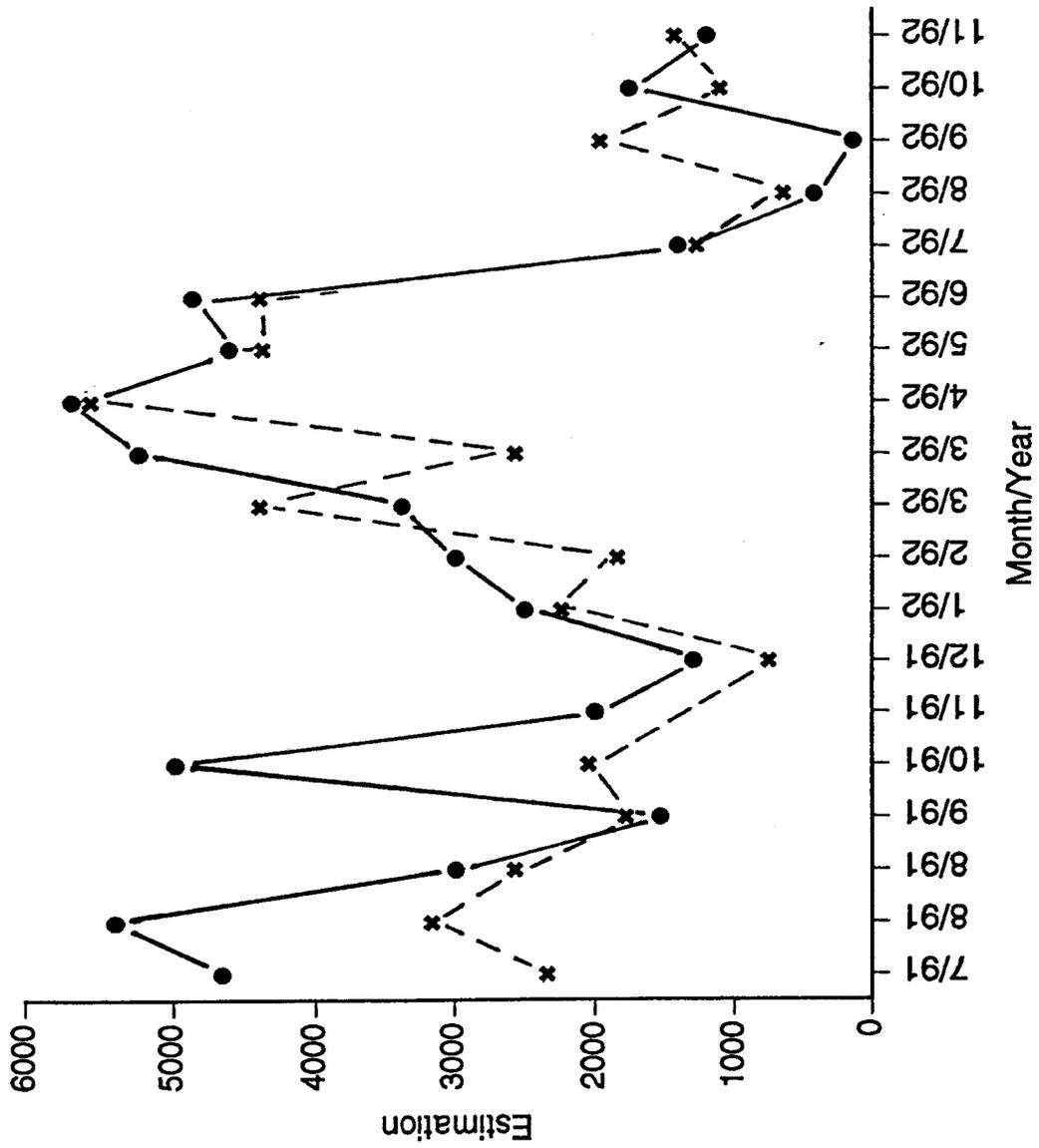












DRAFT

SECTION 2:

ENDANGERED HUMPBACK CHUB, *GILA CYPHA*, AS PREY OF
INDRODUCED FISHES IN THE LITTLE COLORADO RIVER, ARIZONA,
WITH NOTES ON FISH STOCKING IN THE GRAND CANYON REGION

ABSTRACT

Endangered humpback chub and other native fishes were a significant dietary components (13.5% of 408 stomachs) of five predatory, non-native fishes from the Little Colorado River, Arizona. Stomach contents varied among species, were low in diversity, and predominated by detritus, algae (primarily Cladophora), and aquatic insects. Twenty-one introduced species occur in Grand Canyon, and more than 25.8 million fish have been stocked there and in reservoirs immediately up- and downstream. Interaction between non-native and native fishes (predation, resource competition, displacement) may constitute a significant impact on the latter.

INTRODUCTION

Interactions between native and introduced species have been implicated in extirpations of indigenous fishes around the globe (reviewed in Courtenay and Stauffer 1984, Welcomme 1988, Pollard 1989, and Rosenfield and Mann 1992). Some mechanisms of direct interaction (e.g., displacement through resource competition) are elusive and difficult to demonstrate convincingly (Douglas et al., 1994), while others such as hybridization or predation may be more easily quantified. Among examples of the last are catastrophic destruction of perhaps hundreds of endemic species in lakes Victoria and Kyoga, Africa, by Nile perch, Lates niloticus (Ogutu-Ohwayo 1985, Barel et al. 1985, Ribbink 1987); elimination of seven local species from Gatun Lake, Panama, by tucanare, Cichla ocellaris (Zaret and Paine 1973); reduction of native salmonids in Lake Ohrid, Yugoslavia, by rainbow trout, Oncorhynchus mykiss (Nijssen and de Groot 1974); and elimination of Galaxias divergens and G. argenteus from New Zealand streams into which brown trout, Salmo trutta, had been introduced (McDowall 1984).

Native fishes of the Colorado River basin of western North America have been impacted similarly. Here an historically depauperate ichthyofauna of 36 species (many polytypic) has been subjected to interactions imposed by a suite of approximately 70 non-native fishes brought intentionally or inadvertently to the region. Coincident with introductions and habitat alteration resulting from development of water resources, the native fauna declined precipitously. Three native kinds are extinct, 22 others are listed as endangered or threatened, and the remainder (with few exceptions) is inarguably imperiled by continuing threats. Predation and competition by introduced fishes has been cited among primary factors resulting in the present faunal status (Dill 1944, Miller 1946, 1961; Moyle et al. 1986, Minckley and Deacon 1968, 1991), but only recently have become a focus of conservation planning in behalf of the native resources. Despite this awareness, management entities have been unwilling with few local exceptions to implement measures to reduce or eliminate predatory and competitive introduced fishes to benefit natives.

In this paper we focus on predation as a mechanism of interaction between endangered native humpback chub, Gila cypha (Cyprinidae), and introduced channel catfish, Ictalurus punctatus (Ictaluridae), in the Little Colorado River, Arizona. Humpback chub is concentrated in that stream (Douglas and Marsh, 1996), and channel catfish is the most abundant co-occurring non-native predator in the system.

The humpback chub is a moderate-sized minnow endemic to larger streams of the Colorado River basin. The species historically was found in canyon-bound reaches of mainstreams and

major tributaries from near Black Canyon, Arizona-Nevada, upstream into Colorado, Utah, and Wyoming. It was generally uncommon, but locally concentrated (Holden and Minckley 1980). A combination of factors including habitat loss and modification, hybridization with congeners, and potential interactions with non-native fishes has resulted in constricted range and local depletion of humpback chub, which persists only in seven reaches among four rivers (USFWS 1990). The largest remaining population is in the Little Colorado River, the major tributary to the Colorado River in Grand Canyon; it also occurs in fewer numbers in the mainstem. Humpback chub has been federally listed as endangered since 1967.

Channel catfish has been introduced worldwide from its native range in central drainages of United States and southern Canada (Glodek 1980, Welcomme 1988). It was first stocked in the lower Colorado River in 1892--93 (Miller and Alcorn 1945), and since planted elsewhere or dispersed to become ubiquitous. Historically valuable as a food fish, it now supports commercial and recreational fisheries of variable importance throughout its range. This opportunistic omnivore also represents, however, a potential threat to indigenous organisms occupying habitats in which the catfish is exotic, and may represent a deterrent to recovery for some imperiled species (Marsh and Brooks 1988). Channel catfish have been present in Grand Canyon for most of this century (USFWS 1980), and was a predominant species prior to closure of Glen Canyon Dam in 1963 (Smith 1959). Recent records indicate rarity to local abundance in the mainstem (Holden and Stalnaker 1975, Arizona Game and Fish Department, and Bio/West, Inc., unpublished); it is common in the Little Colorado River (P. C. Marsh and M. E. Douglas, unpubl.).

Predation by channel catfish on humpback chub is suggested by crescent-shaped wounds interpreted as bite marks (Kaeding and Zimmerman 1983, Karp and Tyus 1990), and documented from stomachs of channel catfish captured in hoop nets (C.O. Minckley, USFWS, pers. comm.); such predation has not been quantified.

A suite of other non-native fishes (APPENDIX 2--A) has been introduced into the Colorado River for food, sport, forage, or by accident. Many have established self-sustaining populations and naturally expanded their ranges, while others are repeatedly stocked to sustain angler harvest (APPENDIX 2--B). These stockings are conducted by the same agencies charged with protection and recovery of imperiled native fishes. Potential predators in addition to channel catfish encountered in or near the Little Colorado River include brown trout, Salmo trutta; black bullhead, Ameiurus melas, yellow bullhead, A. natalis, striped bass, Morone saxatilis (all uncommon); and rainbow trout, Oncorhynchus mykiss (common). There are no published reports of humpback chub among prey of these species.

We report results of stomach analyses from predatory non-native fishes captured in the Little Colorado River during 1991-1992, and provide an assessment of the potential impact of this predation on endangered humpback chub. We also examine other potential mechanisms of interaction between native and introduced fishes, and record the history of fish non-native stocking in the Grand Canyon region.

STUDY SITE AND METHODS

The Little Colorado River headwaters are in mountainous highlands of east-central Arizona and western New Mexico, from where flow infiltrates underground during most months and does not reach Grand Canyon except during flood conditions. Perennial flow (ca. $6.2 \text{ m}^3 \text{ s}^{-1}$) in the Grand Canyon reach originates in a series of springs beginning at Blue Spring, about 21 km upstream from the Little Colorado-Colorado confluence, augmented downstream by smaller sources. The Little Colorado River at base flow is a saline (conductivity exceeding $5,000 \text{ umhos/cm}$), travertine-forming stream whose water chemistry changes downstream as a result of CO_2 degassing and carbonate degassing (Cole and Kubly 1976); its complex limnology is not well understood. Water clarity scarcely approaches a meter due to suspended carbonates, and is nil during even minor spates as a result of suspended sediments. During our studies, discharge ranged from base flow to approximately $425 \text{ m}^3 \text{ s}^{-1}$, and water temperature was 8 to 25 C.

Native fishes of the Little Colorado River in Grand Canyon include humpback chub, bonytail (*Gila elegans*, extirpated), roundtail chub (*G. robusta*, extirpated), Colorado squawfish (*Ptychocheilus lucius*, extirpated), speckled dace (*Rhinichthys osculus*), and flannelmouth (*Catostomus latipinnis*), bluehead (*Pantosteus discobolus*) and razorback (*Xyrauchen texanus*) suckers. All species that persist are common, with exception of razorback sucker, which is rare.

Non-native fishes include brown and rainbow trouts, carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*), channel catfish and black and yellow bullheads, plains killifish (*Fundulus zebrinus*), green sunfish (*Lepomis cyanellus*) and striped bass. Other species have been introduced or otherwise recorded in tributaries and/or up- and downstream in Grand Canyon (APPENDIX 2--A; Minckley 1991), but none has yet been found in the Little Colorado River.

We established camps at Salt Canyon (river km 10.6 [RK, measured upstream from the Colorado confluence), Powell Canyon (RK 3.0) and near the Colorado confluence (RK 0.6), which allowed access to the 21-km of perennial flow in the Little Colorado

River. A series of precipitous (to 3 m) travertine falls at RK 15 marks the upstream limit of distribution of humpback chub in the Little Colorado River; only carp, speckled dace, fathead minnow, and rainbow trout were found above this point. Sampling above this reach thus was limited to short-term survey-type collections in summer.

Fishes were captured during 19 trips at approximately monthly intervals from July 1991 to December 1992. Hoop nets (0.76 or 1.2 m dia, 2.4 or 3.0 m-length, 4 or 6 hoop, single or double throat) were deployed in all available habitat types of sufficient depth (> about 0.4 m). Trammel nets (7.6 to 45.7 m length, 1.8 m depth, 1.3 to 3.8 mm inner and 30 mm outer meshes) were set routinely in the Little Colorado-Colorado confluence area and occasionally near Powell and Salt canyons (below) in water deeper than about 0.5 m. Angling with baited hooks and artificial lures was performed sporadically throughout the stream.

All fishes were removed from capture devices, identified, counted, measured (TL to nearest mm), and weighed (nearest g). Native species were released near the point of capture after processing. Non-native fishes typically were scanned for presence of PIT tags (which could be present if tagged native fishes were consumed), then sacrificed and either dissected immediately and examined for stomach contents, or preserved in 95% ethanol for later study (the latter primarily of specimens < 100 mm TL). The entire digestive tract was examined and foods determined categorically. Fish prey were examined to determine identity and TL. Material returned to the laboratory was examined microscopically for larval fishes.

RESULTS AND DISCUSSION

Predation by Introduced Fishes.--Identifiable humpback chub remains were in 13 (3.2%) of 408 total digestive tracts of five predator species examined (Table 2--1). Other fishes (speckled dace, bluehead and flannelmouth suckers and undetermined remains) were found in stomachs of 51 predators, five of which had also eaten humpback chub. Mean lengths of humpback chubs in stomachs (102 mm TL; n = 27) did not differ significantly (two-sample t-test, Snedecor and Cochran 1967) from that of other ingested fishes (92 mm TL; n = 37). No larval or small post-larval fishes were found in any predator stomachs. Sample sizes for brown trout, black bullhead, and yellow bullhead were too small (10 to 12) to provide definitive results.

Three of 174 rainbow trout contained humpback chub (prey length 40--45 mm), and two of 12 black bullheads also contained chubs (49--55 mm TL). Speckled dace and unidentified fish were

consumed by two of 10 brown trout, and fish remains were detected in two of 10 yellow bullheads.

Eight of 202 channel catfish each contained one to seven chubs, 85 to 200 mm TL; remains of other species were in 25 stomachs. Channel catfish that consumed humpback chub and other fishes averaged 500 mm TL and were larger than those that had not eaten fish, a result supported by Tyus and Nikirk (1990).

Algae (primarily Cladophora) predominated in rainbow trout (47%), and fish were the most abundant prey item of the other species (10--20%; Table 2--2). Rainbow trout and channel catfish also consumed a variety of other items, including vegetation, an amphipod (Gammarus lacustris), aquatic insect larvae, and terrestrial invertebrates. Brown trout contained only terrestrial insects and fish (20% each); black bullheads ate detritus (8%), aquatic insects (16%), and fish (17%); and yellow bullheads contained odonate naiads (10%), and fish (20%). Proportion of empty stomachs varied among species from six to 70% (Table 2--2).

Food habits of potential piscivores were unremarkable. The relatively low diversity of food items likely reflected a paucity of food in the Little Colorado River. Diets of individual species were qualitatively consistent with other reports from the Colorado River basin (AZGFD 1987, Marsh 1981, Minckley 1973, 1982, Tyus and Nikirk (1990) and elsewhere (Calhoun 1966). All studies concluded that channel catfish were opportunistic omnivores and that fish were a small part of their diet.

Our failure to detect larval and smaller juvenile prey may reflect the transient presence in predator guts of visually identifiable remains of these fragile life stages. Humpback chub is represented in several areas by seemingly sustaining populations, but assessment of the effects of predation on early life stages on long-term population viability cannot be made until suitable methods to quantify this predation are worked out.

Predatory fishes represent a threat to humpback chub in the Little Colorado River and they may exert a major negative effect on the population there. For example, our data conservatively indicate that about 3% of rainbow trout and channel catfish combined ate an average of 2.3 humpback chubs, and other species also ate humpback chub. If a humpback chub meal is taken once a week, a predator population of 1,000 would annually consume 3,588 humpback chub. Numbers of predatory fishes likely number in the thousands. Most humpback chubs in predator stomachs were juveniles, but channel catfish ate humpback chub as large as 200 mm TL and other fish up to 250 mm (Table 2--2). Recent population estimates generated under five different models for adult (> 150 mm TL) humpback chub in the Little Colorado River were 4,508 to 10,444 (Douglas and Marsh 1996). Predation thus may limit recruitment by removing juveniles from the population

and increase total mortality of adults.

Non-native Fishes and Stocking in the Grand Canyon.--Twenty introduced non-native species are known from the Colorado River in Grand Canyon (APPENDIX 2--A). Rainbow, cutthroat, brook, and brown trouts, carp, and channel catfish were present prior to downstream closure of Boulder (Hoover) Dam in 1935 and filling of Lake Mead. Salmonids were stocked directly into Grand Canyon beginning in the 1920s (APPENDIX 2--B). A suite of warm- and coldwater sport (salmonids and centrarchids, plus striped bass) and forage species was stocked to establish recreational fisheries in Lake Mead, and these had access to lower Grand Canyon. Fathead minnow and plains killifish were first found in Grand Canyon between 1935 and 1963. Glen Canyon Dam was completed upstream in 1963, and sport-forage fish introductions to Lake Powell and the tailwaters in Glen Canyon (Lees Ferry reach) began immediately (APPENDIX 2--B). Smallmouth bass was first stocked into Lake Powell in 1982, and a proposal to introduce rainbow smelt (*Osmeria*: *Osmerus mordax*) has recently been entertained. Other, new species undoubtedly will be considered in the future.

Numbers of individuals introduced (nearly 26 million) are staggering, even when spread over a period of years. More than 900,000 salmonids were stocked in Grand Canyon between 1920 and 1978, and 2.6 million have been planted in Glen Canyon since 1964. Nearly 2.5 million fish were stocked in Lake Mead (beginning in 1935) and 19.8 million have been stocked into Lake Powell since 1963. Introductions to all but Grand Canyon continue apace.

CONCLUSION

Native Colorado River fishes that persist in the Grand Canyon are common only in tributaries. Populations in the mainstem are small or concentrated near tributary mouths. Established or continually replenished stocks of predatory fishes in the mainstem undoubtedly impose severe constraints on native fishes by predation on young, and perhaps in other ways. Conditions in some tributaries like the Little Colorado River remain relatively unaltered by human development. Although these streams apparently retain a natural character (particularly hydrologic features) thought to favor native relative to introduced fishes (Minckley and Meffe 1987), predation impacts may limit native species recruitment and abundance.

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TABLE 2--1: Number and mean, minimum, and maximum total length (TL, mm) of introduced piscivores and their fish prey in the Little Colorado River, Arizona, July 1991-June 1995. Some prey (ND) were in states of digestion that prevented species identification, measurement, or both.

Predator	N	Mean	Min	Max	Prey	N	Mean	Min	Max
Rainbow trout	3	356	332	398	Humpback chub	3	43	40	45
	2	372	370	373	Speckled dace	2	60	45	75
	2	353	335	370	Fathead minnow	5	42	30	60
	1	355	355	355	Carp	1	60	60	60
	1	375	375	375	Flannelmouth sucker	1	78	78	78
	1	350	350	350	Bluehead sucker	1	ND	ND	ND
	4	351	319	383	ND Cyprinidae	9	46	30	65
	1	341	341	341	ND Catostomidae	1	43	43	43
	10	345	313	389	ND	16	96	34	>150
Totals	25	352	313	398		39	59	30	>150
Channel catfish	8	554	375	790	Humpback chub	22	115	85	200
	5	453	271	594	Speckled dace	6	67	60	75
	1	482	482	482	Fathead minnow	1	60	60	60

Predator	N	Mean	Min	Max	Prey	N	Mean	Min	Max
	1	476	476	476	Carp	1	116	116	116
	2	525	455	594	Flannelmouth sucker	2	175	150	200
	4	599	582	605	Bluehead sucker	5	211	150	250
	2	480	477	482	ND Cyprinidae	6	58	40	80
Totals	33	500	271	790		54	114	58	250
Yellow bullhead	1	167	167	167	ND Cyprinidae	3	39	37	41
	1	171	171	171	ND	1 > 10 0	>10 0	>1 00	>10 0
Totals	2	1669	167	171		4	54	37	>10 0
Black bullhead	2	152	134	169	Humpback chub	2	52	49	55
Brown trout	1	341	341	341	Speckled dace	1	77	77	77
	1	566	566	566	ND	1	118	118	118
Totals	2	454	341	566		2	98	77	118

TABLE 2--2: Frequency of occurrence of food items as percentage of total stomachs examined for each of five species of predatory non-native fishes collected in the Little Colorado River, Arizona, July 1991-June 1995. ND = not determined.

Food item	Rainbow trout	Brown trout	Channel catfish	Black bullhead	Yellow bullhead
Detritus	0	0	3	8	10
Vegetation	9	0	5	0	0
Algae ^a	47	0	10	0	0
<u>Gammarus</u>	12	0	2	0	0
Corydalidae	1	0	2	0	0
Simuliidae	19	0	4	0	0
Chironomidae	14	0	1	0	0
Gastropoda	1	0	0	0	0
Oligochaeta	0	0	1	0	0
Odonata	0	0	1	0	0
Tipulidae	0	0	1	8	0
Coleoptera	3	0	1	0	0
Ceratopogonidae	0	0	1	8	0
Trichoptera	1	0	0	0	0
ND aquatic insects	1	0	9	0	0
ND terrestrials	3	20	4	0	0
Humpback chub	2	0	4	17	0
Speckled dace	1	10	2	0	0
Carp	1	0	1	0	0
Bluehead sucker	1	0	2	0	0
Flannelmouth sucker	1	0	1	0	0
Fathead minnow	1	0	1	0	0

Food item	Rainbow trout	Brown trout	Channel catfish	Black bullhead	Yellow bullhead
ND Fish	6	10	5	0	10
Fish eggs	1	10	1	0	0
Number of stomachs	174	10	202	12	10
Number and percent empty	60/34	7/70	111/55	5/42	6/60
Mean and range of total length (mm)	354 210-491	397 296-566	286 37-796	158 70-228	166 75-212

*Primarily Cladophora

APPENDIX 2--A. Dates of first introductions to the Colorado River basin of non-native fishes known from Grand Canyon, Arizona. Compiled from USFWS (1980), Minckley (1991), and authorities indicated. Acronyms as follows: AZGFD (Arizona Game and Fish Department), NVDOW (Nevada Department of Wildlife), and UTDRW (Utah Division of Wildlife Resources).

Species	Date(s)	Location	Authority
CLUPEIDAE			
<u>Dorosoma petenense</u>	1953	Lake Mead	LaRivers 1962
SALMONIIDAE*			
<u>Oncorhynchus clarki</u>	1962	Lake Mohave	NVDOW files
<u>O. kisutch</u>	1966	below Davis Dam	NVDOW files
<u>O. mykiss</u>	1922	Grand Canyon	Williamson and Tyler 1932
<u>Salmo trutta</u>	1924	Grand Canyon	ibid
<u>Salvelinus fontinalis</u>	1920	Grand Canyon	ibid
CYPRINIDAE			
<u>Cyprinus carpio</u>	1890	lower river	Gilbert and Scofield 1898
<u>Cyprinella lutrensis</u>	< 1953	lower river	Shapovalov and Dill 1959
<u>Notemigonus crysoleucas</u>	< 1953	lower river	ibid
<u>Pimephales promelas</u>	1950s	lower river	Miller and Lowe 1967
<u>Richardsonius balteatus</u>	1950	lower river	Miller 1952
ICTALURIDAE			
<u>Ameiurus melas</u>	1904	lower river	AZGFD 1977
<u>A. natalis</u>	1899	lower river	Beland 1954

<u>Ictalurus punctatus</u>	1892-93	lower river	Miller and Alcorn 1945
FUNDULIDAE			
<u>Fundulus zebrinus</u>	1950	lower river	Miller 1952
POECILIIDAE			
<u>Gambusia affinis</u>	1922	California	Dill 1944
CENTRARCHIDAE			
<u>Lepomis cyanellus</u>	1937-42	lower river	Jonez and Sumner 1954
<u>L. macrochirus</u>	1937	Lake Mead	Wallis 1951
<u>Micropterus salmoides</u>	1890	Utah	Sigler and Miller 1963
	1935	Lake Mead	Jonez and Sumner 1954
PERCIDAE			
<u>Stizostedion vitreum^b</u>	1951	Utah	Sigler and Miller 1963
PERCICHTHYIDAE			
<u>Morone saxatilis</u>	1959	lower river	St. Amant 1959

^aOncorhynchus apache, endemic to headwaters of the Salt and Little Colorado rivers (Colorado River drainage), Arizona, was transplanted by AZGFD in 1963, 1968, and 1978 to North Canyon Creek, a Colorado River tributary in Grand Canyon (Minckley and Brooks 1985). A population persists there, but the species has not otherwise been recorded in Grand Canyon.

^bWalleye was present in the Colorado River in Utah prior to closure of Glen Canyon Dam in 1963, and later became established in the reservoir (UTDWR, unpublished). An individual was captured in 1971 at Lees Ferry, Arizona (AZGFD, unpublished), but the species has not since been encountered in Grand Canyon.

APPENDIX 2--B. Non-native fish stocking in the Colorado River from Lake Powell, Arizona-Utah, to Hoover (Boulder) dam site, Arizona-Nevada, including the Grand Canyon reach, through 1991. Compiled from Williamson and Tyler 1924, Miller and Alcorn 1953, Jonez and Sumner 1953, AZGFD 1977, Allan and Roden 1978, USFWS 1980, and agency files. Acronyms for stocking agency as follows: AZFC (Arizona Fish Commission), AZGFD (Arizona Game and Fish Department), NPS (National Park Service, Grand Canyon National Park), NVDOW (Nevada Department of Wildlife), UTDWR (Utah Division of Wildlife Resources), USFC (U.S. Fish Commission), USFS (U.S. Forest Service), and USFWS (U.S. Fish and Wildlife Service, including when named Bureau of Sport Fisheries and Wildlife). Stockings were variously of embryos, larvae, juveniles, and adults (not differentiated here). Four localities are indicated, up- to downstream: Powell (Lake Powell), Glen (Glen Canyon dam site downstream to Lees Ferry), Grand Canyon (Lees Ferry downstream to Separation Canyon), and Mead (Separation Canyon downstream to site of Hoover [Boulder] Dam).

Species	Date(s)	Number	Agency	Locality
<u>Dorosoma petenense</u>	1968-69	201500	UTDWR	Powell
	1954-55	11650	NVDOW	Mead
<u>Oncorhynchus kisutch</u>	1969-72	20000	AZGFD	Glen
	1969-73	426151	AZGFD NVDOW	Mead
<u>Q. nerka</u>	1963-65	660000	AZGFD UTDWR	Powell
<u>Q. mykiss</u>	1963-80	15688501	AZGFD UTDWR	Powell

<u>O. clarki</u>	1964-91	1924489	AZGFD USFWS	Glen
	1922-63	461800	AZGFD NPS USFS USFWS	Grand Canyon
	1944-91	3336600	AZGFD NVDOW USFWS	Mead
	1925-78	> 600000	AZGFD	Grand Canyon
	1978-80	60857	AZGFD	Glen
	1972-77	200996	NVDOW	Mead
<u>O. mykiss x O. clarki</u>	1975-77	96176	NVDOW	Mead
<u>Salmo trutta</u>	1924-78	295000	AZGFD NPS	Grand Canyon
	1978-80	78818	NVDOW	Mead
<u>Salvelinus fontinalis</u>	1977-87	606009	AZGFD	Glen
	1920-31	90000	NPS	Grand Canyon
<u>Cyprinus carpio</u>	1881-91	unknown	AZFC USFC	Mead
<u>Micropterus dolomieu</u>	1982-88	272672	UTDWR	Powell
<u>Micropterus salmoides</u>	1963-64	2924000	UTDWR	Powell
	1935-81	794929	AZGFD NVDOW	Mead

<u>Lepomis macrochirus</u>	1937-42	952770	USFWS	USFWS	Mead
<u>Pomoxis nigromaculatus</u>	1964-91	51021	AZGFD UTDWR	AZGFD UTDWR	Powell
<u>Morone saxatilis</u>	1974-79 1969-72	815318 60334	UTDWR AZGFD	UTDWR AZGFD	Powell Mead

APPENDIX 2--B. Non-native fish stocking in the Colorado River from Lake Powell, Arizona-Utah, to Hoover (Boulder) dam site, Arizona-Nevada, including the Grand Canyon reach, through 1990. Compiled from Williamson and Tyler 1924, Miller and Alcorn 1953, Jones and Sumner 1953, AZGFD 1977, USFWS 1980, and agency files. Acronyms for stocking agency as follows: AZFC (Arizona Fish Commission), AZGFD (Arizona Game and Fish Department), NPS (National Park Service, Grand Canyon National Park), NVDFG (Nevada Department of Fish and Game), UTDWR (Utah Division of Wildlife Resources), USFC (U.S. Fish Commission), USFS (U.S. Forest Service), and USFWS (U.S. Fish and Wildlife Service, including when named Bureau of Sport Fisheries and Wildlife). Stockings were variously of embryos, larvae, juveniles, and adults (not differentiated here). Four localities are indicated, up- to downstream: Powell (Lake Powell), Glen (Glen Canyon dam site downstream to Lees Ferry), Grand Canyon (Lees Ferry downstream to Separation Canyon), and Mead (Separation Canyon downstream to site of Hoover [Boulder] Dam).

Species	Date(s)	Number	Agency	Locality
<u>Dorosoma</u> <u>petenense</u>	1954	274	NVDFG	Mead
	1955	11376	NVDFG	Mead
	1968	1500	UTDWR	Powell
	1969	200000	UTDWR	Powell
<u>Oncorhynchus</u> <u>kisutch</u>	1969	36700	AZGFD	Mead
	1970	56116	NVDFG	Mead
	1971	84335	AZGFD	Glen, Mead
	1972	169000	AZGFD	Mead
	1973	100000	AZGFD	Mead

Q. nerka^a

1963	600000	UTDWR	Powell
1964	35000	UTDWR	Powell
1922	5000	USFS	Grand Canyon
1923	20000	NPS	Grand Canyon
1924	6000	NPS	Grand Canyon
1925	50000	NPS	Grand Canyon
1930	100000	NPS	Grand Canyon
1931	25000	NPS	Grand Canyon
1932	25000	NPS	Grand Canyon
1940	50000	AZGFD	Grand Canyon
1942	30000	AZGFD	Grand Canyon
1944	5200	AZGFD	Mead
1948	15000	AZGFD	Grand Canyon
1950	50400	AZGFD	Grand Canyon
1958	51000	AZGFD	Grand Canyon
1963	1835000	UTDOW	Powell
	34400	USFWS	Grand Canyon
1964	3691380	UTDOW	Powell
1965	4423525	UTDWR	Powell
	7830	AZGFD	Glen
	2550	USFWS	Mead
1966	2140000	UTDWR	Powell
	1500	AZGFD	Glen
	650	USFWS	Glen
1967	549844	UTDWR	Powell
	575	USFWS	Glen
1968	201364	UTDWR	Powell
	8300	AZGFD	Glen
	2493	USFWS	Glen
1969	251238	UTDWR	Powell

Q. mykiss

158219	AZGFD	Glen, Mead
41650	NVDFG	Mead
24375	AZGFD	Glen
154000	NVDFG	Mead
848000	UTDWR	Powell
54535	AZGFD	Mead
13643	NVDFG	Mead
4585	AZGFD	Glen
146392-	NVDFG	Mead
180486		
233400	UTDWR	Powell
3675	AZGFD	Glen
164542-	NVDFG	Mead
172477		
249857-	NVDFG	Mead
254240		
782,536-	NFDFG	Mead
801-861		
50000	UTDWR	Powell
100000	AZGFD	Glen
650440	NVDGF	Mead
18600	UTDWR	Powell
95000	AZGFD	Glen
112034-	NVDFG	Mead
144321		
50000	AZGFD	Glen
13210	UTDWR	Powell
1970		
1971		
1972		
1973		
1974		
1975		
1976		
1977		
1978		
1980		
1925	AZGFD	Grand Canyon
1972	NVDFG	Mead
1975	NVDFG	Mead

O. clarki

<u>O. mykiss</u> x <u>O. clarki</u> hybrid	1976	120373	NVDFG	Mead
	1977	14416-15514	NVDFG	Mead
	1978	60000	AZGFD	Grand Canyon
	1975	28908	NVDFG	Mead
	1977	67268	NVDFG	Mead
<u>Salmo trutta</u>	1924	50000	NPS	Grand Canyon
	1930	145000	NPS	Grand Canyon
	1977	unknown	AZGFD	Grand Canyon
	1978	100000	AZGFD	Grand Canyon
<u>Salvelinus fontinalis</u>	1920	5000	NPS	Grand Canyon
	1927	60000	NPS	Grand Canyon
	1931	25000	NPS	Grand Canyon
	1977	47880	AZGFD	Glen
<u>Cyprinus carpio</u>	1881-91	unknown	USFC AZFC	Mead
<u>Micropterus dolomieu</u> ^a	1982	3159	UTDWR	Powell
	1984	30600	UTDWR	Powell
	1985	104115	UTDWR	Powell
	1986	27017	UTDWR	Powell
	1987	34770	UTDWR	Powell
	1988	71031	UTDWR	Powell
<u>Micropterus salmoides</u>	1935	14625	USFWS	Mead
	1937	325000	USFWS	Mead
	1938	21000	USFWS	Mead

<u>Lepomis macrochirus</u>	1939	80000- 200000	USFWS	Mead
	1940	56000	USFWS	Mead
	1941	32000	USFWS	Mead
	1942	49000	USFWS	Mead
	1963	924000	UTDWR	Powell
	1964	2000000	UTDWR	Powell
	1964	197000	NVDFG	Mead
	1937	25000	USFWS	Mead
	1940	18000	USFWS	Mead
	1941	320000	USFWS	Mead
	1942	12145	USFWS	Mead
<u>Pomoxis nigromaculatus</u> ¹	1964	9350	UTDWR	Powell
	1965	34700	UTDWR	Powell
<u>Morone saxatilis</u>	1969	10000	NVDFG	Mead
	1970	16300	NVDFG	Mead
	1971	1034	NVDFG	Mead
	1972	1000	AZGFD	Mead
		2000	NVDFG	Mead
	1974	49885	UTDWR	Powell
	1975	94878	UTDWR	Powell
	1976	55062	UTDWR	Powell
	1977	138653	UTDWR	Powell
	1978	254290	UTDWR	Powell
	1979	222550	UTDWR	Powell

¹Not yet recorded from the Colorado River in Grand Canyon.

DRAFT

SECTION 3:

**CATOSTOMIDAE OF THE GRAND CANYON REGION OF ARIZONA:
POPULATION ESTIMATES, MOVEMENTS AND
SURVIVABILITY**

INTRODUCTION

THE Colorado River Basin comprises nearly 650,000 km² of the most arid terrain in western North America (Fig. 1--1a). As with most major basins, it is composed of several discrete divisions (Minckley et al., 1986). For example, the upper basin Colorado and Green rivers (and tributaries) form a distinct zoogeographic entity, for they terminated into closed basins prior to Pliocene. Southward, a "contemporary middle segment" drains southwestward and is composed of the White, Virgin, and Little Colorado rivers (and parts of the Bill Williams drainage). It effectively straddles both upper and lower Colorado River basins (which are artificially demarcated at the northern terminus of Grand Canyon). The lowermost section of the basin consists of the Colorado and Gila rivers. Major changes have occurred in these various sections as a result of dam construction and chronic dewatering for agriculture and urban development. The 2400 km of riverine habitat suitable for large-river fishes has now been reduced to 965 km (Miller, 1982).

Because of their uniqueness, fishes of the Colorado basin attracted early scientific interest (reviewed by Minckley et al., 1986). Numerous ichthyologists established (or enhanced) reputations by describing new species from collections made during military campaigns, government boundary surveys, and expeditions seeking westward routes of transportation (Minckley and Douglas, 1991). Minckley et al. (1986:580) separated endemic Colorado River basin fishes into three major categories: "Big-river-forms" which range throughout the system in larger streams; "small-stream-low-elevation-forms" which occupy smaller tributaries at low-to-intermediate elevations; and finally, "small-stream-high-elevation-forms" found at high-to-intermediate elevations and which either straddle drainages or have near relatives in adjacent ones. In this manuscript, all three study species {i.e, flannelmouth sucker [*Catostomus latipinnis*], bluehead sucker [*Catostomus (Pantosteus) discobolus*], and razorback sucker [*Xyrauchen texanus*]} are components of Minckley et al.'s "big-river fauna;" each was described from materials collected during the period of western exploration (see Appendix 3--1).

The big-river fish fauna of the Colorado is comprised of seven species (four cyprinids and three catostomids). Four of these are now listed as endangered, one is a candidate for listing, one is under review, and one is believed safe (see Table 3--1) (USFWS, 1994). The species which comprise the latter two categories (*C. latipinnis* and *C. discobolus*, respectively) are ecologically enigmatic (Appendix 3--1; see below). This paucity of information stems from several factors. Native fish work in western North America has focused primarily upon threatened or

endangered (i.e., T/E) species. Derivation of baseline data for species not as yet pushed to the brink of extinction should also be a major imperative. It seldom is.

Another factor contributing to lack of baseline data on these species is simply ruggedness of the terrain drained by the Colorado River and its tributaries. These streams are often difficult to access dependably, and a sampling strategy is thus impossible to implement on a consistent basis. In addition, the vast distances of the intermontane west strongly influence logistics of research and have a generally negative impact on sampling. Both aspects (i.e., inaccessibility and distance) compound field work and make its design and implementation both difficult and expensive (see also Douglas, 1993).

The third study species, *Xyrauchen texanus*, is relatively well known ecologically (reviewed by Minckley, 1991; Minckley et al., 1991). A substantial (but now rapidly declining) population of this species was isolated within that portion of the Colorado River which became Lake Mojave when Davis Dam was closed in 1951. It has been a focal point of research at Arizona State University for two decades (Minckley, 1983). *Xyrauchen texanus* is not prevalent in the Grand Canyon, and consensus (Minckley et al. 1991:310; Appendix 3--1) argues that it has never been historically plentiful in this region of the Colorado River, its endangered status notwithstanding.

The present study was thus undertaken with two goals: To estimate within the Little Colorado River (LCR) area of Grand Canyon National Park (GCNP) and the Navajo Nation, population sizes for each study species by month, season, and year of the four-year study period (where applicable). From these data, seasonal and yearly movement patterns, and survival probabilities by size-class would also be evaluated and contrasted.

METHODS AND MATERIALS

Study area and data collection.--The study was confined to the Little Colorado River (LCR) and its confluence with the mainstem Colorado River (Fig. 1--1b), 99 river km (RKM) below Glen Canyon Dam. The study area resides in both Grand Canyon National Park (GCNP) and the Navajo Nation (Coconino County, AZ); its description, to include water chemistry, riparian vegetation, and channel topography, are described in Douglas and Marsh (1996; see Section 1 of this report).

Briefly, base camps were established in the LCR gorge at 0.55, 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 3--2). To capture fishes, hoop and trammel nets were set routinely (the latter primarily at confluence) (net dimensions provided in Douglas and Marsh, 1996; see Section 1 of this report). Fishing effort was recorded at each camp as number of net-hours fished. All captured fishes were identified, measured (TL to nearest mm), weighed (nearest g), and sexed. Large-river endemics greater than 150 mm TL (= adults) were injected with passively induced transponder (i.e., PIT) tags (Prentice et al., 1990) and released near points of capture.

Capture matrices.--Adult *C. latipinnis* and *C. discobolus* were grouped separately into three categories: Newly-tagged fish, recaptured fish, and those with old tags. The first represents fish PIT-tagged by ASU personnel at time of capture (i.e., individuals previously not captured). The second represents fish captured by ASU personnel but already PIT-tagged (i.e., recaptured; source of original tag unknown). The third includes those fish tagged previously with either a Carlin or floy-tag and subsequently PIT-tagged by ASU personnel; the old tag was removed and retained.

For purposes of this report, all three groups start their capture histories when first handled by ASU personnel. In this sense, those fish PIT-tagged by other research groups or agencies were considered "tagged" by ASU personnel at time of first recapture. Obviously, fish tagged and recaptured by ASU personnel have a prior capture history.

For a given species, all three categories were computationally merged, sorted by PIT-tag number, and discrepancies corrected (such as individuals listed as "captured" when in actually they were "recaptured"). Individuals of both species were often recaptured several times (maximum number was 12 for both species). Individuals were then 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, initial capture of an individual, and all subsequent recaptures, are represented as a row vector in the CH-matrix.

The CH-matrix was sorted two different ways for analysis: First, individuals were segregated by season and year (where winter = December, January, February; spring = March, April, May; summer = June, July, August; and autumn = September, October, and November). In all, 16 seasons were represented (four each over four years). Individuals were also partitioned into 50 mm (TL) size-classes, starting at 150 mm TL. For *C. latipinnis*, there were nine total size classes, while for *C. discobolus* there were six.

Population estimates.--For *C. latipinnis* and *C. discobolus*,

Cormack-Jolly-Seber (CJS) population estimates were generated by month (n=49), season (n=16 and n=4), and by each year (n=4) of the study. Estimates were also adjusted by monthly fishing effort. However, to adjust estimates, months were often grouped together to accommodate low recaptures. For *Xyrauchen texanus*, CJS estimates were generated for only six of the 49 months, due to zero sample sizes for many sampling periods.

Estimates were generated for the entire LCR rather than by river reach (as defined in Douglas and Marsh, 1996; see Section of this report). The program POPAN-4 for Windows (A. N. Arnason and C. J. Schwarz, Dept. Computer Sci., Univ. Manitoba, Canada, 1995, unpubl.) was used to generate these estimates, as well as standard deviations, 95% confidence limits, and survival estimates. Open estimates were used exclusively because geographic and demographic closure of populations could not be substantiated, particularly given the temporal span over which sampling was conducted. Differences between open- and closed population estimates are reviewed by Douglas and Marsh (1996; see Section 1 of this report).

Fishing effort and population estimates were transformed to common logs. ANCOVA was used to test population estimates for differences among and between seasons, and between years, with fishing effort as the covariate. The rationale and prerequisites for use of ANCOVA are discussed in Douglas and Marsh (1996; see Section 1 of this report).

Probabilities of yearly survival (adjusted for fishing effort) were calculated by size class for both *C. latipinnis* and *C. discobolus*. Probabilities could not be calculated for 1995 in that for this to occur, capture/ recapture data are required for 1996. Survival probabilities were not calculated for *Xyrauchen texanus*, due to paucity of data.

RESULTS

Numbers of *C. latipinnis* and *C. discobolus* captured, recaptured with PIT-tags, and recaptured with old tags are presented in Table 3--2. Results of merging, sorting, and condensing these data into CH-matrices are also tabulated. Consequences of partitioning each CH-matrix by season (n=16) is presented in Table 3--3, while effect of partitioning by size class (i.e., 50 mm increments beginning at 150 mm TL) are reported in Table 3--4. Results for each species are detailed below.

Xyrauchen texanus.--The 32 capture/ recapture records for this species (and/or hybrids between this species and *C. latipinnis*) are presented in Appendix 3--3. There are 25 uniquely-identified individuals, with seven recaptures. Population estimates

unadjusted for fishing effort are presented in Table 3--5 for six of the 49 months. These estimates are consistently small (≤ 12 individuals) and fluctuate across seasons. Small numbers of recaptures precluded adjusting these estimates for fishing effort, or calculating them for all months of the study. Nevertheless, if the pattern of captures are examined, then *X. texanus* displays a seasonal predictability that contrasts with its large size and vagility. For example, 72% (23/32) of captures occurred in spring (March--April--May), 19% (6/32) in autumn (September--October--November), 6% (2/32) in summer (June--July--August), and 3% (1/32) in winter (December--January--February) (Appendix 3--3). Clearly, spring and autumn were preferred seasons for movement, particularly the former. However, this seasonal predictability is in itself intermittent over years. For example, of the 23 spring captures noted above, 61% (14/23) were in 1995, 35% (8/23) were in 1994, and 4% (1/23) were in 1992. In addition, 85% (21/25) of the individuals in Appendix 3--3 are male, while 12% (3/25) are female (one individual was not sexed). This suggests that males may be more vagile than females. And finally, of the 32 recorded captures, 65% (n=20) occurred approximately 3 km (or greater) above the confluence (one occurred almost 11 km above).

Catostomus latipinnis.--Preliminary tests indicated that fishing effort had a significant effect on population estimates for this species. Season also had a significant effect on these estimates, at all levels of fishing effort. However, the population estimate/fishing effort relationship was nonsignificant over seasons (i.e., interactions between these terms were nonsignificant). A standard ANCOVA was then performed; results indicated that estimated populations of *C. latipinnis* varied significantly over the 16 seasons [$F=2.44$; $df=16$; $P<0.01$; Proc GLM, Statistical Analysis System (SAS, ver. 6.08), Cary, NC, 1989, unpubl.]. Pairwise linear contrasts of population estimates consolidated by four seasons revealed that two (of six) were significant: Summer vs autumn ($F=4.41$; $P<0.04$) and autumn vs spring ($F=4.86$; $P<0.03$). Because of the manner in which seasons were partitioned, 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. There were no significant differences between these years in overall population estimates.

Cormack-Jolly-Seber populations estimates, unadjusted and adjusted for fishing effort, are plotted over all 49 months of the study in Figures 3--1 and 3--2, respectively. Adjusted population estimates and their standard errors are presented by month in Appendix 3--2. Those months grouped due to low recapture rates are also indicated. Both Figure 3--1 and 3--2 reveal similar global trends (i.e., analogous elevations and depressions). When these plots are compared, it is clear that adjusting population estimates by fishing effort for *C.*

latipinnis had little overall global effect. However, local discrepancies are apparent between the two plots. For example, when adjusted values are examined the greatest population estimate for this species occurs in spring (month 35), whereas for unadjusted values it occurs in summer (month 36). Similarly, peaks and valleys at months 28--35 are reversed in the two plots. These discrepancies underscore both advantage and necessity of adjusting estimates by fishing effort (discussed in Section 4 of report).

Figure 3--3 presents CJS estimates (both unadjusted and adjusted for fishing effort) plotted over 16 seasons. Again, the global perspective is similar for both plots, but local discrepancies are apparent. These largely mirror those mentioned above. For adjusted values, the elevated spring estimate (season 12; Fig. 3--3b) is shifted to the following summer (season 13) in unadjusted values (Fig. 3--3a). However, fluctuations at months 28--35 in the monthly plots smooth themselves out seasonally such that both plots now reflect an overall depression at seasons 10--11.

Catostomus discobolus.--Preliminary tests revealed that neither fishing effort nor season significantly affected population estimates for this species. The population estimate/fishing effort relationship was also nonsignificant over seasons. Pairwise linear contrasts of estimates merged into four seasons were nonsignificant as well. When pairwise contrasts were compiled over years, no significant differences were found.

Figures 3--4 and 3--5 present CJS populations estimates for *C. discobolus* that are unadjusted and adjusted for fishing effort, respectively, over all 49 months. Adjusted values and their standard errors are presented in Appendix 3--2, and months grouped to accommodate adjustment by fishing effort are indicated. Adjustment of estimates for this species (Fig. 3--5) had more effect than for *C. latipinnis* (Fig. 3--2). Both plots reveal seasonal (and assumedly normal) fluctuations. However, Figure 3--5 demonstrates a strong and steady decline from month 23 until month 45 (with minor elevations during this span).

Figure 3--6 presents CJS estimates (both unadjusted and adjusted for fishing effort) plotted over 16 seasons. The downward trend in estimated numbers is less apparent here, due to dramatic seasonal variability in both plots. Nevertheless, some sense can be made of these fluctuations. Unadjusted seasonal estimates (Fig. 3--6a) peaked consistently in autumn (three times), once in spring, and once in winter. Adjusted estimates (Fig. 3--6b) peaked twice in autumn and once each in summer and winter. This species demonstrates a consistent (albeit statistically nonsignificant) increase in population numbers during autumn, probably as a result of increased movements during this season by normally sedentary individuals.

Species comparisons.--*Catostomus discobolus* displayed considerably more variance in CJS estimates than did *C. latipinnis*. This is because its recaptures were only 11.8% (484/4,097; Table 3--2), as compared to 41.5% for the latter (1,550/32,739; Table 3--2). Similarly (and as expected given the above), standard errors of monthly CJS estimates (Appendix 3--2) were also greater for *C. discobolus* than for *C. latipinnis*.

Survival probabilities for nine size-classes of *C. latipinnis* and five size-classes of *C. discobolus* are presented in Table 3--6, and plotted for each species in Figs. 3--7 and 3--8, respectively. Probabilities in both table and figures are adjusted for fishing effort. The standard errors of the survival probabilities for *C. discobolus* could not be calculated, due to small sample sizes. Survival rates for *C. discobolus* for 1991--1993 are remarkably uniform across size-classes. Greatest variability is reflected in size-class 1 (Fig. 3--8; Table 3--6). Uniformity is also apparent in *C. latipinnis*, in spite of large (but uniform) fluctuations in early size-class survivability (Fig. 3--7). Beyond size-class 4, fluctuations stabilize somewhat for this species, with lines reflecting positive slopes. However, both species reveal poor survivability in 1994; for *C. discobolus*, it is uniform across all size classes whereas for *C. latipinnis*, it is manifested from size-class 3 upward.

DISCUSSION

Suckers, family Catostomidae, are primarily benthic fishes. The basal stock of this clade is believed to be a deep-bodied fish of large, low-gradient rivers. A major adaptive event in the radiation of this group was the gradual diversification of mountain suckers from the basal stock (Smith and Koehn, 1971; Smith, 1992). Both forms (larger, more primitive suckers vs slender tributary forms) are found today in North America.

Smith and Koehn (1971) argued that the most evolutionarily advanced North American catostomids inhabit the Colorado River on the Colorado Plateau. Here, two cases of parallel divergence exist within both clades. In one instance, *C. latipinnis* diverges from its sister-taxon *C. insignis*, while in the other, *C. discobolus* separates from its sister-taxon *C. clarki*. Both shifts involve similar changes in morphological characters, and each reflects segregation of sister-taxa into upper and lower parts of the Colorado River basin. The three study species of this report fall within the two large clades [i.e., deeper-bodied forms of low-gradient rivers (*X. texanus* and *C. latipinnis*) vs a more slender and highly evolved mountain sucker (*C. discobolus*)]. Life history aspects of each are documented in Appendix 3--1. All three are part of an indigenous, but declining, Colorado River fish community (see Appendix 4--1; also Minckley, 1991).

During this study, population estimates were relatively stable for *C. latipinnis*. However, for *C. discobolus* population estimates declined over the 49 month duration of this study. The cause for this decline [also noted in a third species, *Gila cypha* (Cyprinidae); see Section 4 of this report] is unknown. Population estimates for a fourth study species (*Xyrauchen texanus*) are extremely small (Table 3--5), but this species was never believed abundant in the Grand Canyon region of the Colorado River (Appendix 3--1).

Catostomus discobolus was captured with regularity in this study, but recaptures of marked individuals were extremely low (Table 3--2). As a result, elevated variances (Appendix 3--2) accompany population estimates for this species. One hypothesis for lack of recaptures is that patterns displayed in Figures 3--4 and 3--6b simply reflect the natural history of this species (discussed in Appendix 3--1). It is alleged to be a spring breeder, moving to faster waters in April--May to reproduce (S. M. Carothers and C. O. Minckley, U.S. Dept. Interior, Water and Power Resources Service, 1981, unpubl.; Minckley, 1991). However, unadjusted seasonal estimates (Fig. 3--6a) reveal only one spring peak and one spring depression, while adjusted seasonal estimates (Fig. 3--6b) reveal no spring peaks and two spring depressions. Possibly, breeding movements of this species are (a) restricted to within the LCR, and (b) of short distances. During diurnal hours, *C. discobolus* remains quiescent in deep pools and eddies, and moves only nocturnally to shallow riffles or other hard-bottomed habitats to feed (Minckley, 1991; Appendix 3--1). Both such habitats are often adjacent to one another in the LCR (M. E. Douglas and P. C. Marsh, pers. obs.). Thus, this species may exhibit reproductive movements that very restricted, much more than those of *C. latipinnis* (discussed below).

A basic principle of both closed and open (i.e., CJS) models (reviewed in Section 1; see Douglas and Marsh, 1996) is that all organisms are equally likely to be captured in each sample [i.e., every animal present in the population at the time of the i th sample (where $i = 1, 2, 3, \dots, k$) has the same probability of capture (p_i)]. Thus, a second hypothesis which explains low recapture rates for *C. discobolus* is that once individuals of this species have been initially captured, they become "trap-shy" (i.e., their probability of capture decreases markedly). In this sense, probability of equal capture would have two components (Pollock et al., 1990): Heterogeneity (which varies over all animals in the population and may be due, for example, to ontogeny, sex, social status, or territoriality), and trap response (which varies according to prior capture history). Evidence of trap response in capture probability has been found in a variety of vertebrates (reviewed by Pollock et al., 1990:69), and can manifest itself in several ways (with predictable outcomes). For example, animals often become "trap-happy" as a response to baited traps, which would encourage

once-trapped animals to re-trap themselves. This phenomenon generates a negative bias in capture probabilities (i.e., true population size is underestimated). On the other hand, "trap-shy" organisms (i.e., those, for example, that learn to avoid traps after initial capture) would generate a positive bias in capture probabilities (and a concomitant over-estimation of population size).

Similarly, another aspect of capture heterogeneity that may manifest itself in this study, particularly with regard to *C. discobolus*, is manifestation of heterogeneous sampling intensities. This situation results when all sections of the study area are not sampled with equal intensity. Given that *C. discobolus* is a rheophilic organism (Appendix 3--1), and that such areas are difficult to sample with nets, then estimates in Appendix 3--2 may indeed represent overestimation. Simulation studies using capture-recapture data for *C. discobolus* may provide more insight into this potential problem.

For *C. discobolus*, a steady decrease in adjusted CJS estimates (Fig. 3--5) began at month 23 (spring, 1993), which was approximately the period when large floods occurred in the LCR. Extremely high water purged travertine deposition from submerged banks and bottom, thereby rendering the water column extremely transparent. Normally, the water column is a translucent turquoise color (see Section 1), which typically results from carbonate moving from water column onto substrate as a precipitate, then back into the water column. This process is dynamic and complex. However, severe flooding and concomitant loss of carbonate precipitation on structure increased water clarity tremendously in the LCR during 1993, and maintained itself in this state through 1995. This situation is non-normal for the LCR; the question is then whether this altered state allowed greater predation on indigenous fishes (particularly those which frequented the LCR), or simply curtailed normal movements such that catch rates (Table 3--3) and resulting adjusted CJS estimates (Appendix 3--2; Fig. 3--5) declined dramatically.

Catostomus latipinnis is physically larger and more robust than *C. discobolus* (Table 3--4), seemingly prefers larger streams, and ostensibly demonstrates a concomitant greater vagility. In spite of these attributes (or as a result of them), the flannelmouth becomes more predictable in space and time. This, in turn, manifests itself in demonstrable seasonal trends. For example, peaks in seasonal unadjusted CJS estimates occurred for *C. latipinnis* in summer of all years examined (Fig. 3--3a). When these estimates are adjusted for fishing effort (Fig. 3--3b), the summer peak is sustained in two of three occurrences (the third peak instead moves forward to spring). In addition, the majority of captures for this species were recorded at confluence, primarily in trammel nets. This may explain why this

species does not reflect the low recaptures and high standard errors of *C. discobolus* (Appendix 3--2).

Survival rates for both species (Table 3--6) are remarkably uniform over all size-classes in 1991--1993. However, survival for both species in 1994 (i.e., those individuals surviving from 1993 to 1994) was lowest of the study. This most assuredly is the result of altered visibility in the water column as a result of severe flooding, and is most apparent for *C. discobolus* (Fig. 3--8). Here, the decline was apparent across all size classes. For *C. latipinnis*, the 1994 reduction was predominantly across size-classes 4--9 (Fig. 3--7).

This study demonstrates the paucity of baseline data which exists for the study species. Three areas of additional research are clearly necessary, and advocated: Genetic studies are required for all three species, such that estimates of variability and patterns of genetic divergence can be mapped Canyon-wide. This is most apparent with regards to *X. texanus*, where hybrids clearly exist between this species and *C. latipinnis*. However, *C. discobolus* exists in other tributaries within the Canyon, and questions exist as to the similarities of these with forms that inhabit the LCR (Appendix 3--1). Similarly, the status of *C. latipinnis* in the LCR is also questioned, as is the number of forms of this species which exist Canyon-wide (Appendix 3--1).

Long-term monitoring studies are also required for both *C. latipinnis* and *C. discobolus*. Each should be studied separately; both studies should be designed with the biology of the study species in mind. For example, studies of *C. latipinnis* should center at confluences of Paria and Little Colorado rivers. The behavior of this species clearly involves long-range movements, much like those of *Ptychocheilus lucius* (Tyus, 1991) and *X. texanus* (Dowling et al., 1996). However, *C. latipinnis* has a propensity to congregate at outflow of tributary rivers and it is here that it can most parsimoniously be sampled using trammel nets. A study involving *C. discobolus* should focus on the LCR, particularly those areas such as fast-water habitats in which good catch-rates were apparent in the current study. Both studies should be of enough duration so that trends in abundance and movements can be statistically verified, and plots of decreasing abundance (i.e., Fig. 3--5) realized before long-term damage can be manifested. In this way, these indigenous forms can be conserved before (not after) they are pushed to the brink of endangerment.

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APPENDIX 3--1.

Flannelmouth sucker (Catostomus latipinnis).--Described originally from the San Pedro River (Arizona) by Baird and Girard (1854). It appears most closely related to species further north and west (Smith and Koehn, 1971). Historically, it was distributed in all moderate-to-large rivers throughout the Colorado River basin (Minckley and Holden, 1980). It is now considered extirpated below Lake Mead, although reintroduction of individuals has been attempted by Arizona Game and Fish Department below Boulder Dam (W. L. Minckley, pers. comm.) (Fig. 1--1b). Fossil remains of *C. latipinnis* have been found in Pleistocene beds of the Little Colorado River Basin (Uyeno and Miller, 1963, 1965). Adult size is 300--400 mm TL, with 500+ mm TL maximum (Minckley and Holden, 1980). Maximum size recorded in this study for *C. latipinnis* was 661 mm TL. Life history attributes of this species are sketchy; it typically inhabits pools and deeper runs of rivers and often enters mouths of small tributaries (Minckley and Holden, 1980). Minckley (1991) provides an excellent review of current information on this species, and this, in turn, affords the basis for our synopsis.

In the Yampa River, ripe adults congregate at the upstream end of cobble bars to spawn (depth = 1 m; velocity = 1 m s⁻¹; McAda and Wydowski, 1985). Postreproductive adults apparently remain in flatwater or eddies near margins of strong currents, generally in waters at least 1 m deep. Young often congregate downstream (or on) riffles and along shoreline of flatwater reaches. They frequent tributaries as well.

In Marble and Grand canyons, ripe *C. latipinnis* were caught from March-May at the mouth of the Paria River and other low-gradient streams (Carothers and Minckley, U. S. Bureau of Reclam., Final Rept., 1981). Postreproductive fish remained in these habitats through summer, but returned to the mainstem in winter when temperature differential equilibrated between tributary and mainstem (Suttkus and Clemmer, 1979). Adult *C. latipinnis* feed upon aquatic invertebrates (primarily dipterans), organic debris, and sand (an apparent by-product of benthic feeding). Those individuals in the mainstem also ingest filamentous alga (*Cladophora glomerata*) which is abundant in Marble and upper Grand canyons (Carothers and Minckley, U. S. Bureau of Reclam., Final Rept., 1981). It is believed that diatoms abundant within the alga are digested.

There is some controversy with regard to maximum estimated age of *C. latipinnis*. Difficulty centers primarily on suitability of materials examined. For example, McAda (1977) and McAda and Wydowski (1985) used scales to determine an age of eight or nine years for upper basin *C. latipinnis*. Usher et al. (1980), Minckley (1983), and McCarthy and Minckley (1987) argued that

scales were inappropriate media from which to determine maximum age, for these were often regenerated and thus gave false readings. In addition, scale annuli were often unreadable after the first few years of life, adding to inherent unreliability of (and elevated variance in) this medium. Usher et al. (1980) and Carothers and Minckley (U. S. Bureau of Reclam., Final Rept., 1981). used opercular bones to estimate a maximum age of 10 years for *C. latipinnis* in Marble/Grand canyons. Minckley (1991) suggested that these ages are underestimated and based conclusions on data from Scopettone (1988) and Minckley (unpubl., cited 1991). In both studies, Green River *C. latipinnis* (n = 30 and five, respectively) were aged using otoliths. In the former, the oldest individual (TL = 530 mm) was estimated to be 30 years, whereas all five individuals (TL = 530--590 mm) in the latter study were aged > 17 years.

Bluehead sucker [Catostomus (Pantosteus) discobolus].--Originally described as *Pantosteus delphinus* (Cope, 1872) from the Green River of Wyoming. In a revision, Smith (1966:42--46) determined that *discobolus* had precedence over *delphinus*, and furthermore, that the bluehead was most properly classified under the genus *Catostomus*, with the original generic name relegated to a subgenus. However, Minckley (1973:167--169), Minckley and Deacon (1968), and other western ichthyologists (i.e., Miller, 1976:5) rejected synonymization of *Pantosteus* with *Catostomus*. Although the issue is still under debate, synonymization remains valid until results of additional studies become available.

This species is distributed throughout the upper Colorado River basin; it is replaced in the lower basin by its closest relative, *Catostomus clarki* (Smith and Koehn, 1971), which occupies a similar niche (Holden and Minckley, 1980). It is one of a clade of very specialized, mostly herbivorous fishes distributed in relatively high-gradient streams of western North America. Feeding adaptations that make this clade distinct include broad, disc-shaped lips and strong jaws sheathed in cartilage. These allow the fish to adhere firmly to rocks in torrential streams, and while so attached, to scrape algae, diatoms and a variety of sessile invertebrates from rock surfaces. Adult size is 250--300 mm TL, with 400+ mm maximum (Holden and Minckley, 1980). Maximum size recorded in this study for *C. discobolus* was 494 mm TL.

Again, life history of this species is enigmatic; available evidence has been summarized by Minckley (1991) and is synopsized below. Adults remain in deep pools and eddies during diurnal hours, and move nocturnally to shallow riffles or other hard-bottomed habitats to feed. In Marble and Grand canyons, adults spawn in swift water of tributaries, over gravel-sand or gravel-cobble bottoms during April-May.

Estimates of maximum age for *C. discobolus* are as variable

as those provided above for *C. latipinnis*. Again, variability often stems from the medium from which age estimations are made. Usher et al. (1980) used operculae to derive an age of eight years maximum for *C. discobolus* from Marble/Grand canyons. However, Scopetonne (1988) and Minckley (unpubl., cited 1991) used opercular bone and otolith, respectively, to age *C. discobolus* from Green and Yampa rivers, respectively. In the former study, a 400 mm specimen was aged at 20 years, while in the latter, a 470 mm individual was aged at 20+ years.

Many researchers believe two distinct forms of *C. discobolus* occur in the upper Colorado River basin. Miller (1964) noted that *C. discobolus* had evolved a uniquely streamlined body form with small scales and expansive fins; yet, an extreme type was also found in the upper basin which exhibited a very narrow caudal peduncle, much like that found in *Gila elegans*. Similarly, Vanicek (1967) and Holden and Stalnaker (1973) also noted the existence of two morphs: one with a relatively deep, laterally compressed peduncle vs a second with a very narrow peduncle that is rounded in cross-section. The latter is apparently restricted to the swifter parts of big rivers. However, variation within this species may, in fact, reflect local ecological conditions rather than phylogenetic diversification (Smith, 1966). A photograph displaying the two different peduncle morphs of *C. discobolus* (and an intermediate morph) is presented in Figure 7--7 of Minckley (1991:138).

Razorback sucker [Xyrauchen texanus].--Is another catostomid originally described in another genus (i.e., as *Catostomus texanus* by Abbott in 1861, renamed *Catostomus cypho* by Lockington (1891), then placed into its own monotypic genus as *Xyrauchen texanus* by Eigenmann and Kirsh (in Kirsh, 1899). It was commonly taken by early collectors (reviewed by Minckley et al., 1991:308) and was utilized by native Americans as a food fish, so much so that it was often given a distinct name by different aboriginal peoples. Reported to be common in the lower basin (Kimsey, 1957), and in reservoirs created by mainchannel Colorado River dams. It was cited by Hubbs and Miller (1953) as being uncommon in the upper basin and becoming scarce. Hybrids between *Catostomus latipinnis* x *Xyrauchen texanus* have long been known. Jordan (1891) named such a specimen as *Xyrauchen umcompahgre*.

Banks (1964:74), in a pre-Flaming Gorge Dam study, noted that razorbacks (i.e., "humpback" suckers) and their hybrids appeared to select the Green rather than the Yampa river, and attributed this to differences in run-off, temperature, and turbidity between the rivers. However, Vanicek (1967; citing early 1960s agency reports) reported that razorbacks were rare in the Green and Yampa rivers. Vanicek (1967:45) also noted that the hybrid sucker (*Catostomus latipinnis* x *Xyrauchen texanus*) was not uncommon in the Green River, and noted that morphological characters of the latter were intermediate between the two

parental species (in agreement with Hubbs and Miller, 1953, who examined eight total specimens, two from the upper Colorado River and six from the upper Green River). Vanicek et al. (1970) collected 16 putative hybrids from the Green River after closure of Flaming Gorge Dam. Holden (1973) reported that hybrids were collected throughout the range of the razorback sucker, usually in quiet, backwater areas in association with the razorback. Holden noted that the razorback was collected only in the middle and lower sections of the upper Colorado River basin, and was considered "rare." Hybrids were readily distinguished by an intermediate lateral line scale count, and a much abbreviated (although clear) keel. Holden collected 40 hybrids and 53 razorbacks during his study.

Razorbacks have never been abundant within Grand Canyon and adjacent areas. Smith (1959) reported it "...rare, or possibly just difficult to collect in Glen Canyon, since extensive collecting turned up only two immature (i.e., YOY) specimens..." Within the Canyon, G. H. Clemmer (unpubl. field notes, 1976, 1980; Special Coll., Hayden Library, ASU) reported taking a hybrid sucker at the mouth of the Paria River. In another study, R.D. Suttikus, G. H. Clemmer, C. Jones, and C. R. Shoop (GCNP survey of fishes, mammals, and herpetofauna, 1976, unpubl.) reported that while no razorback sucker were taken during their study, three hybrids were. These researchers believed that "...the razorback has been forced out of existence in the Grand Canyon section of the Colorado River. The low water temperatures that continue to prevail because of the base releases from Glen Canyon Dam are too cold for spawning. Secondly, the razorback apparently does not utilize many of the small tributaries that are available in the Canyon area. Thirdly, the dam is a barrier that prevents upstream movement to suitable spawning areas. We postulate that during the early part of the period when the Powell Reservoir was being filled, the dam acted as a barrier but water temperatures remained suitable for spawning. Thus, razorback sucker, being greatly outnumbered by flannelmouth sucker, hybridization between the two forms resulted. Now, since spawning conditions are completely unfavorable for the razorback, it is being genetically swamped out by the flannelmouth."

Remains of five indigenous fish species were found within Stanton's Cave (GCNP: RM 50): *Gila cypha*, *G. elegans*, *Ptychocheilus lucius*, *C. latipinnis*, and *P. discobolus* (Miller and Smith, 1984). It is interesting to note that *Xyrauchen texanus* was not found in that excavation. This suggests that *X. texanus* was not a resident of the Grand Canyon's indigenous fish community. Rather, it was a transient through the Canyon, moving from more satisfactory habitat below, to similar habitat above.

APPENDIX 3--2

Computational statistics from CJS analysis of adult *G. cypha*.
 NO. = numerical designation for month; DATE (FROM/ TO) = sampling
 periods; NH(I) = CJS population estimate at time (i) adjusted for
 fishing effort; SE NH(I) = standard error of nh(i).

NO.	DATE (FROM/ TO)	<i>C. latipinnis</i>		<i>C. discobolus</i>	
		NH(I)	SE NH(I)	NH(I)	SE NH(I)
01	01 July--14 July 1991	*	*	* ¹	*
02	21 July--03 Aug. 1991	1,586	618	14,162 ¹	3,801
03	11 Aug.--23 Aug. 1991	1,409	584	14,162 ¹	3,332
04	13 Sep.--25 Sep. 1991	502	155	14,162 ¹	3,332
05	15 Oct.--24 Oct. 1991	949	248	14,162	6,812
06	07 Nov.--16 Nov. 1991	1,983	682	24,544 ¹	8,322
07	09 Dec.--18 Dec. 1991	1,529	1,710	24,544 ¹	8,322
08	08 Jan.--15 Jan. 1992	1,064	567	24,544 ¹	8,322
09	11 Feb.--19 Feb. 1992	1,281 ¹	941	24,535	11,842
10	05 Mar.--13 Mar. 1992	1,281 ¹	941	37,770	11,513
11	26 Mar.--03 Apr. 1992	889	222	37,774 ¹	5,824
12	20 Apr.--29 Apr. 1992	1,872	778	37,774 ¹	5,824
13	18 May -- 27 May 1992	2,771	766	26,267	5,692
14	15 June--24 June 1992	2,272	952	26,267 ¹	5,692
15	14 July--23 July 1992	653	571	26,267 ¹	5,692
16	10 Aug.--19 Aug. 1992	5,221	2,178	37,729	39,811
17	14 Sep.--23 Sep. 1992	987	163	39,003	8,762
18	12 Oct.--22 Oct. 1992	760	238	38,989	8,471
19	09 Nov.--18 Nov. 1992	1,757 ¹	1,015	48,415 ¹	14,914
20	10 Feb.--17 Feb. 1993	1,757 ¹	1,015	48,415 ¹	14,914
21	02 Mar.--10 Mar. 1993	769	335	48,233	10,611
22	22 Mar.--31 Mar. 1993	1,550	495	48,206	8,805
23	12 Apr.--21 Apr. 1993	3,647	1,293	48,188	11,069
24	10 May -- 19 May 1993	3,177	1,228	18,238	4,573
25	08 June--16 June 1993	4,133	1,327	10,532	2,403
26	12 July--21 July 1993	4,098	1,314	11,115	2,467
27	10 Aug.--18 Aug. 1993	560	554	9,656	2,581
28	13 Sep.--22 Sep. 1993	1,481	555	12,717	2,783
29	12 Oct.--21 Oct. 1993	1,466	435	7,825	1,670
30	08 Nov.--17 Nov. 1993	2,869	1,558	12,187	2,928
31	06 Dec.--15 Dec. 1993	1,090	767	6,832	1,460
32	11 Jan.--20 Jan. 1994	1,994	542	8,645	1,872
33	10 Feb.--19 Feb. 1994	1,915	705	17,698	3,964
34	15 Mar.--24 Mar. 1994	3,700	914	17,698	4,058
35	12 Apr.--21 Apr. 1994	7,886	2,606	17,690	4,135
36	10 May -- 19 May 1994	7,131	2,259	7,115	1,545

27	14	June--23	June	1994	4,528	1,036	7,145 ¹	1,531
38	12	July--21	July	1994	2,435	606	7,145 ¹	1,531
39	09	Aug.--18	Aug.	1994	2,234	553	13,115 ¹	3,312
40	13	Sep.--22	Sep.	1994	2,860	845	13,115 ¹	3,312
41	11	Oct.--20	Oct.	1994	1,988	392	13,115 ¹	3,312
42	01	Nov.--10	Nov.	1994	1,654	590	16,344 ¹	4,898
43	06	Dec.--15	Dec.	1994	2,297	650	16,344 ¹	4,898
44	10	Jan.--19	Jan.	1995	1,505	462	16,344 ¹	4,898
45	07	Feb.--16	Feb.	1995	4,542	5,284	13,958	3,555
46	28	Feb.--09	Mar.	1995	3,021	1,232	30,433	*
47	21	Mar.--30	Mar.	1995	1,793	507	9,452	2,388
48	11	Apr.--20	Apr.	1995	797	353	5,143	4,446
49	26	May -- 25	May	1995	*	*	10,779	4,110
50	13	June--27	June	1995	*	*	*	*

* = not calculated

¹ = combined with previous month

APPENDIX 3--3

Collection records for *Xyrauchen texanus* captured in the Little Colorado River (Navajo Nation, Coconino County, AZ) or at its confluence with the Colorado River (Marble Canyon of Grand Canyon National Park). CAPTURE = PIT tag number of captured individuals; RECAPTURE = PIT tag numbers of recaptured individuals; CAMP = C(Confluence), P(Powell) or S(Salt); GEAR = T(Trammel), H(Hoop); DATE = month-day-year; METERS = meters upriver; TL = total length; WT = weight; SX = M(Male) or F(Female);

CAPTURE	RECAPTURE	CAMP	GEAR	DATE	METERS	TL	WT	SX
1FOC7A1840		C	T	101493	60	580	1929	F
	1FOC7A1B40	C	T	41994	80	560	1968	F
1F1F660D4F		C	T	101993	80	490	1266	M
1F20076159		C	T	101893	30	530	1650	M
1F46621524		P	H	41495	2980	499	.	M
1F7B5B404B		P	H	41495	2980	511	.	M
7F7A12452B		C	T	41695	20	435	886	-
7F7D1B7106		S	H	70891	10900	348	350	M
7F7E430B4D		P	H	101591	3000	510	1178	M
7F7F182F5A		C	T	42592	630	558	1578	F
7F7F47652E		C	T	61692	.	513	1314	M
	7F7F47652E	P	H	41594	4940	520	1278	M
	1FOC705213	C	T	41594	60	465	1300	M
	7F7D1B6C1A	P	H	41495	2980	468	.	M
	7F7D1B780C	C	T	111293	.	522	1296	M
	7F7D1B780C	P	H	41594	4940	520	1550	M
	7F7D1B780C	P	H	42094	3060	540	1648	M
	7F7D2B077D	P	H	41495	2980	522	1352	M
	7F7D2C4C6F	P	H	41495	2980	491	1192	M
	7F7D294E76	P	H	121093	3080	495	1182	M
	7F7D437110	P	H	41495	2980	450	.	M
	7F7E427D1D	P	H	41495	2980	497	.	M
	7F7E430B4D	P	H	111091	3100	509	1088	M
	7F7F0B5D0C	P	H	41495	2980	485	.	M
	7F7F264F09	P	H	41495	2980	451	.	M
	7F7F27285C	P	H	41395	3080	535	1300	M
	7F7F290A2B	P	H	41395	3080	465	968	M
	7F7F3E5367	C	T	30295	40	548	1660	F
	7F7F323842	C	T	31894	80	520	1100	M
	7F7F323842	C	T	32094	40	520	1100	M
	7F7F33064D	P	H	41395	3080	524	1234	M

Table 3.1: Conservation status of indigenous big-river fishes (sensu Minckley et al., 1986) of the Colorado River basin.

FAMILY	GENUS/SPECIES	COMMON NAME	STATUS
Cyprinidae	<i>Ptychocheilus lucius</i>	Colorado Squawfish	Endangered
Cyprinidae	<i>Gila elegans</i>	Bonytail Chub	Endangered
Cyprinidae	<i>Gila cypha</i>	Humpback Chub	Endangered
Catostomidae	<i>Xyrauchen texanus</i>	Razorback Sucker	Endangered
Cyprinidae	<i>Gila robusta</i>	Roundtail Chub	Candidate
Catostomidae	<i>Catostomus latipinnis</i>	Flannelmouth Sucker	Scrutiny
Catostomidae	<i>Catostomus discobolus</i>	Bluehead Sucker	Secure(?)

Table 3.2: Individual *Catostomus latipinnis* and *C. discobolus* grouped into three categories: CAPTURED, RECAPTURED, and OLD TAGS. The first represents fish PIT-tagged by ASU personnel at time of capture. The second represents fish already PIT-tagged when captured (i.e., recaptured; source of original tag unknown). The third includes fish previously tagged with either Carlin or floy-tags and subsequently PIT-tagged by ASU personnel (see text). TOTAL is a summation of the three categories. CH-MATRIX represents TOTAL collapsed into a capture-history matrix where each unique PIT-tag number is represented but once.

SPECIES	CAPTURED	RECAPTURED	OLD TAG	TOTAL	CH-MATRIX
<i>C. latipinnis</i>	2,179	1,550	10	3,739	2,578
<i>C. discobolus</i>	3,613	484	0	4,097	3,697

Table 3.3: Individual *Catostomus latipinnis* and *C. discobolus* grouped by season (= SEASON) from respective capture-history matrices (where 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 refers to numerical designation for season, and TOTAL represents numbers of individuals summed for each species for each year.

NUMBER	SEASON/ YEAR	<i>C. latipinnis</i>	<i>C. discobolus</i>
01	Summer 1991	236	85
02	Autumn 1991	166	151
03	Winter 1991	65	78
	TOTAL 1991	467	314
04	Spring 1992	75	629
05	Summer 1992	125	261
06	Autumn 1992	171	210
07	Winter 1992	1	7
	TOTAL 1992	372	1107
08	Spring 1993	131	628
09	Summer 1993	250	88
10	Autumn 1993	73	123
11	Winter 1993	139	219
	TOTAL 1993	593	1058
12	Spring 1994	255	620
13	Summer 1994	323	40
14	Autumn 1994	218	70
15	Winter 1994	102	65
	TOTAL 1994	898	795
16	Spring 1995	248	423
	TOTAL 1995	248	423
	TOTAL	2,578	3,697

Table 3.4: Individual *Catostomus latipinnis* and *C. discobolus* grouped from respective capture-history matrices by size class (= SIZE CLASS) in 50 mm increments beginning from 150 mm TL.

SIZE CLASS	<i>C. latipinnis</i>	<i>C. discobolus</i>
150--200	258	1,249
201--250	271	1,689
251--300	251	599
301--350	184	134
351--400	345	26
401--450	417	--
451--500	403	--
501--550	314	--
551--600+	135	--
TOTAL	2,578	3,697

Table 3.5: CJS estimates for *Xyrauchen texanus* (and potential hybrids) during 1991--1995 in the Little Colorado River (Navajo Nation, Coconino Co., AZ) and its confluence with the Colorado River (Marble Canyon of Grand Canyon National Park). NO. = numerical designation for month; DATE (FROM/ TO) = sampling periods; NH(I) = CJS population estimate at time (i); SE NH(I) could not be calculated.

NO.	DATE (TO/ FROM)	NH(I)
29	12 Oct.--21 Oct. 1993	8
30	08 Nov.--17 Nov. 1993	4
31	06 Dec.--15 Dec. 1993	12
34	15 Mar.--24 Mar. 1994	12
35	12 Apr.--21 Apr. 1994	5
46	28 Feb.--09 Mar. 1995	4

Table 3--6: Survival probabilities for five size-classes of *Catostomus discobolus*, and nine size-classes of *Catostomus latipinnis*, calculated by year, from 1991--1994 (1995 survivability could not be calculated; see text). SIZE CLASS = size stanzas for each class; PHI = survival probability adjusted for fishing effort; SE PHI = standard error of survival probability adjusted for fishing effort.

SIZE CLASS	1991		1992		1993		1994	
	PHI	SE PHI						
<i>C. discobolus</i>								
150--200	0.45	0.**	0.49	0.**	0.67	0.**	0.02	0.**
201--250	0.57	0.**	0.51	0.**	0.40	0.**	0.04	0.**
251--300	0.49	0.**	0.43	0.**	0.47	0.**	0.02	0.**
301--350	0.50	0.**	0.44	0.**	0.55	0.**	0.02	0.**
351--400+	0.51	0.**	0.47	0.**	0.52	0.**	0.03	0.**
<i>C. latipinnis</i>								
150--200	0.98	0.25	0.44	0.09	0.87	0.19	0.91	0.94
201--250	0.46	0.18	0.44	0.12	0.44	0.12	0.41	0.53
251--300	1.00	0.20	0.95	0.16	1.00	0.21	1.00	1.30
301--350	0.67	0.21	0.64	0.17	0.70	0.26	0.35	0.35
351--400	0.73	0.26	0.57	0.14	0.76	0.20	0.66	0.90
401--450	0.75	0.22	0.94	0.23	0.89	0.32	0.43	0.51
451--500	0.86	0.11	0.74	0.11	0.74	0.13	0.47	0.79
501--550	0.73	0.15	0.84	0.17	1.00	0.**	0.23	0.10
551--600+	1.00	0.**	0.84	0.31	0.26	0.15	0.48	0.81

** = not calculable

FIGURE LEGENDS

Figure 3--1: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *C. latipinnis* by month in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring (March-April--May) of 1992, 1993, 1994, and 1995.

Figure 3--2: Cormack-Jolly-Seber population estimates (adjusted for fishing effort) for adult (> 150 mm TL) *C. latipinnis* by month in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring (March-April--May) of 1992, 1993, 1994, and 1995.

Figure 3--3a: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *C. latipinnis* by season (n = 1--16) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

Figure 3--3b: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *C. latipinnis* by season (n = 1--16) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

Figure 3--4: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *C. discobolus* by month in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring (March-April--May) of 1992, 1993, 1994, and 1995.

Figure 3--5: Cormack-Jolly-Seber population estimates (adjusted for fishing effort) for adult (> 150 mm TL) *C. discobolus* by month in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring (March-April--May) of 1992, 1993, 1994, and 1995.

Figure 3--6a: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *C. discobolus* by season (n = 1--16) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

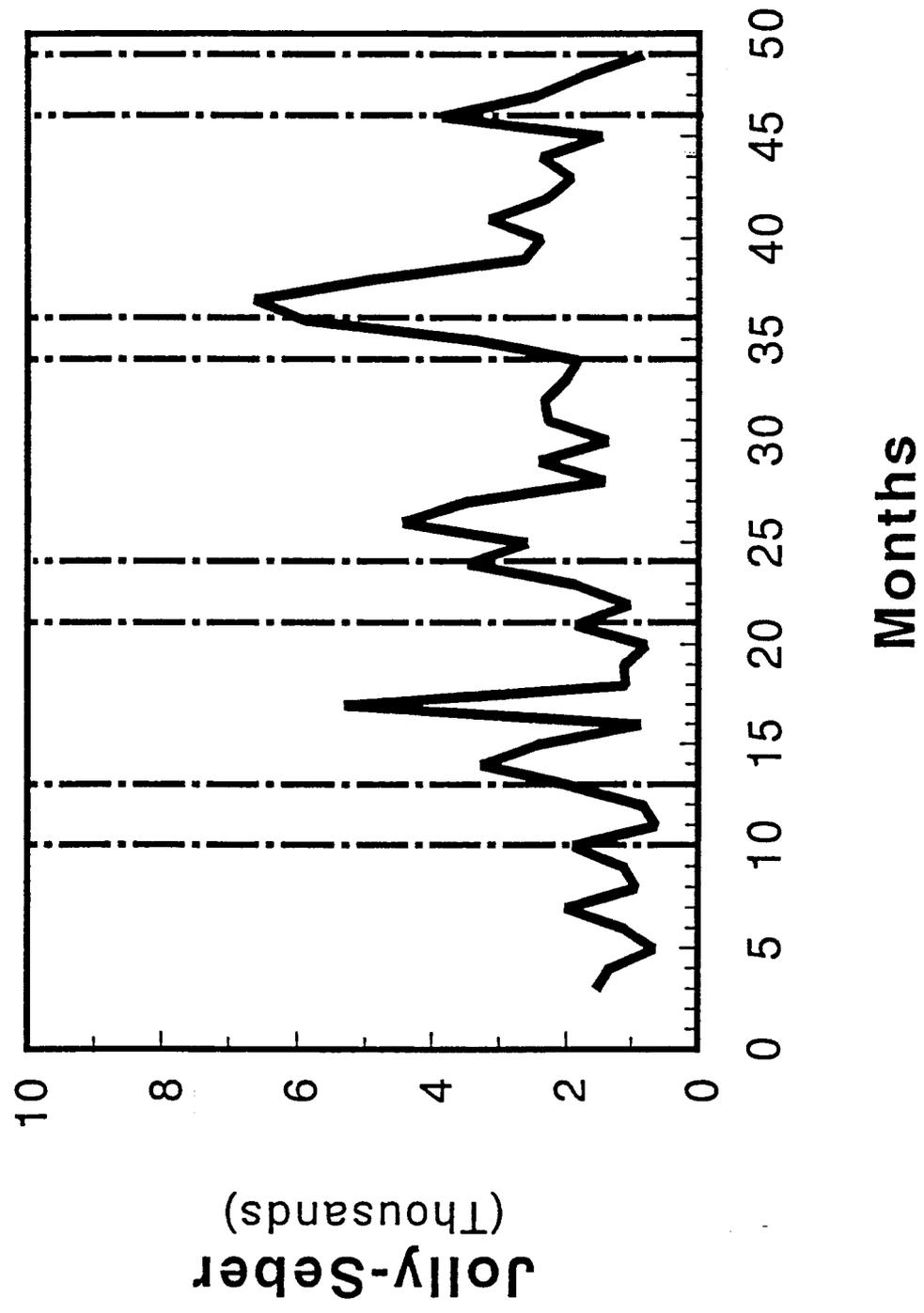
Figure 3--6b: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *C. discobolus* by season (n = 1--16) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

Figure 3--7: Yearly survival probability by size--class for adult *C. latipinnis* (> 150 mm TL) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Probability values are for years 1991--1994.

Figure 3--8: Yearly survival probability by size--class for adult *C. discobolus* (> 150 mm TL) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Probability values are for years 1991--1994.

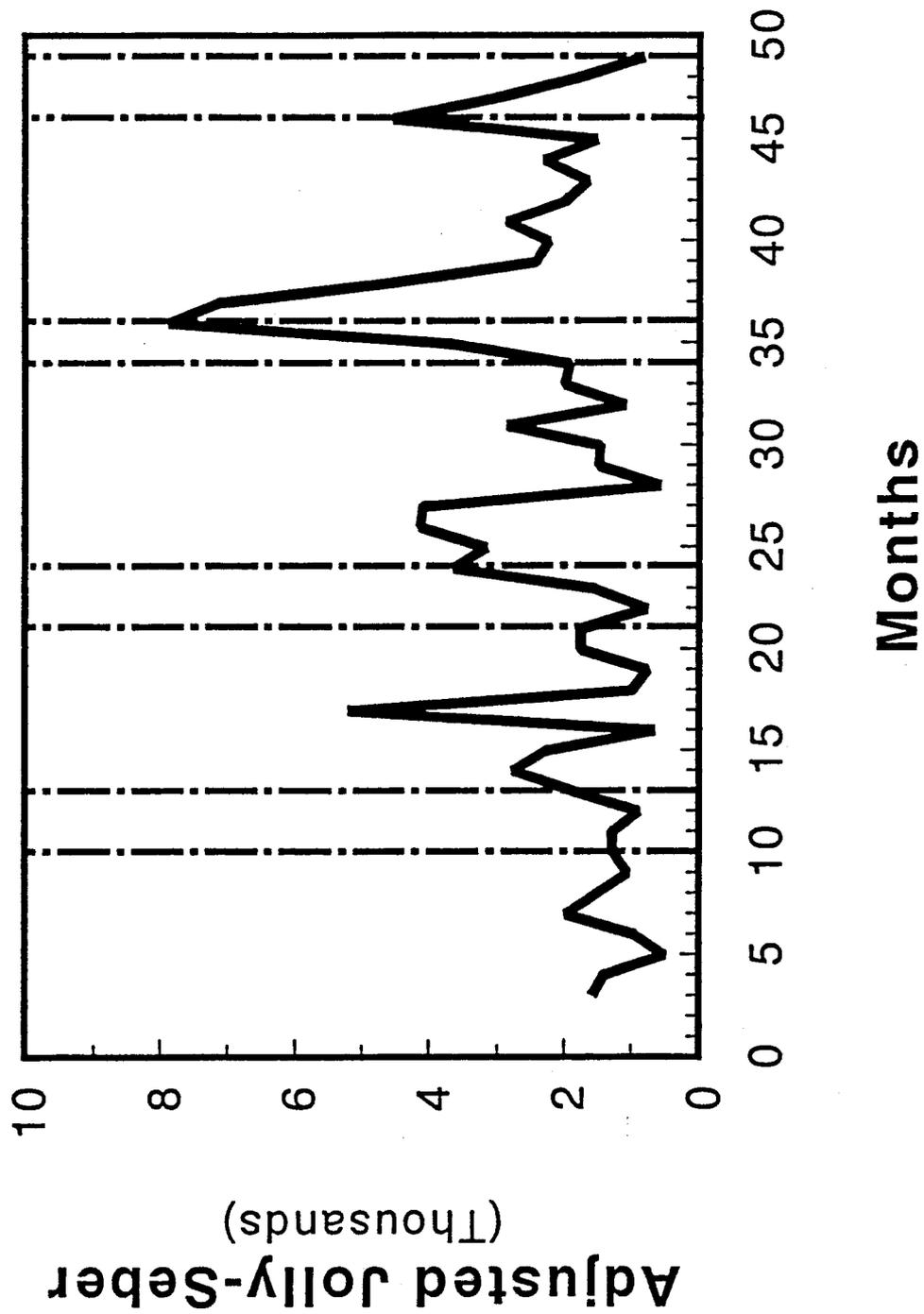
Catostomus latipinnis

Monthly Population Estimates (1991-95)



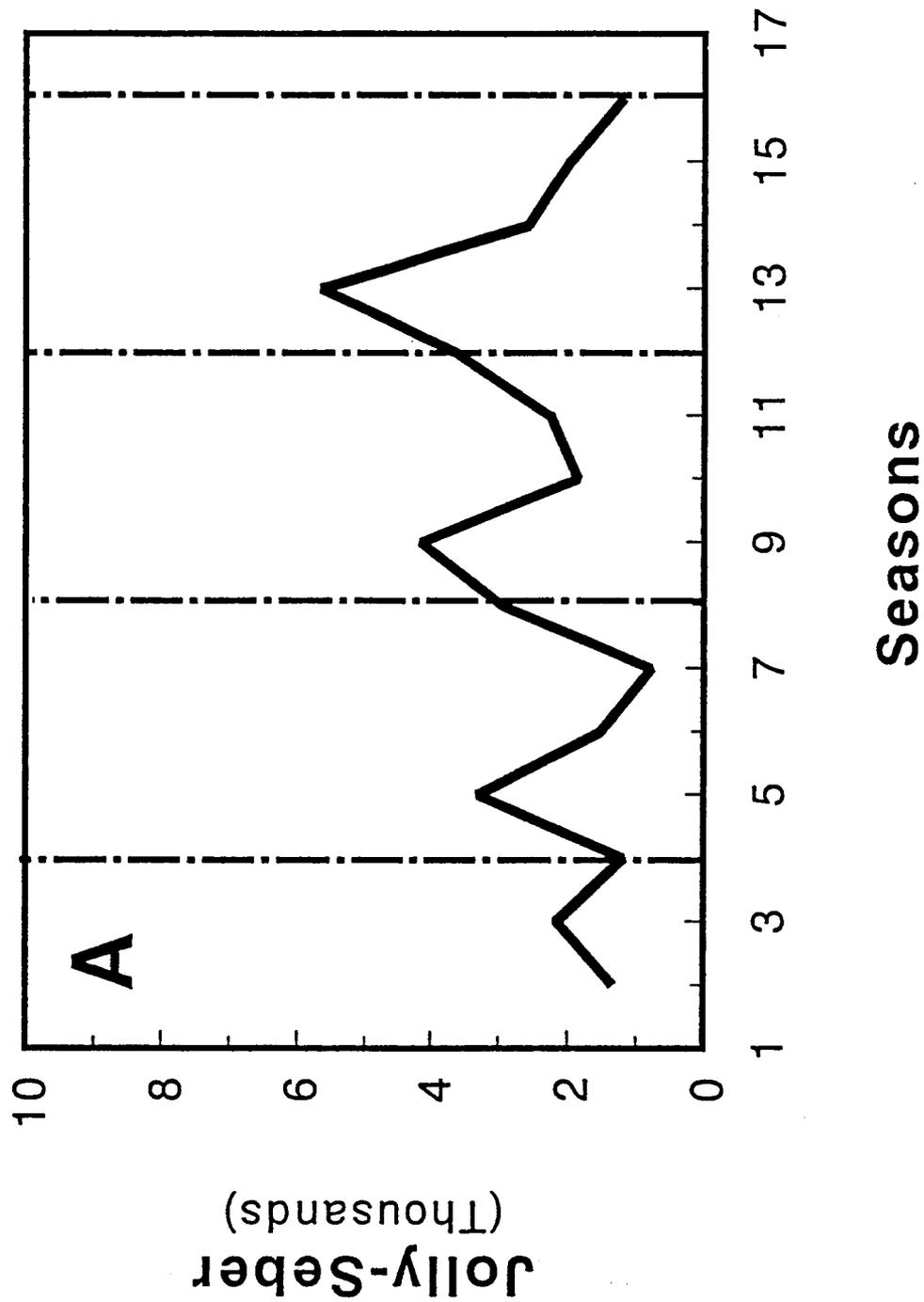
Catostomus latipinnis

Monthly Population Estimates (1991-95)



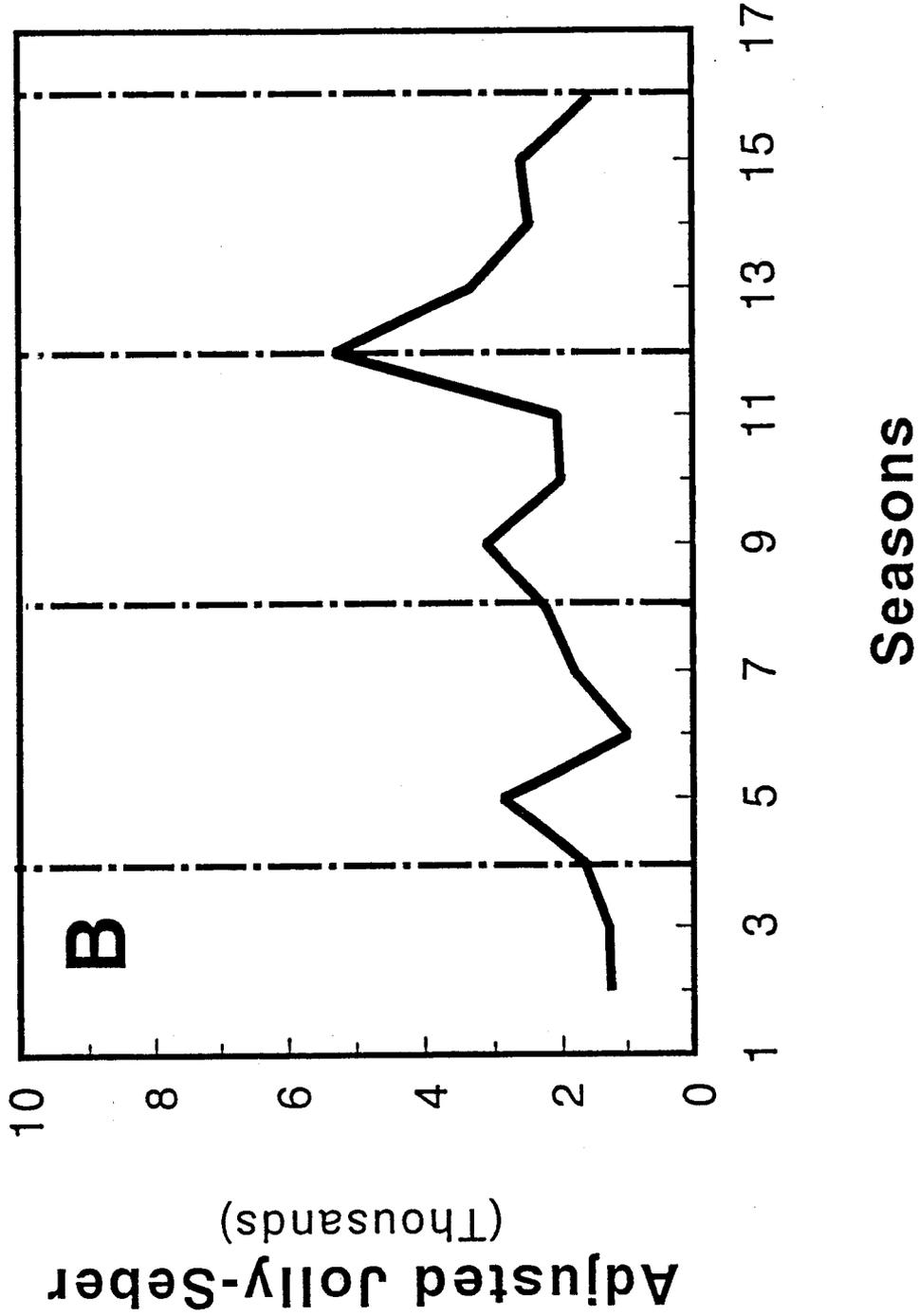
Catostomus latipinnis

Seasonal Population Estimates (1991-95)



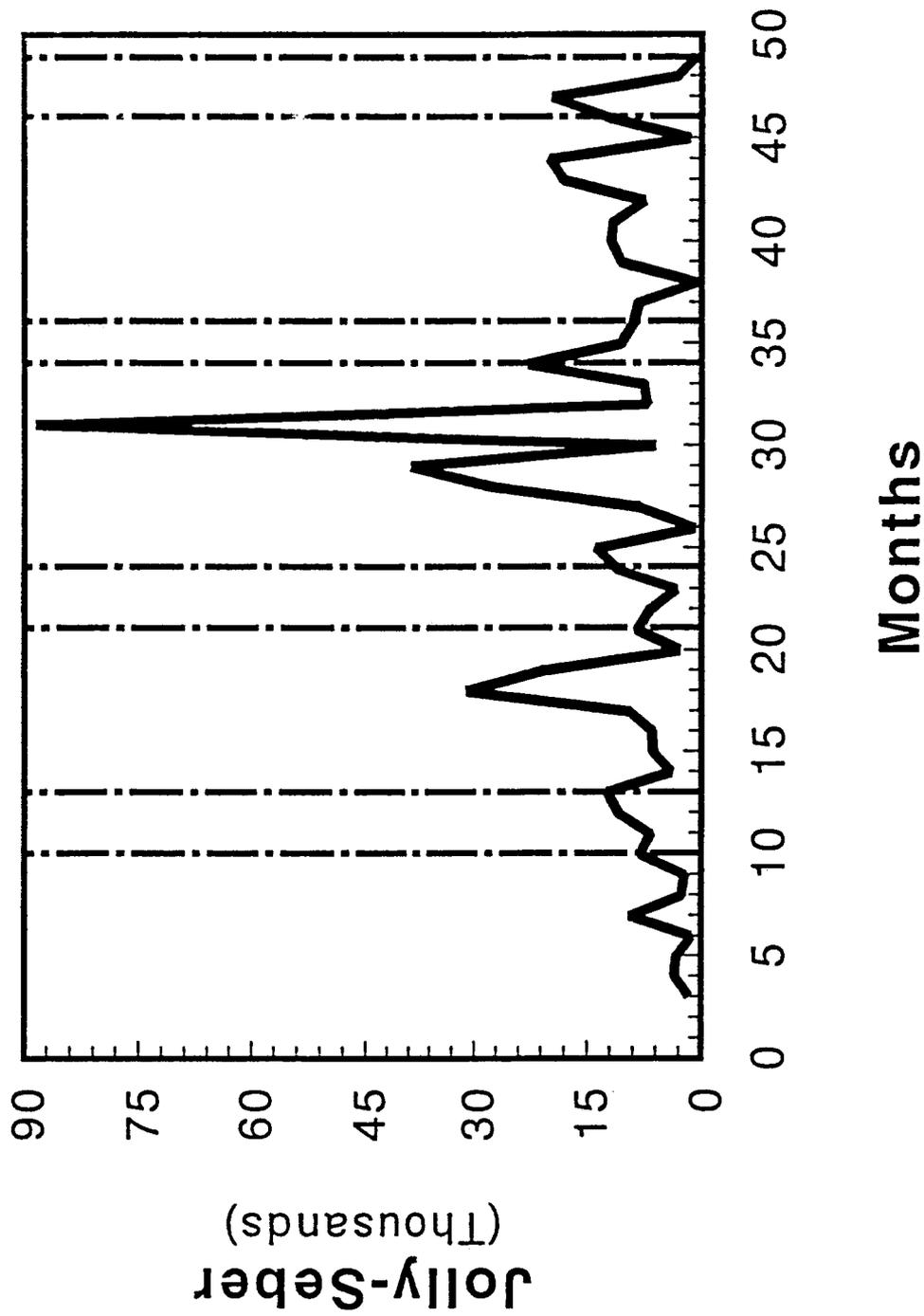
Catostomus latipinnis

Seasonal Population Estimates (1991-95)



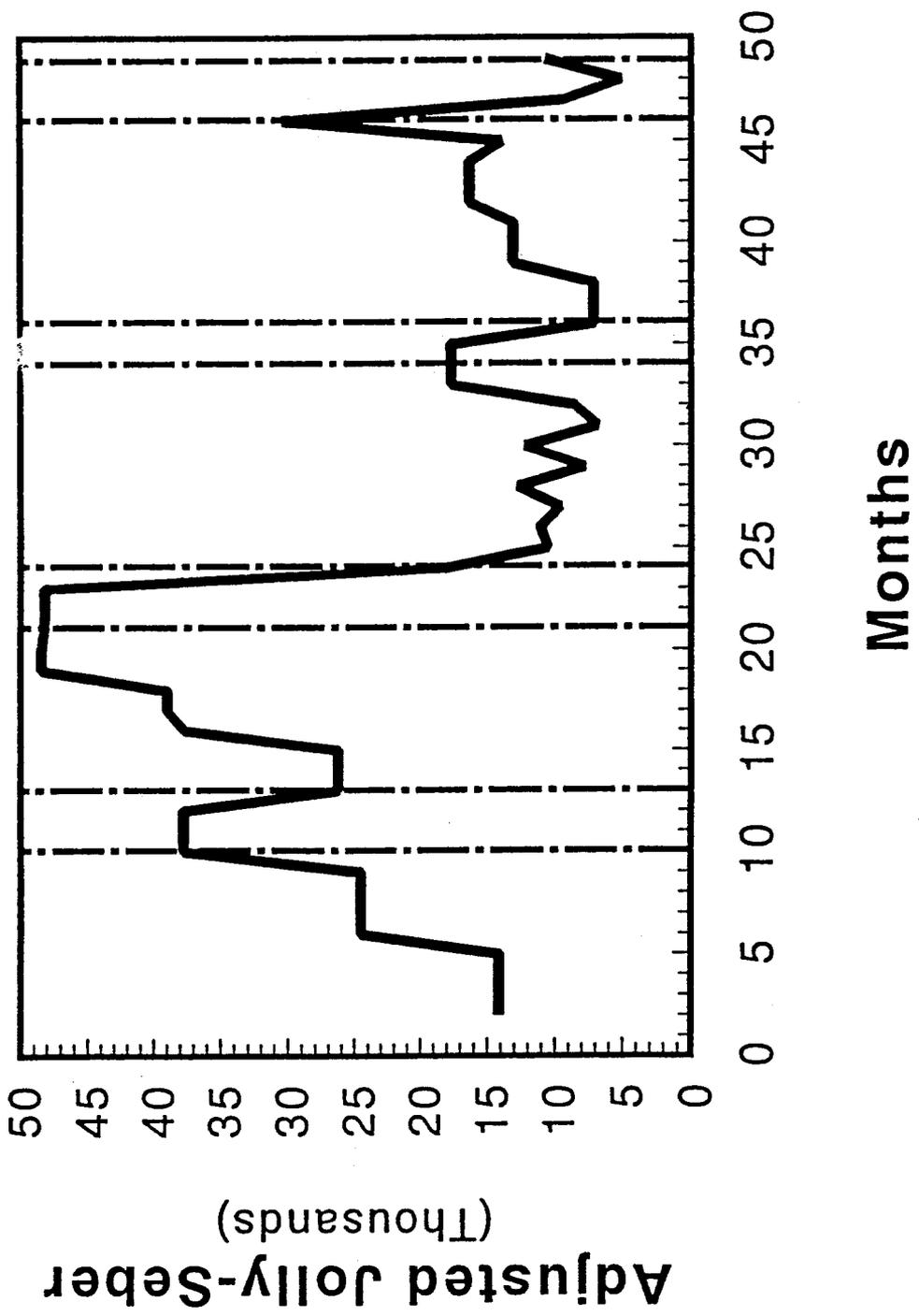
Pantosteus discobolus

Monthly Population Estimates (1991-95)



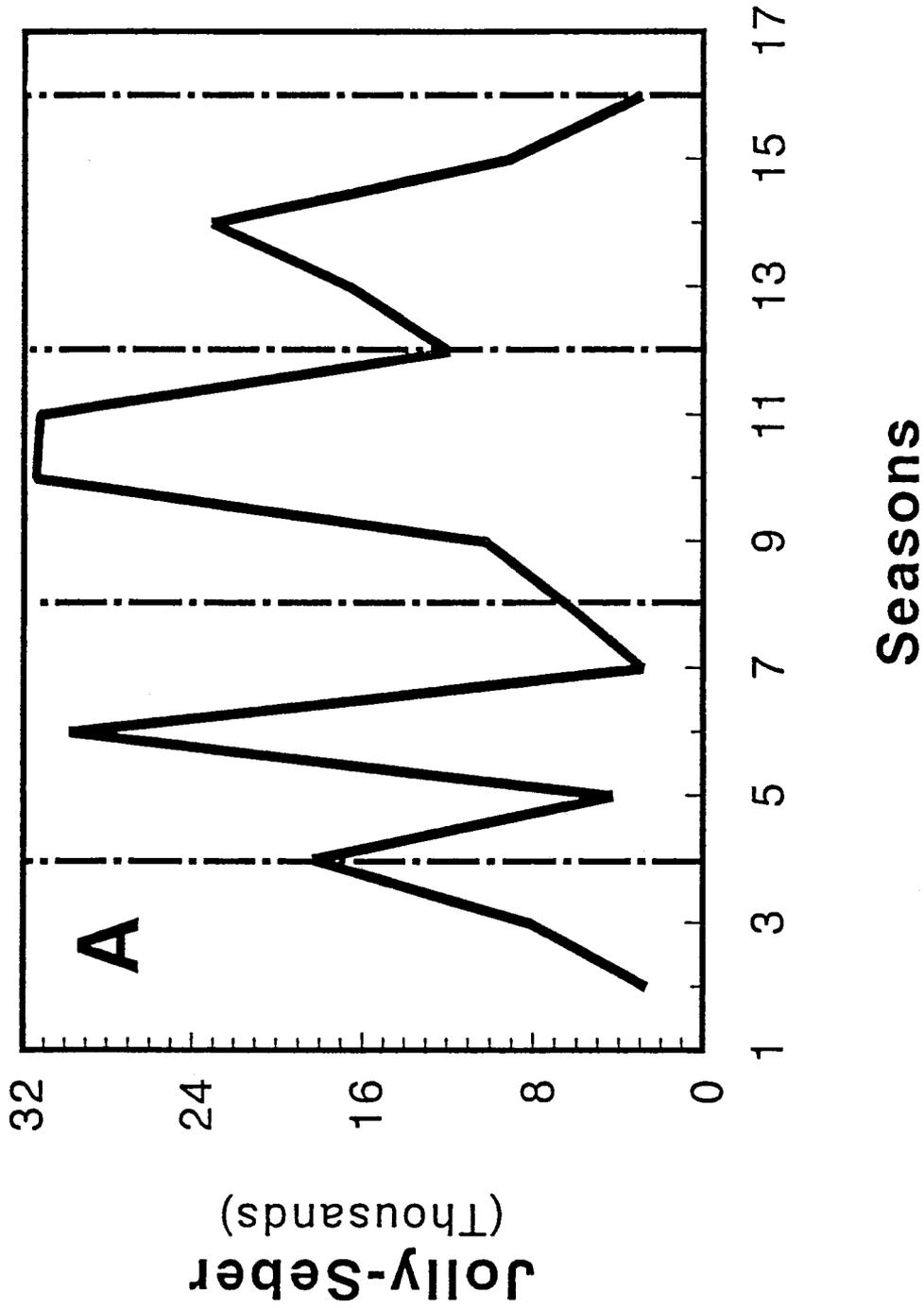
Pantosteus discobolus

Monthly Population Estimates (1991-95)



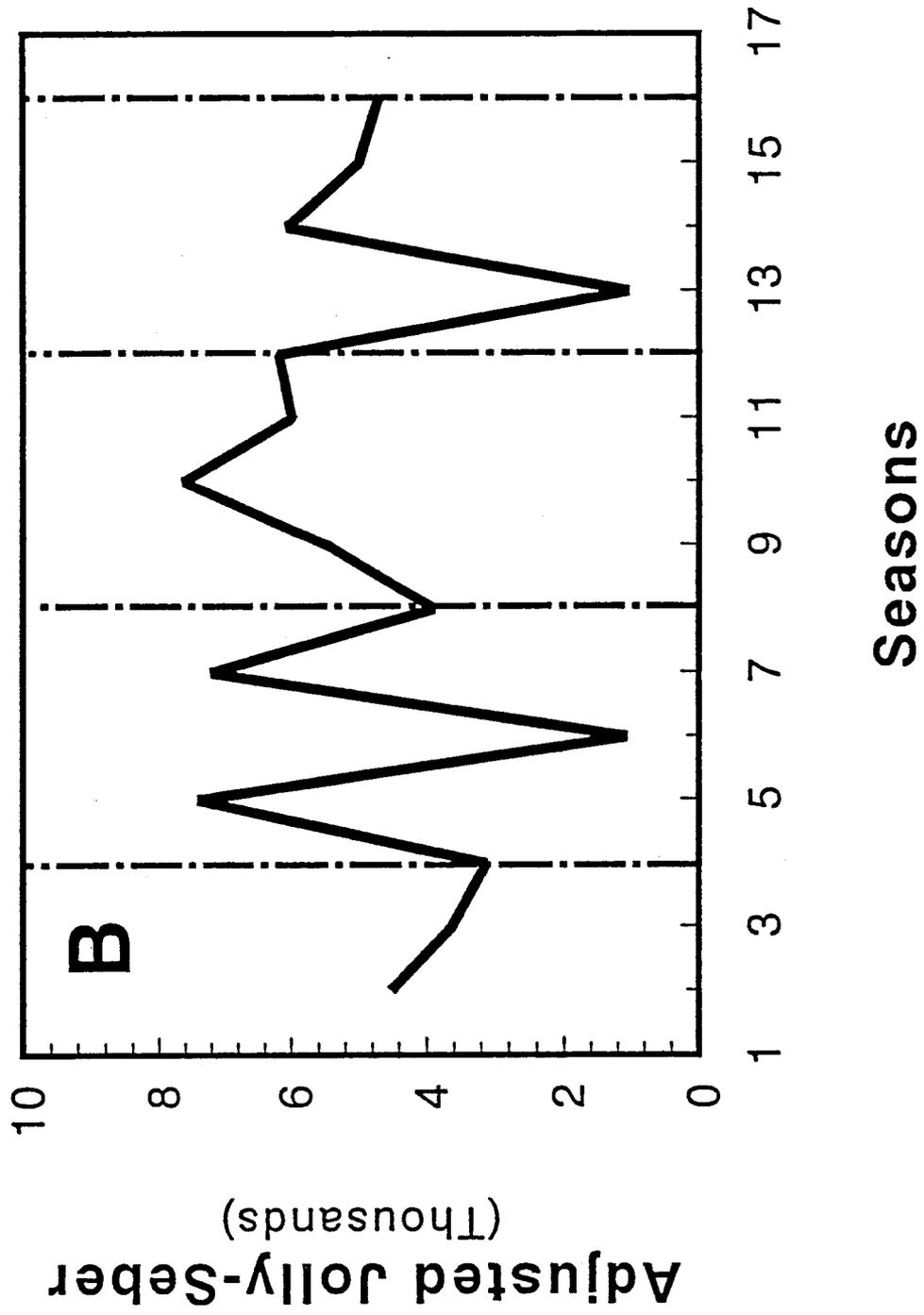
Pantosteus discobolus

Seasonal Population Estimates (1991-95)

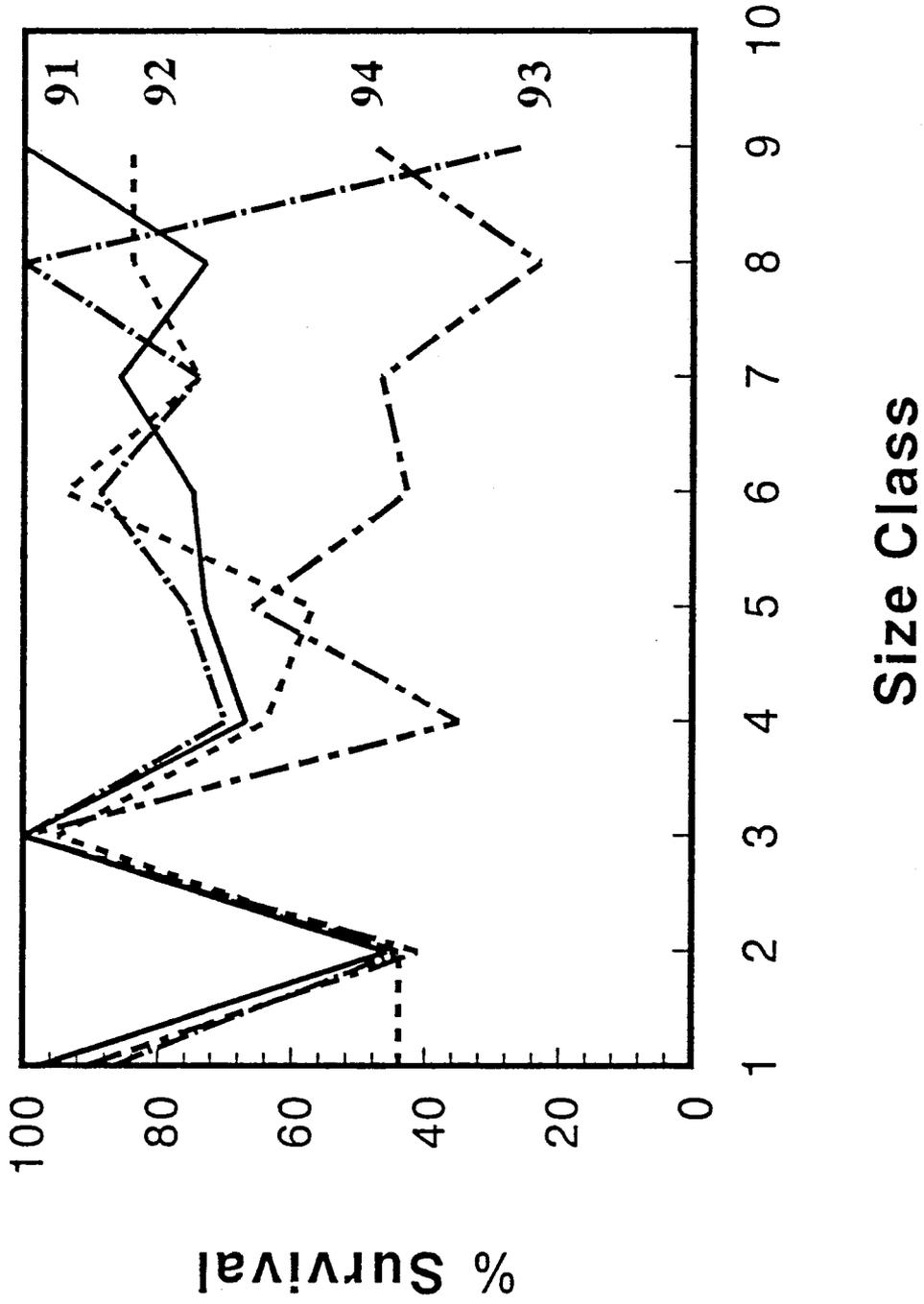


Pantosteus discobolus

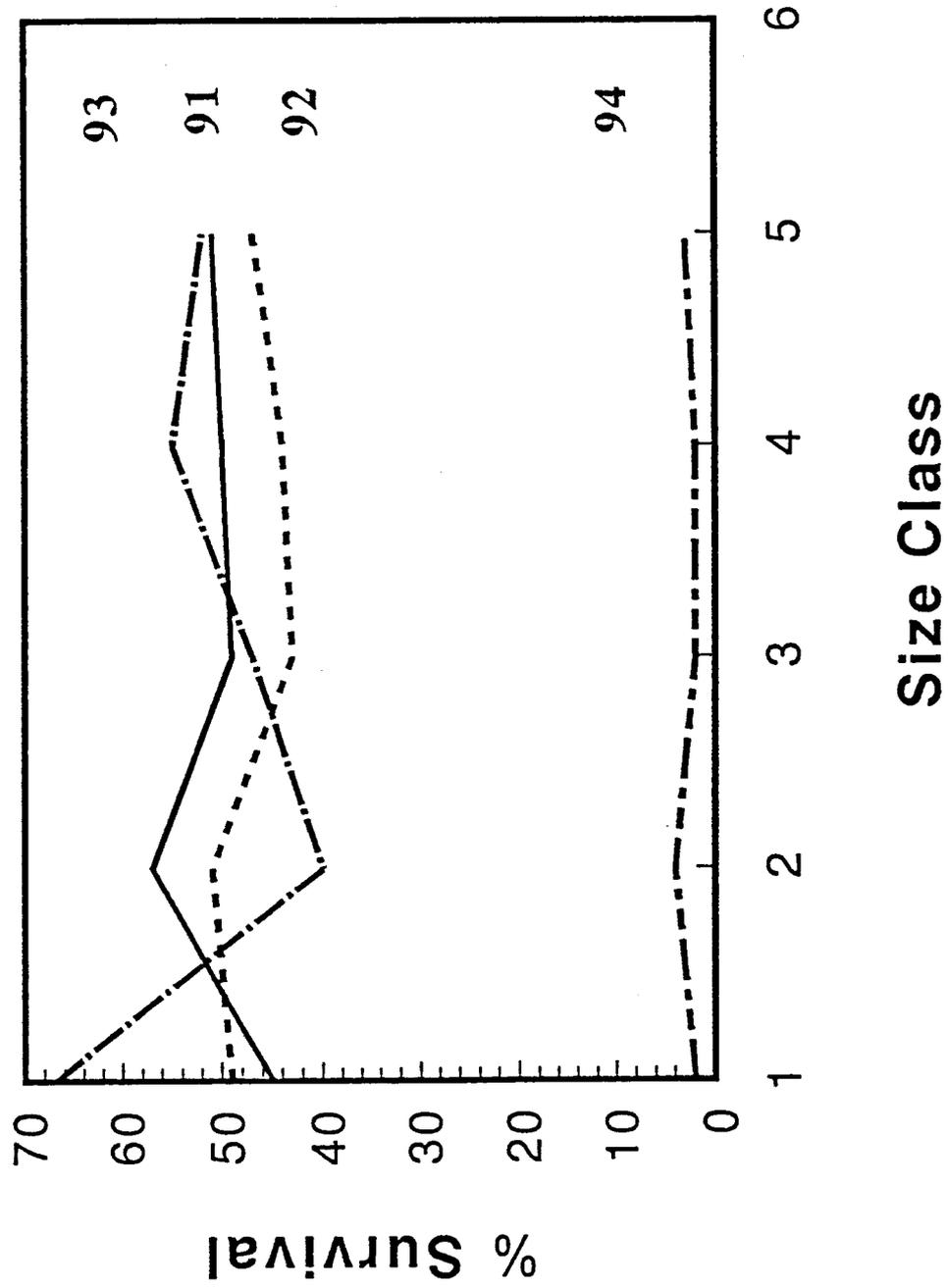
Seasonal Population Estimates (1991-95)



Catostomus latipinnis
Survival Probability by Size



Pantosteus discobolus
Survival Probability by Size



DRAFT

SECTION 4:

**SURVIVABILITY OF AN ENDANGERED SPECIES (GILA CYPHA) IN
THE GRAND CANYON REGION OF ARIZONA: RESULTS OF
A FIVE-YEAR MARK/ RECAPTURE STUDY**

INTRODUCTION

In the past decade, advances in analysis of capture-recapture data have reflected maturation of ecological thought. Previously, capture-recapture algorithms were developed to estimate population sizes, for at that time ecological perspectives centered upon distributions and abundances of organisms (e.g., Andrewartha and Birch, 1954). However, perspectives have gradually shifted towards quantification of life history parameters (e.g., Stearns, 1992), with particular focus on trait differences amongst individuals. Here, the idea is that observed differences in life history traits lead in a proximal sense to an increase in survival, and in an ultimate sense to an increase in fitness (Endler, 1986). This viewpoint juxtaposes both immediate and future success of an organism, and places each within the same context (Hutchinson, 1965). Concomitantly, mark-recapture data have been used to estimate and compare probabilities of survival within and between populations (reviewed by Seber, 1986). The capacity for mark-recapture theory to track current ecological thought was fostered initially by development of the Cormack-Jolly-Seber (i.e., CJS) approach (reviewed by Lebreton et al. 1993), which has been subsequently modified and extended by a variety of researchers to increase precision and decrease bias (see Anderson et al., 1994). Now, survival probabilities are not only modelled, but also tested against specific biological hypotheses (Lebreton et al. 1992; Kingsolver, 1995). A recent proliferation of algorithms has occurred (reviewed by Lebreton et al. 1992:86), which now allows application of survival analysis to a variety of intractable ecological and evolutionary problems. Interestingly enough, many of the latter do not even involve use of marked organisms (reviewed by Nichols, 1992).

Burnham et al. (1987) developed a series of sampling protocols, models, and tests of hypotheses which allowed survival rates to be approximated within context of a specific treatment (i.e., simulated release of trout above and below dams). This study did much to coalesce survival theory and enhance its application. Although a simulation, it has a basis of fact, in that a decade of fish release programs in the Columbia River of northwestern United States were implemented to decipher effects of hydroelectric dams, spillways, bypass systems, and related system structures on survival rates of marked fishes. Determination of survival rates for these fishes was thus a necessary economic and biological consideration.

In this paper, a more prosaic approach is followed, in which actual capture-recapture data are used to generate survival probabilities for size-classes of a cyprinid fish (the humpback chub, *Gila cypha*) endemic to the Grand Canyon of the Colorado River in western North America. While the study species is found

in other canyon-bound reaches of the Colorado River basin (see Douglas and Marsh, 1996: Fig. 2a; Section 1, Fig. 1--2a), its distribution is severely restricted and it is seldom locally abundant, particularly when compared to other indigenous fishes. The study population resides within the Marble Canyon section of Grand Canyon National Park (GCNP) at confluence of the Colorado and Little Colorado rivers [LCR: 99 RKM (river kilometers) below Glen Canyon Dam; Fig. 1--2b]. Here, it uses the lower 14.8 RKM of the LCR (on the Navajo Nation, Coconino County, AZ), as both breeding habitat and refugium, often remaining within the LCR for extensive periods, to include overwinter (Douglas and Marsh, 1996; see Section 1 of this report). A derivation of survival rates for different size-classes of this endangered fish would enhance management strategies designed to reduce anthropogenic impacts (see below).

Life history and ecology of *G. cypha* have been (and are being) impacted by operation of the dam. Other natural and recreational resources downstream from the dam are likewise being impinged by current dam management. As a result, a lengthy and costly environmental impact statement (EIS) on dam operation was mandated by Congress in 1989, under the National Environmental Protection Act (NEPA). The present study formed one component of the Bureau of Reclamation's Glen Canyon Environmental Studies (GCES; reviewed by Wegner, 1991), in which Phase II (see Patten, 1991) was authorized to specifically ascertain if flow releases from the dam could be modified to minimize impacts on natural and cultural resources downstream.

The primary focus of this paper is development of Cormack-Jolly-Seber (CJS) open population estimates for *G. cypha* during each of the 50 months, 16 seasons, and four years of this study. From these data, probabilities of yearly survival are then estimated for five different adult size-classes. The hypothesis under test is that overall survival rate is low for this species, particularly given massive anthropogenic modifications of the mainstem Colorado River (reviewed in Douglas and Marsh, 1996, and references therein; see Section 1 of this report, and Appendix 4-1).

METHODS AND MATERIALS

Gila cypha is a biological enigma (Douglas and Marsh, 1996), and for a variety of reasons. It was only described in 1946 (Miller, 1946), has often been confused with congenitors in the basin (Douglas et al., 1989; reviewed by Holden, 1992:44--45), inhabits only inaccessible, canyon-bound reaches of the system (Holden and Minckley, 1980; Douglas and Marsh, 1996), and was listed as endangered in 1967. In addition, earlier (pre-impoundment) fisheries studies on indigenous fishes were published in non-reviewed "grey literature" that is now

unobtainable (see Douglas, 1993, and references therein). These factors, in synergy, have limited available information on *G. cypha* and impeded development of a comprehensive data base to augment its conservation. The cryptic life history and rugged habitat of this species, coupled with its bizarre functional morphology (Minckley, 1991; Douglas, 1993; Douglas and Marsh, 1996; Fig. 1--1), have now established it as a charismatic icon symbolizing the intermontaine "canyon country" of western North America (Fig. 4--1).

The study river

The LCR drains 141,155 km² of eastern and northern AZ and western NM, and flows 412 km from headwaters to confluence with the Colorado River (GCNP, Coconino Co., AZ; Figs. 2a, 2b). The LCR is seasonally dry in much of its upper 390 km, a result of modern land-use practices and water impoundments initiated at the turn of the century (Miller, 1961). However, flow in the lower 21 km is perennial, from numerous groundwater springs which drain 72,520 km² of the Black Mesa north and east of Flagstaff, AZ. The largest (i.e., Blue Springs, at LCR RKM 21; Fig. 2b) has a discharge of 6.1-6.6 m³/sec (Johnson and Sanderson, 1968).

At base flow, the LCR is saline (conductivity exceeds 5000 umhos/cm⁻¹) and travertine-forming. Carbonate precipitates into the water column and onto submerged surfaces; the river at base flow thus has a distinct turquoise color. Carbonate deposition (a function of CO₂ degassing and photosynthetic activity of algae and cyanophyceans) produces an intricate and confusing water chemistry (Kubly and Cole, 1979). Travertine accumulations over geologic time define pools, runs, and rapids, and generate scalloped waterfalls and cascades. Broad sandbars and other depositional features more typical of erosive southwestern streams are dispersed amongst this, and shift seasonally (and dramatically) according to duration and extent of flooding. Dominant riparian vegetation is a mixture of native and nonnative species (see Carothers and Brown, 1991; Johnson, 1991; Douglas and Marsh, 1996). The lower LCR passes through a narrow gorge that progressively widens and deepens as it drops towards Marble Canyon. A series of precipitous (to three m) travertine falls at RKM 14.9 (Atomizer Falls complex, Fig. 1--2b) mark upstream distribution of *G. cypha*. Above this point are found only introduced common carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*), rainbow trout (*Oncorhynchus mykiss*), and indigenous speckled dace (*Rhinichthys osculus*).

Base camps and data collection

Biologists worked from three base camps in the LCR gorge: Near confluence (RKM 0.55), at Powell Canyon (RKM 3.1), and at Salt Canyon (RKM 10.8). Those at confluence fished the lower 1.2 km of river, while Powell camp personnel fished upriver from 1.3--7.6 km. Salt camp biologists fished from 8.0--14.9 km. There were 50 sampling periods (6--14 day duration) at approximate monthly intervals from July 1991 to June 1995 (see Table 4--4). Hoop nets (dimensions in Douglas and Marsh, 1996) were deployed in all available habitat types of sufficient depth (i.e., > 0.4 m). Trammel nets (see Douglas and Marsh, 1996) were set routinely in the confluence. Fishing effort for a particular trip was recorded as number of net-hours per camp.

All captured fishes were identified, measured (TL to nearest mm) and weighed (nearest g). Indigenous species were examined for tags, secondary sexual characteristics, ripeness, and general health and condition. Those greater than 150 mm TL (= 'adults') were injected with passively integrated transponder (i.e., PIT) tags (see Prentice et al., 1990) and released near points of capture. Nonnative fishes were scanned for presence of PIT tags (a result of consuming tagged native fishes), then sacrificed and either dissected immediately or preserved for later study (see Section 2 of this report).

Analytical protocol

Adult *G. cypha* were grouped initially as newly-tagged (i.e., PIT-tagged by ASU personnel at time of capture), recaptured (i.e., already PIT-tagged when captured by ASU personnel), or with old tags (i.e., Carlin or floy-tag from previous investigations which was removed and retained; the fish was then PIT-tagged). For this study, all three groups start their capture histories when first handled by ASU personnel.

All three categories were computationally merged and sorted by PIT-tag number." Individual *G. cypha* were often recaptured several times during this study (maximum number of recaptures for one individual was 20). Individuals were then condensed into a capture-history (CH) matrix (Burnham et al., 1987), in which each unique PIT-tag (= individual) comprised a row vector and each of the 50 sampling periods a column. If an individual was captured (or recaptured) during a given sampling period, that respective column of the matrix was scored '1', otherwise '0.'

The CH-matrix was sorted two different ways: First, individuals were segregated by season and year (where winter = December, January, February; spring = March, April, May; summer = June, July, August; and autumn = September, October, and November). In all, 16 total seasons were represented (four each over four years, beginning with summer, 1991 and terminating with spring, 1995). Individuals were also partitioned into five 50 mm

(TL) size-classes, starting at 150 mm TL.

Open Cormack-Jolly-Seber (CJS) population estimates were generated for each species by month ($n=50$), by season ($n=16$ and $n=4$), and by year ($n=4$) over all four years of the study. In each case, estimates were generated for the entire LCR rather than by river reach (as defined in Douglas and Marsh, 1996). The program POPAN--4 for Windows (A. N. Arnason and C. J. Schwarz, Dept. Computer Sci., Univ. Manitoba, Canada, 1995, unpubl.) was used to generate estimates, standard deviations, 95% confidence limits and survival probabilities. Open estimates were used exclusively because geographic and demographic closure could not be substantiated over the span of the study. In this study, it was not necessary to group individuals (as in Section 3) to elude difficulties stemming from small or '0' recapture values for a given month.

Probabilities of survival were calculated for each size class over four of the five years of the study (i.e., 1991--1994). Survival estimates for 1995 were not produced in that capture/recapture data were required for 1996 to produce this analysis.

RESULTS

Numbers of *G. cypha* captured, recaptured with PIT-tags, and recaptured with old tags are presented in Table 4--1. Results of merging, sorting, and condensing these data into CH-matrices are also tabulated. Consequences of partitioning each CH-matrix by season ($n=16$) are presented in Table 4--2, while effects of partitioning these matrices by adult size class (i.e., 50 mm increments beginning at 150 mm TL) are reported in Table 4--3.

Preliminary tests indicated that fishing effort had no significant effect on population estimates for *G. cypha*. However, a seasonal effect was significant at all levels of fishing effort. The population estimate/ fishing effort relationship was also nonsignificant over seasons (i.e., no significant interaction between these two terms). A standard ANCOVA was performed; estimated populations of *G. cypha* varied significantly over the 16 seasons [$F=2.49$; $df=16$; $P<0.01$; Proc GLM, Statistical Analysis System (SAS, ver. 6.08), Cary, NC, 1989, unpubl.]. Pairwise linear contrasts of population estimates consolidated by four seasons were nonsignificant, however. Because of the manner in which seasons were partitioned, 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. There were no significant differences between these years in overall population estimates.

Preliminary statistics (Table 4--1) indicate that 58%

(10,795/ 18,626) of individuals were recaptures. The minimum number of multiple recaptures were 57% [100 - (7,993/ 18,626)]. Capture/ recaptures by season and year are presented in Table 4--2. A severe dropoff in numbers is indicated for the 1994 year and spring of 1995, particularly when compared to values for previous years. Numbers of captures/ recaptures divided into size classes are presented in Table 4--3. The majority of individuals (38%; 3,037/ 7,993) fall within the smallest size class, while the fewest individuals (11.3%; 903/ 7,993) are within the middle group (TL = 251--300 mm). Arrangement of size classes by decreasing percentage is: 1--5--4--2--3 (Table 4--3).

Computational statistics derived from a CJS analysis of capture/ recapture data are presented in Table 4--4. Included within this table are dates of monthly sampling periods, and monthly population estimates (and standard errors) of adult *G. cypha*, corrected for fishing effort. Unadjusted estimates and those adjusted for fishing effort are plotted for all 50 months of the study in Figures 4--2 and 4--3, respectively. Both plots record seasonal (and thus apparently normal) fluctuations in adult population numbers during the first 26 months of the study. However, both plots also record a sharp and steady decrease in these estimates from this point until end of the study. This decrease is most dramatic in the plot of population estimates adjusted for fishing effort (Fig. 4--3).

Figure 4--4 is a plot of unadjusted and adjusted CJS estimates over 16 seasons. The sharp decline in population estimates by month (Figs. 4--2, 4--3) is still apparent even when months are coalesced into seasons. When unadjusted estimates are plotted, the decline begins in season 9 (i.e., summer 1993), whereas with adjusted estimates, it begins at season 10 (i.e., autumn, 1993).

Yearly survival probabilities for five adult size-classes of *G. cypha* are recorded in Table 4--5 (along with standard errors). These estimates are plotted in Figure 4--5. Years 1991--1993 show a remarkable uniformity of survival across all size-groups, with 1993 revealing a decline in survival probabilities from size class 3 through size class 5. However, the greatest reduction in survival rates is found for 1994 (i.e., 1993 individuals surviving into 1994). Here, four of five size classes are remarkably reduced over those recorded for the previous three years. The sharp increase noted for size class five in this year is the result of a weak sample size (i.e., a standard error of zero; Table 4--5).

DISCUSSION

Survival probabilities for a given population are developed from a capture/ recapture database (i.e., CH-matrix) from which

organisms are grouped in some way for analysis, such as by sex, ontogeny, or geography. A rate of survival is then generated for each grouping variable over sampling periods. In practice, sampling periods are often coalesced as well into more reasonable periods over which survival can be expected to operate (i.e., over seasons or years, for example). The CH-matrix is also springboard for development of CJS population estimates, which can also be derived for groups within the population (as above). These estimates are baseline data from which to interpret survival probabilities (see Appendix 3--2).

During the analytical process, it is important for CJS estimates to be weighted (or adjusted by) the capture effort exerted per sampling period, particularly when this effort fluctuates between periods. Clearly, this is less of a problem when capture effort is exerted uniformly over each sampling period. When it isn't (as in this study; see also Sections 2 and 3), then effort must somehow be accommodated, either during derivation of estimate(s), or afterwards. Occasionally, the software utilized in the analyses has the capability to adjust the matrix of estimates against a vector composed of sampling efforts (i.e., POPAN-4's UFIT algorithm). Alternatively, the researcher must do it *post-hoc* (i.e., via ANCOVA; Section 1 of this report). Values of the population estimate(s) are often changed radically by this adjustment. For example, in a separate study (Section 3 of this report), unadjusted and adjusted CJS estimates were derived for *Catostomus latipinnis* and *C. discobolus* (Figs. 3--1, 3--2, and 3--4, 3--5, respectively; Section 3). Plots of both estimates for each species showed similar global patterns across 49 months of sampling (i.e., peaks and valleys were analogous for unadjusted and adjusted estimates). However, the magnitude of amplifications and depressions differed between plots, as did their local onset (i.e., peaks and depressions initiated and/ or terminated differentially between plots). In general, when compared to an unadjusted value, use of fishing effort as a covariate magnified the value of a given estimate for a sampling period.

With regard to the current study, an open (i.e., CJS) model was used to produce population estimates for *G. cypha* unadjusted and adjusted for fishing effort (the latter on a monthly, seasonal, or yearly basis). Previous population estimates for this species in the LCR (reviewed in Section 1, Table 1--5; Douglas and Marsh, 1996) were derived without taking fishing effort into consideration, and without testing for closure (when closed population estimates were used) (but see Section 1, Table 1--4). As a result, previous estimates (other than those presented by Douglas and Marsh, 1996; Section 1 of this report) must be viewed with skepticism.

Population estimates for *G. cypha* (both unadjusted and adjusted) show similar trends (Figs. 3--2, 3--3). Before month 27

(summer, 1993), each demonstrates a similar pattern of peaks and depressions on a global level. After month 27, each also reveals a gradual decrease in population estimates which continues unabated to the end of the study. However, this decrease is most apparent when the plot is examined of estimates adjusted for effort (Fig. 3--3). Here, the decrease is so pronounced initially, that it falls at month 27 from the highest estimate recorded in the study (i.e., 9,848; Table 4--4), to the lowest value recorded to that point (i.e., 4,278; Table 4--4). This decrease then continues unabated, eventually recording its lowest value at month 49 of 50 (i.e., 442; Table 4--4).

Both plots of population estimates evaluated over 16 seasons demonstrated similar trends. The decrease seen in both plots of monthly estimates (Figs. 4--1, 4--2) are also reflected in Figures 4--3 and 4--4. Seasonal plots adjusted for fishing effort showed that season 16 recorded the lowest estimate over the entire study. Again, seasonal trends simply reflect monthly trends.

A similar decrease in population estimates was recorded for *C. discobolus* (Fig. 3--5; Section 3 of this report). However, it was not recorded for *C. latipinnis* in the same study (Fig. 3--2; Section 3 of this report). It was hypothesized that *C. discobolus* reflected a drop in population estimates at month 25 which was concomitant with a change in water chemistry in the LCR. Floods early in 1993 removed travertine deposits (Douglas and Marsh, 1996; Section 1) on banks and bottom, thus disrupting movement of carbonate from water column into precipitates and back again. Under normal occurrences, this carbonate movement maintains a milky, turquoise color in the water column and greatly inhibits visibility underwater. Once this intricate water chemistry was disrupted by intense flooding, the water column became transparent and visibility increased remarkably. Population estimates for *C. latipinnis* were not as affected as those of the other two species because the former uses the LCR to a lesser degree than the latter two. The question that was posed for *C. discobolus* at that time (Section 3 of this report) is apropos for the present study. The tremendous decrease in population estimates recorded for each of these two species is most assuredly tied to water chemistry, but the latter is not the cause. Rather, the question is whether the decrease is a result of behavioral alteration on the part of both species, or as a result of predation. *Gila cypha*, in particular, is noted as being photonegative. It is normally active during crepuscular periods and at night. It is also active at all times when the Colorado River and/or the LCR is muddy from flood conditions (reviewed by Douglas and Marsh, 1996; Section 1 of report). However, one would also assume that this species would still be active at night, much as it would be when water conditions were normal. In fact, it is the nocturnal activity that results in the capture/recaptures recorded in Table 4--1. Thus, given the above, it is

difficult to argue that behavior of *G. cypha* was sufficiently altered by differences in water column visibility such that normal movement patterns were terminated and estimated population sizes decreased (recorded in Table 4--4; plotted in Figure 4--3).

An alternative hypothesis is that decreases in estimated population size are the result of predation. Yearly survival estimates plotted by size class of *G. cypha* are remarkably similar (Fig. 4--5), with exception of 1994. Here, values are uncommonly reduced from those of previous years. Interestingly enough, survival rates for all four years show the same global pattern of lowered values for smaller *G. cypha*, with increasing survival as size increases. But, for 1994, all size classes are reduced considerably over those of previous years. In fact, survival rates for 1994 never climb above 47% for any size class (Table 4--5), whereas in previous years, survival rates never dropped below 52% (and this was for the smallest size class). Clearly, 1994 was a problematic year for *G. cypha*.

There are two introduced fishes in the Colorado and Little Colorado rivers [i.e., rainbow trout (*Oncorhynchus mykiss*) and channel catfish (*Ictalurus punctatus*)] that have a history of predation upon *G. cypha*. Twenty-five of the former (313--398 mm TL; mean = 352 mm TL) and 33 of the latter (271--790 mm TL; mean = 500 mm TL) were found with stomach contents containing fish remains (13.5% of stomachs examined, Table 3--1; Section 3 of report). Channel catfish, in particular, are believed to predate on larger *G. cypha*, based on presence of crescent-shaped bite marks on dorsal and/or ventral aspects of specimens (Kaeding and Zimmerman, 1983; Karp and Tyus, 1990; C. O. Minckley, pers. obs.). Channel catfish that predated upon *G. cypha* were among the largest taken by ASU personnel, confirming the fact that this predator can easily ingest fishes to 200 mm TL (Section 3 of this report). However, it is difficult to visualize predation having such a uniform effect on all size classes of *G. cypha* as that recorded in Fig. 4--5.

The most parsimonious explanation for reduced population estimates from month 25 to end of study is that altered water chemistry had an unobserved effect upon *G. cypha*. Quite possibly reduction in carbonate content of the water column cued the altered behavior of this species. Alternatively, diurnal water clarity was so traumatic to the study species that it inhibited nocturnal movements as well. Increased water clarity may have disturbed normal behaviors by allowing increased interactions with introduced fishes. Douglas et al. (1994) reviewed literature which indicated that aversion to nonnatives by native species does not require direct interaction (i.e., competition for resources). The mere presence of the nonnative may be reason enough to induce altered behavior.

Data reported herein point to the need for additional

studies on *G. cypha*. First, long-term monitoring of this population must continue, and at a level that will track potential population declines shown in Fig. 4--4. Current thought on long-term monitoring is that it will occur only once or (at best) twice each year, and for a limited duration. Clearly, this is not enough to segregate normal movement variability in this species from non-normal occurrences such as those in Fig. 4--4. Also, more information is required on behavior of this species, to include its interactions with nonnatives. The latter are clearly the greatest problem facing indigenous fish communities (Appendix 4--1). Given this, and the fact that resource agencies are reluctant (or unable) to implement control measures for introduced fishes, it becomes clear that this problem will remain a considerable one in the years to come.

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Appendix 4--1

Gila cypha is part of an indigenous Colorado River fish fauna in jeopardy (see Table 3--1). Reasons for decline are documented in a variety of sources (summarized in Minckley and Deacon, 1991), and emphasize physical and biological modifications of the basin by modern humans. With regard to physical disturbance, the river has been impounded for industrial and recreational purposes and pumped for agricultural ones. Repercussions of these activities are manifold. For example, the continuity of the river is now broken, its sediment load interdicted, thermal regime depressed, flow oscillations damped, and volume depleted. These cannot have anything but a negative impact upon a fauna that has lived and evolved for millenia within the waters of this basin.

However, Minckley (1991:141) argues persuasively that, as devastating to riverine habitat as physical alterations have been (and continue to be), they cannot be considered primary cause for disappearance of indigenous Colorado River fishes. The two largest liabilities resulting from physical modification of riverine habitat have been reductions of nursery habitats for these fishes, and depression of mainstem temperatures below those tolerable for their reproduction and larval development. In spite of these developments, the indigenous fish community has been remarkably persistent. It has likewise demonstrated similar persistence throughout an evolutionary period equally as tumultuous, if not more so, than the extant one (reviewed by Minckley et al., 1986). The endemic species which comprise the large-river community are regarded primarily as generalist species (Smith, 1981) with a demonstrated capacity for completion of their life histories in a variety of habitats (as in Moyle and Sato, 1991; Williams, 1991), to include federal hatcheries (Johnson and Jensen, 1991). Their resilience to, and adaptability with, environmental fluctuations and perturbations is strong (albeit not infinite).

While physical alterations to the riverine ecosystem have been pervasive, debilitating, and ongoing, they do not measure up to damage caused by prolific introductions of nonnative fishes into the basin. This aspect of mankind's intervention has clearly been the most crippling to indigenous freshwater fishes. Numbers (and effects) of these introductions are of staggering proportions, and have been documented by Minckley (1991:142---145), Minckley and Douglas (1991), and Douglas and Marsh (1996; Section 1 of report). The history of freshwater fish introductions within Grand Canyon National Park is documented in Chapter 3 of this report, which also substantiates predatory effects of adult nonnatives on the indigenous fauna.

While most introductions were to create sport fisheries in the numerous reservoirs and tailwaters that now compose much of

the Colorado River mainstem, smaller nonnative "forage" fishes were also introduced, often accidentally (Douglas et al., 1994). These are often overlooked when effects of introduced fishes are examined, but they are equally as detrimental to natives as are larger forms. For example, adult red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), and redbelly shiner (*Richardsonius balteatus*) have trophic requirements similar to those of indigenous juvenile cyprinids. In addition, larvae and juveniles of these introduced cyprinids also compete spatially and trophically with those of indigenous fishes (T. W. Joseph, J. A. Sinning, R. J. Behnke, and P. B. Holden, Environ. Protection Agency Rept., 1977, unpubl.).

In backwaters of the Yampa and Green rivers, adult red shiner (36--79 mm TL) predated significantly upon larval cypriniforms (Ruppert et al., 1993). Given red shiner's high predation rate (larval native fishes were found in 15% of stomachs examined), and the fact that it is ubiquitous in its distribution with a specificity for nursery habitats of indigenous fishes, this species most probably has a significantly negative impact on overall survival of indigenous larvae. In the Canyon, red shiner predominate only below Diamond Creek (RM 226) (R. A. Valdez, pers. comm.).

Another small, introduced fish, the Plains killifish (*Fundulus zebrinus*), was first collected in the upper drainages of the LCR in 1938. In the interim, it has gradually dispersed downriver to the confluence and is now found within additional tributaries of the main canyon (R. R. Miller, GCNP report, 1975, unpubl. field notes, Spec. Coll., Hayden Library, ASU). Although there have been no studies on interactions between this species and indigenous fishes within the Colorado River drainage, *F. zebrinus* has a documented history of predation on (and competition with) indigenous fishes of the Rio Grande drainage, particularly *Camptostoma ornatum* (Hubbs and Wauer, 1973).

The fathead minnow (*Pimephales promelas*), a third nonnative forage fish, was first recorded within Colorado River drainages of the White Mountains (Arizona) circa 1952 (R. R. Miller, in Smith, 1959:196; see also R. R. Miller and G. R. Smith, 1972, unpubl. field notes, Special Coll., Hayden Library, ASU). Carothers and Minckley (Table 6--1: S. M. Carothers and C. O. Minckley, U.S. Dept. Interior, Water and Power Resources Service, 1981, unpubl.) listed it as being "locally common" within Grand Canyon. Recent studies (R. A. Valdez, pers. comm.) suggest the focus of its mainstream distribution is centered about the confluence of the LCR (i.e., RKM 99).

Ruppert et al. (1993) found mostly algae and organic debris in an analysis of stomach contents of 42 adult fathead minnows (32--60 mm TL) collected from backwaters of the Yampa and Green rivers. However, spatial requirements of this species certainly

overlap those of larval and juvenile native forms, thus suggesting potential for competitive displacement. This would result in serious population declines being registered by the native (as demonstrated in Douglas et al., 1994).

Table 4--1: Adult *Gila cypya* divided into three categories: CAPTURED, RECAPTURED, and OLD TAGS. The first represents fish PIT-tagged by ASU personnel at time of capture. The second represents fish already PIT-tagged when captured (i.e., recaptured; source of original tag unknown). The third includes fish previously tagged with either Carlin or floy-tags and subsequently PIT-tagged by ASU personnel (see text). TOTAL is a summation of the three categories. CH-MATRIX represents TOTAL collapsed into a capture-history matrix where each unique PIT-tag number is represented but once.

SPECIES	CAPTURED	RECAPTURED	OLD TAG	TOTAL	CH-MATRIX
<i>G. cypha</i>	7,670	10,795	161	18,626	7,993

Table 4--2: Adult *Gila cypha* from CH-matrix coalesced by season (= SEASON), where 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 refers to numerical designation for season, and TOTAL represents numbers of adults summed for each year.

NUMBER	SEASON/ YEAR	<i>G. cypha</i>
01	Summer 1991	1706
02	Autumn 1991	389
03	Winter 1991	368
	TOTAL 1991	2463
04	Spring 1992	1251
05	Summer 1992	564
06	Autumn 1992	274
07	Winter 1992	33
	TOTAL 1992	2122
08	Spring 1993	975
09	Summer 1993	1185
10	Autumn 1993	199
11	Winter 1993	194
	TOTAL 1993	2553
12	Spring 1994	280
13	Summer 1994	106
14	Autumn 1994	53
15	Winter 1994	88
	TOTAL 1994	527
16	Spring 1995	328
	TOTAL 1995	328
	TOTAL	7,993

Table 4--3: Individual *Gila cypha* from CH-matrix grouped by size (= SIZE CLASS) in 50 mm increments beginning at 150 mm TL. INDIVIDUALS = numbers of individuals per size class.

SIZE CLASS	INDIVIDUALS
150--200	3,037
201--250	1,153
251--300	903
301--350	1,168
351--400+	1,732
TOTAL	7,993

Table 4--4: Computational statistics from CJS analysis of adult *G. cypha*. NO. = numerical designation for month; DATE (FROM/TO) = sampling periods; N(I) = sample size at time (i); M(I) = marked subs of N(i); R(I) = number of recaptures from those who returned to population; Z(I) = number seen before (i), after (i), but not at (i) NH(I) = population estimate at time (i) adjusted for fishing effort; SE NH(I) = standard error of nh(i).

NO.	DATE (FROM/TO)	N(I)	M(I)	R(I)	Z(I)	NH(I)	SE NH(I)
01	01 July--14 July 1991	440	0	267	0	6312	832
02	21 July--03 Aug. 1991	875	75	482	192	6847	404
03	11 Aug.--23 Aug. 1991	653	186	373	488	6822	403
04	13 Sep.--25 Sep. 1991	334	119	234	742	5963	387
05	15 Oct.--24 Oct. 1991	232	119	147	857	5963	432
06	07 Nov.--16 Nov. 1991	133	71	81	933	5961	414
07	09 Dec.--18 Dec. 1991	129	67	69	947	5961	448
08	08 Jan.--15 Jan. 1992	114	39	79	977	4979	340
09	11 Feb.--19 Feb. 1992	282	51	179	1005	6853	387
10	05 Mar.--13 Mar. 1992	269	65	187	1119	7354	488
11	26 Mar.--03 Apr. 1992	495	133	307	1173	8743	484
12	20 Apr.--29 Apr. 1992	833	310	472	1170	8743	434
13	18 May -- 27 May 1992	318	156	178	1486	8577	478
14	15 June--24 June 1992	786	365	375	1299	9725	454
15	14 July--23 July 1992	231	125	123	1549	6327	342
16	10 Aug.--19 Aug. 1992	108	71	58	1601	5706	325
17	14 Sep.--23 Sep. 1992	82	43	35	1616	5706	447
18	12 Oct.--22 Oct. 1992	247	94	128	1557	6986	371
19	09 Nov.--18 Nov. 1992	161	79	81	1606	6487	353
20	10 Feb.--17 Feb. 1993	67	34	43	1653	6457	531
21	02 Mar.--10 Mar. 1993	697	358	356	1338	8890	427
22	22 Mar.--31 Mar. 1993	148	92	83	1602	5963	332
23	12 Apr.--21 Apr. 1993	407	258	205	1427	6466	345
24	10 May -- 19 May 1993	722	291	342	1341	9128	435
25	08 June--16 June 1993	521	189	210	1494	9157	458
26	12 July--21 July 1993	627	233	295	1481	9848	464
27	10 Aug.--18 Aug. 1993	807	359	260	1417	9848	462
28	13 Sep.--22 Sep. 1993	114	68	55	1609	4278	288
29	12 Oct.--21 Oct. 1993	143	67	57	1597	4278	262
30	08 Nov.--17 Nov. 1993	158	81	61	1573	4278	265
31	06 Dec.--15 Dec. 1993	181	110	68	1524	4277	261
32	11 Jan.--20 Jan. 1994	133	72	59	1520	3888	248
33	10 Feb.--19 Feb. 1994	162	101	58	1478	3888	249
34	15 Mar.--24 Mar. 1994	224	141	72	1395	3953	261
35	12 Apr.--21 Apr. 1994	382	261	117	1206	3953	254
36	10 May -- 19 May 1994	328	252	109	1071	3830	253
37	14 June--23 June 1994	205	145	61	1035	3157	231
38	12 July--21 July 1994	104	82	27	1014	2401	193
39	09 Aug.--18 Aug. 1994	76	52	23	989	2044	172

40	13 Sep.--22 Sep.	1994	95	79	37	933	2029	171
41	11 Oct.--20 Oct.	1994	85	68	21	902	2029	175
42	01 Nov.--10 Nov.	1994	75	55	19	868	1937	172
43	06 Dec.--15 Dec.	1994	41	33	15	854	1819	179
44	10 Jan.--19 Jan.	1995	169	127	48	742	1941	174
45	07 Feb.--16 Feb.	1995	177	138	48	651	1941	177
46	28 Feb.--09 Mar.	1995	72	61	23	638	1440	155
47	21 Mar.--30 Mar.	1995	211	156	56	505	1582	162
48	11 Apr.--20 Apr.	1995	519	395	44	166	1582	168
49	26 May -- 25 May	1995	226	166	11	44	442	89
50	13 June--27 June	1995	133	55	0	0	910	128

Table 4--5: Survival probabilities for five size-classes of *Gila cypha* by year, from 1991--1994 (1995 survivability could not be calculated). SIZE CLASS = size stanzas for each class; PHI = survival probability adjusted for fishing effort; SE PHI = standard error of survival probability adjusted for fishing effort.

SIZE CLASS	1991		1992		1993		1994	
	PHI	SE PHI						
150--200	0.57	0.03	0.59	0.03	0.52	0.04	0.18	0.04
201--250	0.63	0.05	0.63	0.04	0.63	0.07	0.37	0.09
251--300	0.74	0.05	0.70	0.04	0.62	0.06	0.47	0.11
301--350	0.76	0.04	0.86	0.04	0.69	0.06	0.42	0.06
351--400+	0.83	0.05	0.81	0.03	0.63	0.03	1.00	0.00

FIGURE LEGENDS

Figure 1: *Gila cypha*, depicted in a poster advertising the 1994 annual meeting of the Western Division of the American Fisheries Society, held at Northern Arizona University, Flagstaff, AZ. Poster drawn by Mr. Zack Znidiak, U.S. Fish and Wildlife Service, Flagstaff, AZ.

Figure 2: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *Gila cypha* by month in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring (March-April--May) of 1992, 1993, 1994, and 1995.

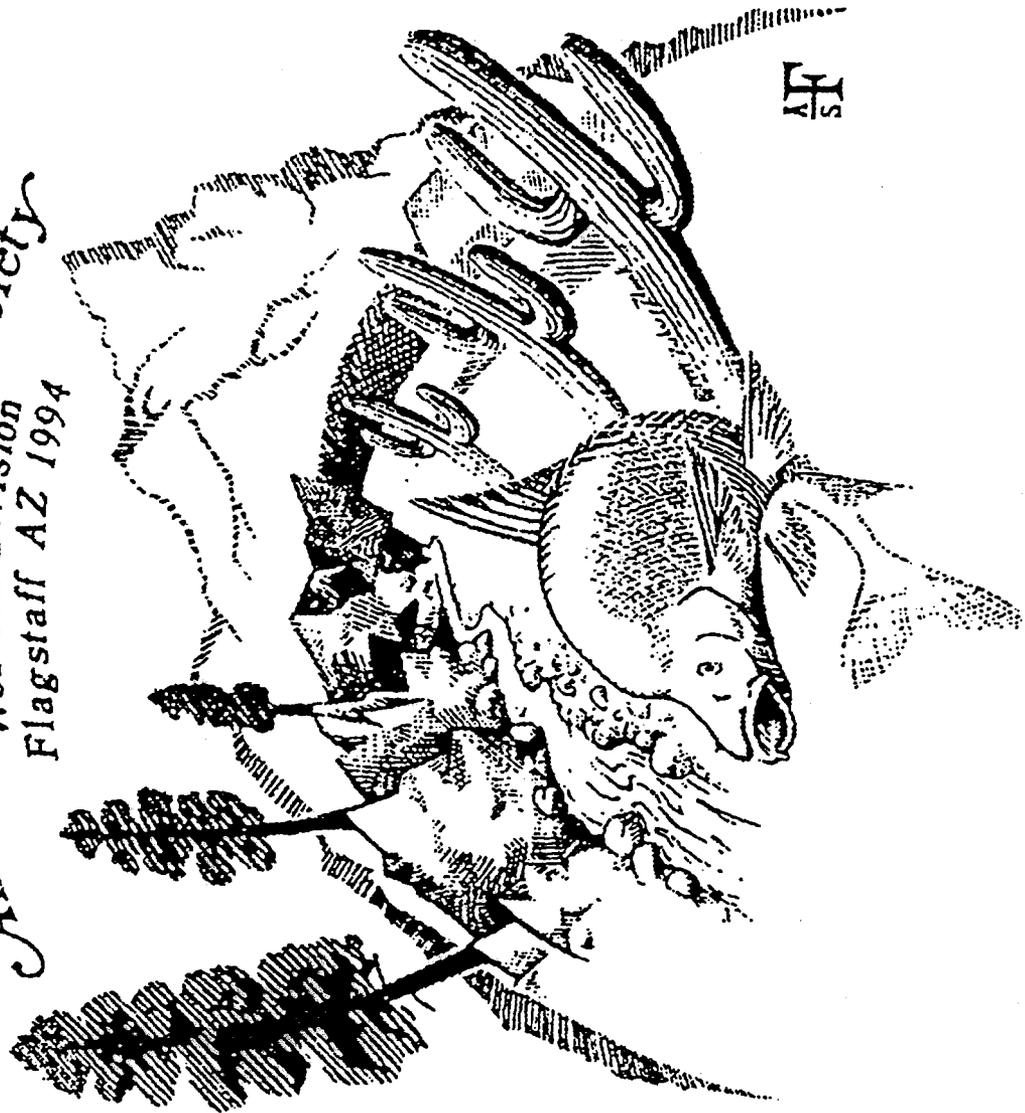
Figure 3: Cormack-Jolly-Seber population estimates (adjusted for fishing effort) for adult (> 150 mm TL) *Gila cypha* by month in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring (March-April--May) of 1992, 1993, 1994, and 1995.

Figure 4A: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *Gila cypha* by season (n = 1--16) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

Figure 4B: Cormack-Jolly-Seber population estimates (not adjusted for fishing effort) for adult (> 150 mm TL) *Gila cypha* by season (n = 1--16) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Vertical lines in graph represent spring of 1992, 1993, 1994, and 1995.

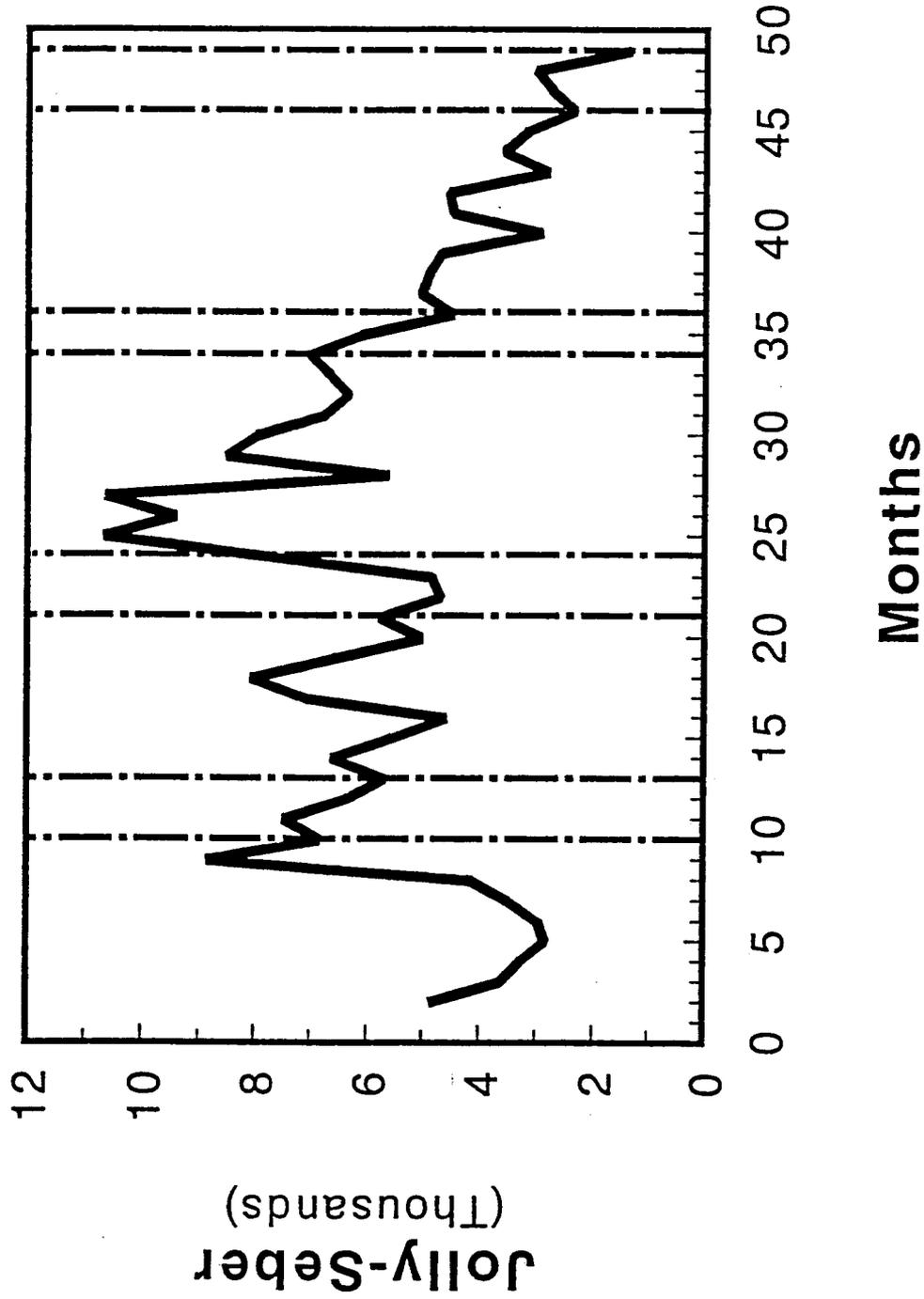
Figure 5: Yearly survival probability by size--class for adult *Gila cypha* (> 150 mm TL) in the lower 14.9 kilometers of the Little Colorado River (Navajo Nation, Coconino Co.), Arizona. Probability values are for years 1991--1994.

American Fisheries Society
Western Division
Flagstaff AZ 1994



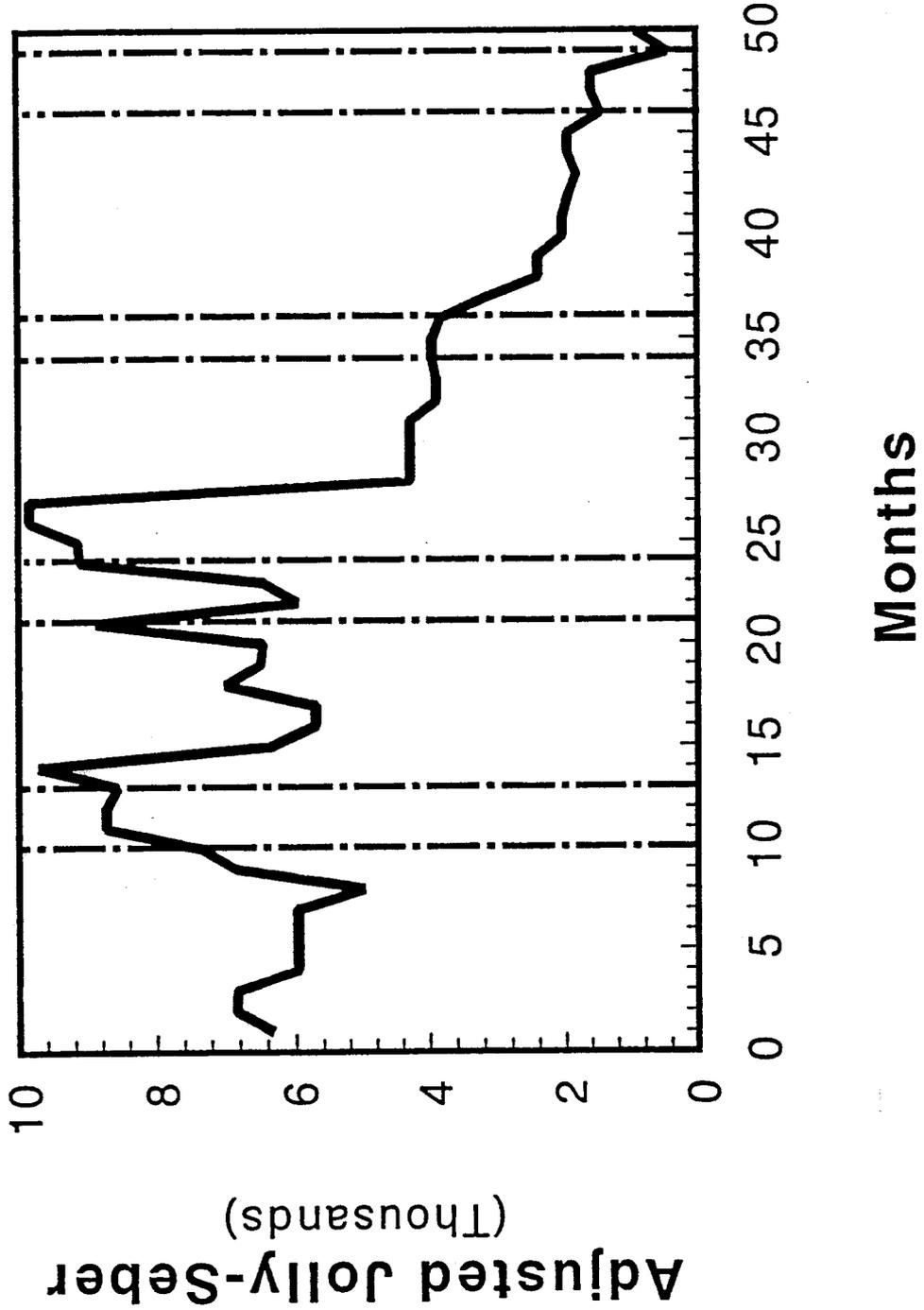
Gila cypha

Monthly Population Estimates (1991-95)



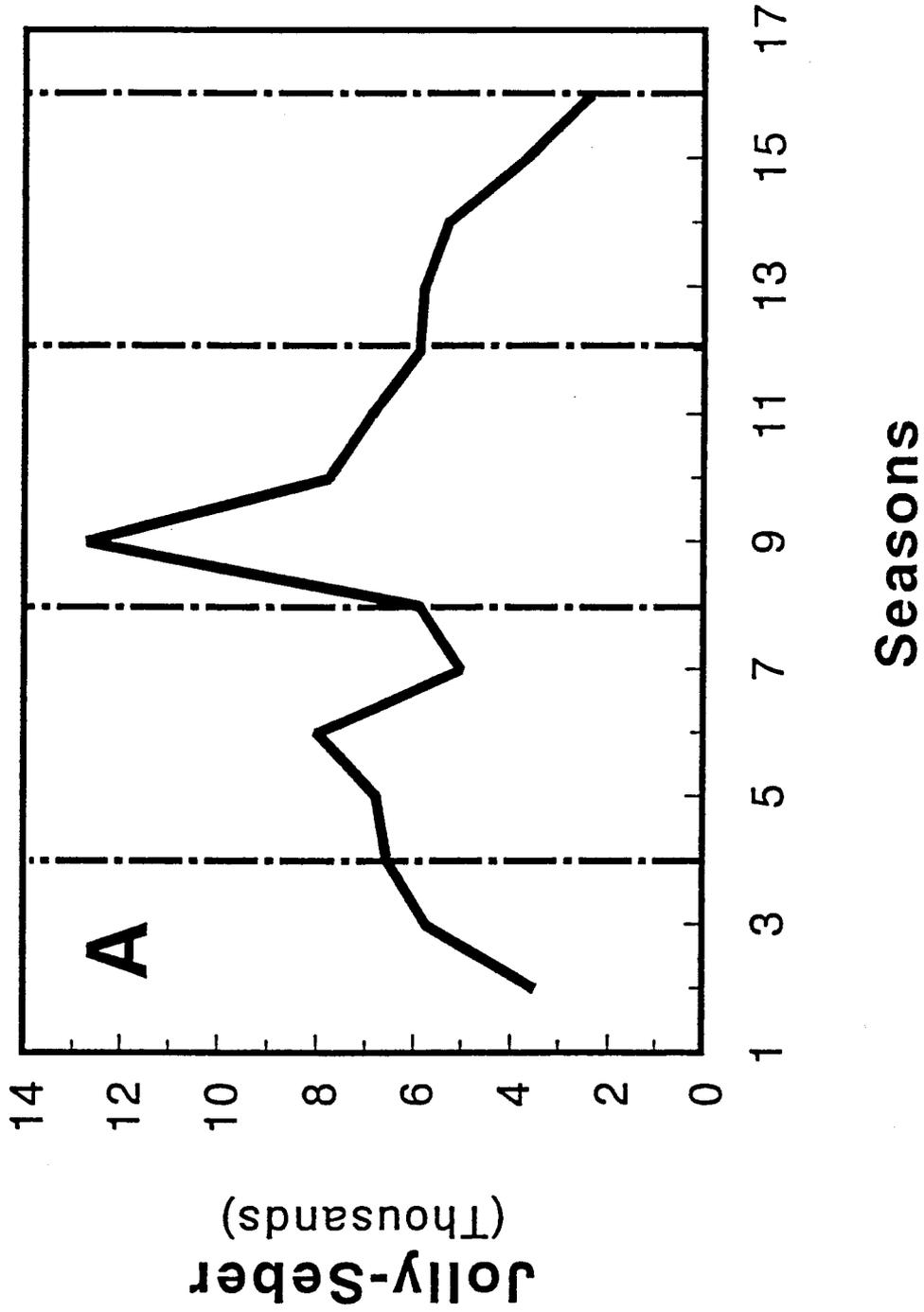
Gila cypha

Monthly Population Estimates (1991-95)



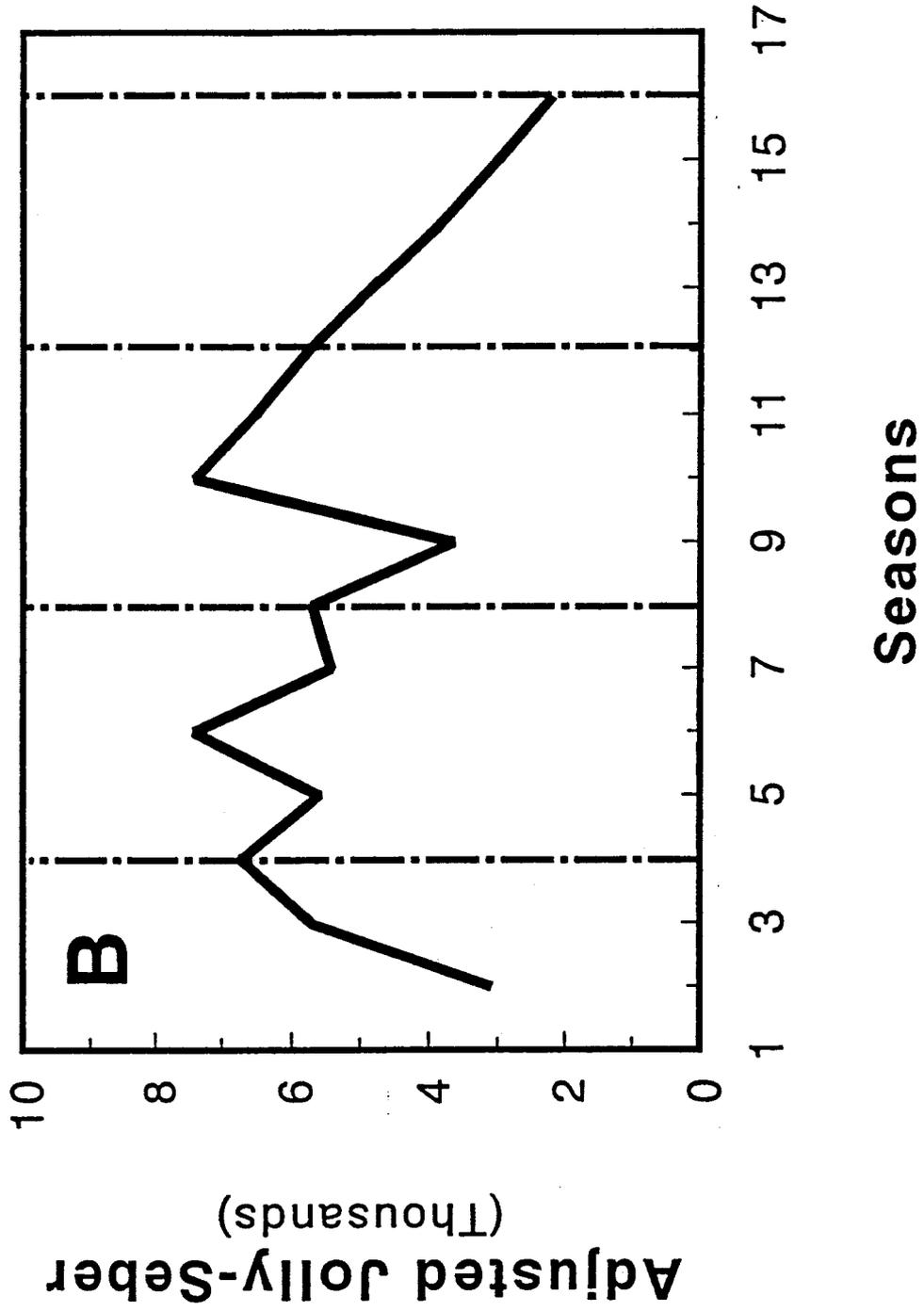
Gila cypha

Seasonal Population Estimates (1991-95)



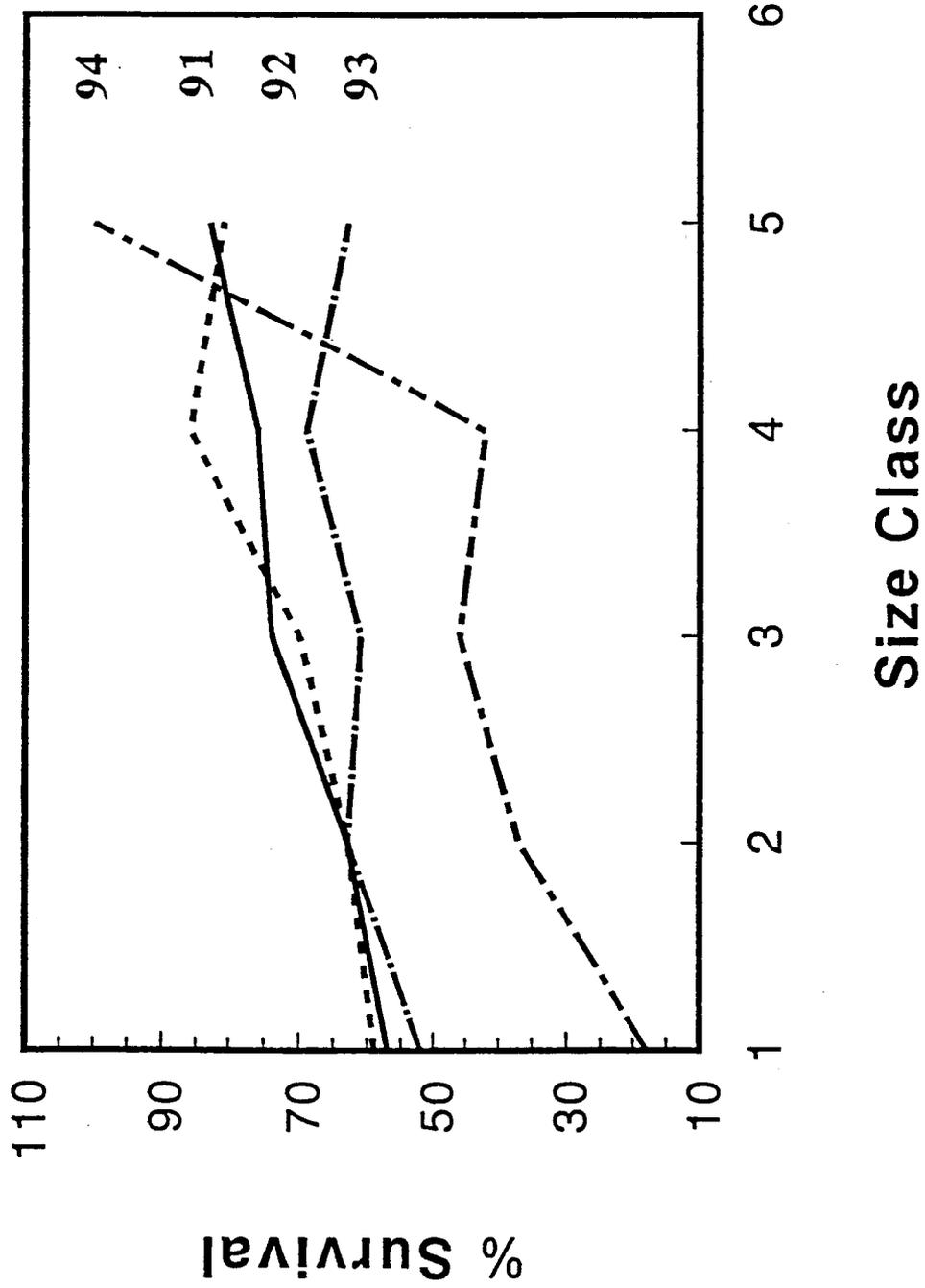
Gila cypha

Seasonal Population Estimates (1991-95)



Gila cypha

Survival Probability by Size



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GLEN CANYON ENVIRONMENTAL
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DRAFT

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FLAGSTAFF, AZ**

Dear David:

Find enclosed a FINAL REPORT for *Ecology and Conservation Biology of Humpback Chub (Gila cypha) in the Little Colorado River*. This draft is submitted as per obligations for Contract Number 1-FC-40-10490.

The report consists of four separate manuscripts: The first (*Population estimates/ population movements of Gila cypha, an endangered cyprinid fish in the Grand Canyon region of Arizona*) was recently published [i.e., *Copeia* 1996(1):15--28], while the second (*Endangered humpback chub, Gila cypha, as prey of introduced fishes in the Little Colorado River, Arizona, with notes on fish stocking in the Grand Canyon region*) has been submitted. The third manuscript (*Catostomidae of the Grand Canyon region of Arizona: Population estimates, movements, and survivability*) is still being developed and will be submitted this summer. The fourth manuscript (*Survivability of an endangered species (Gila cypha, Cyprinidae) within the Grand Canyon region of Arizona: Results of a five-year mark-recapture study*) is also scheduled for submittal in summer, 1996.

Thank you very much for your assistance as project manager during the progress of our research. Please get in touch if there are any problems with the report, or if I have in any way omitted anything of importance.

Sincerely,

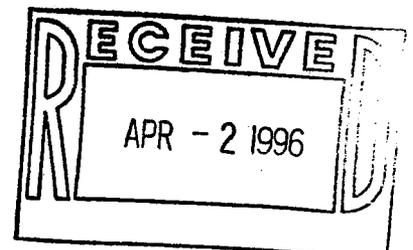
Michael E. Douglas

Michael E. Douglas, Ph.D.
Co-Principal Investigator

Enclosures: as stated

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