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Population Estimates/Population Movements of *Gila cypha*, an Endangered Cyprinid Fish in the Grand Canyon Region of Arizona

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Gila cypha **(the humpback chub) is a unique but endangered cyprind 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 County, 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 1991–1992, 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 postreproductive 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 River 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; 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. Although 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), 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 the gorge sections of the Green and Yampa rivers in Utah and Colorado (Green River Wilderness Area and Dinosaur National Mon-

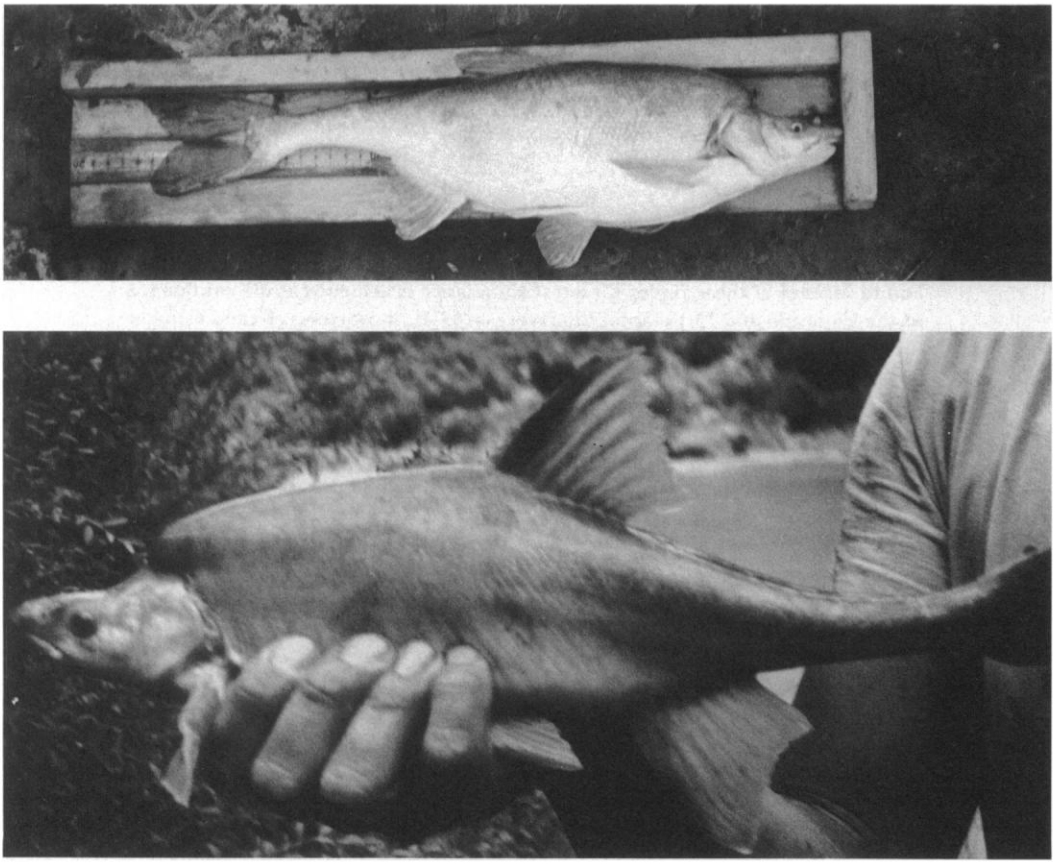

Fig. 1. (Top) An adult female humpback chub (*Gila cypha*) captured by trammel net at confluence of Little Colorado and mainstream Colorado rivers (Grand Canyon National Park, Coconino County, AZ). (Bottom) Adult male humpback chub (*Gila cypha*) captured by hoop net in Little Colorado River near Salt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

ument, respectively); the Colorado River in Utah above Lake Powell (Canyonlands National Park); and 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. 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. 2B). Although the life history of *G. cypha* is enigmatic (discussed in Douglas, 1993), the Grand Canyon population is least known of all. For example, chub inhabiting the Colorado River at the LCR confluence were not even recognized as a reproducing population until 1975 (R. R. Miller, field notes, Special Coll., Hayden Library, Arizona State University, unpubl.). 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 dis-

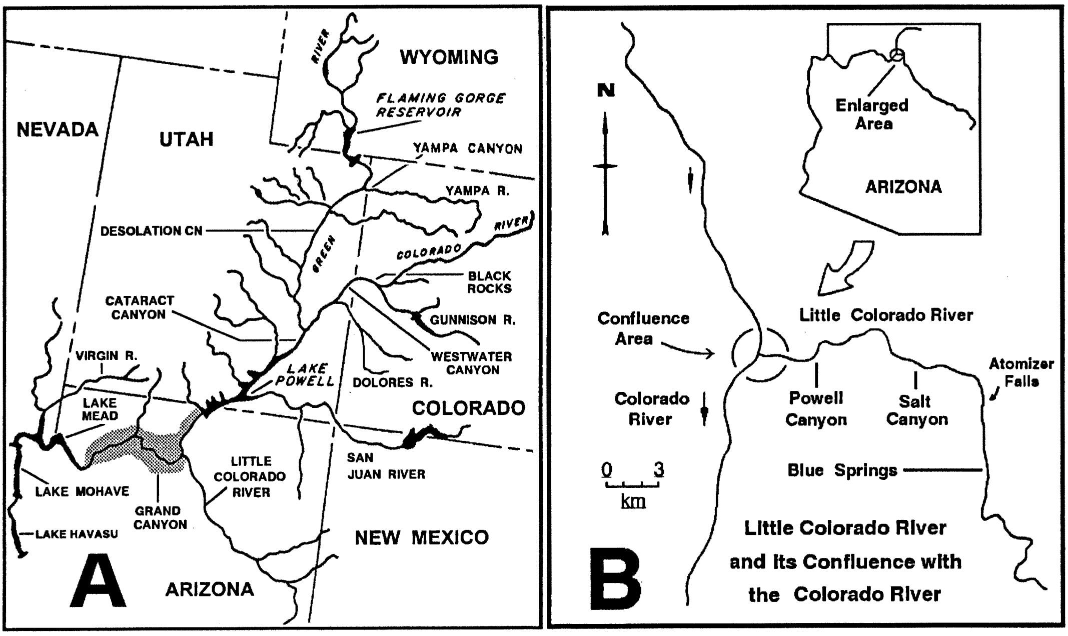

Fig. 2. (A) Map of the Colorado River basin, depicting dams, reservoirs, and component rivers. (B) Map of the lower Little Colorado River, from Blue Springs (21 km above confluence; Navajo Indian Reservation, Coconino County, AZ) to its confluence with the Colorado River in Marble Canyon (Grand Canyon National Park, Coconino County, AZ). Confluence is 99 km below Glen Canyon dam.

cussed in the context of Glen Canyon Dam, built in 1963 to impound Lake Powell at the northern extent of Grand Canyon.

Materials and Methods

Study river.—The LCR drains 141,155 km^2 of eastern and northern Arizona and western New Mexico and flows 412 km from headwaters to confluence with the Colorado River (GCNP, Coconino County, AZ; Fig. 2). 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 km^2 of the Black Mesa north and east of Flagstaff, AZ. The largest of these (i.e., Blue Springs, at LCR RKM 21; Fig. 2B) has a discharge of 6.1–6.6 m^3/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 CO_2 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 qlandulosa*), 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 toward Marble Canyon. A series of precipitous travertine falls at RKM 14.9 (Atomizer Falls, Fig. 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, whereas 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 Dec. 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 (7.6–45.7 m length, 1.8 m depth, 1.3–3.8 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 (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 = Dec., Jan., Feb.; spring = March, April, May; summer = June, July, Aug.; and autumn = Sept., Oct., Nov.). Numbers of *G. cypha* tagged/recaptured in a given reach during a given trip were condensed into a capture history (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 the fact that 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 Institute, Inc., 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, although this analysis is a logical culmination of population estimates by reach, by month summed over reach, and 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 Institute, Inc., 1985), with effort at Salt Canyon greater than that at Confluence (Sidak's multiple range test; SAS Institute, Inc., 1985). However, efforts at Salt and Powell Canyon reaches were statistically similar. Population estimates (normalized by river km) also differed significantly among reaches, with greatest overall values at Confluence ($F = 4.19$; $P < 0.01$; SAS Institute, Inc., 1985).

Analysis of covariance.—Differences in normalized population estimates could result from increased effort. To test estimates with fishing effort fixed, we first evaluated two specifications: (1) that slopes of the between-camp regressions of population vs effort were homo-

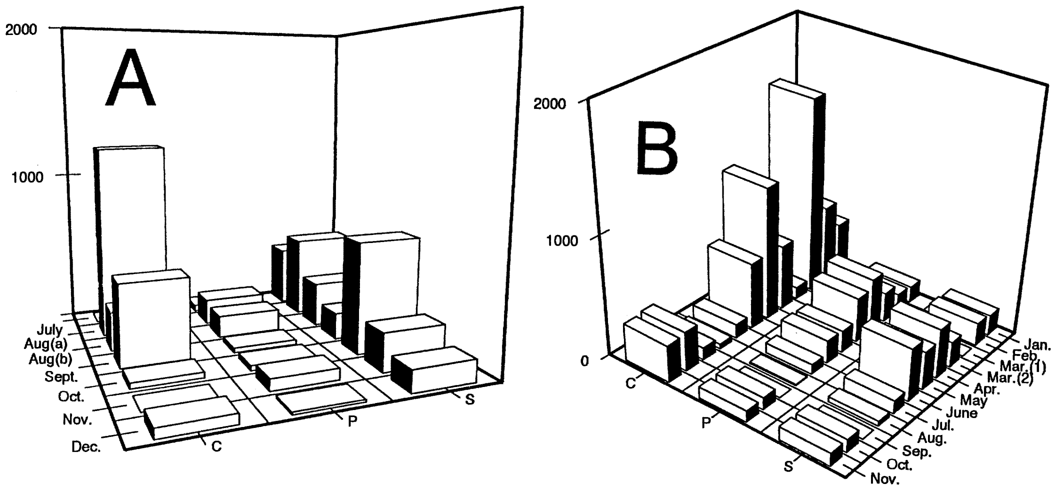

Fig. 3. (A) Three-dimensional plot of population estimates by reach (where C = Confluence; P = Powell; and S = Salt) during July–Dec. 1991. (B) Three-dimensional plot of population estimates by reach (where C = Confluence; P = Powell; and S = Salt) during Jan.–Nov. 1992.

geneous (i.e., regression lines parallel; see Somers and Jackson, 1993), and (2) that interaction between fishing effort and population estimates was nonsignificant. The resulting ANCOVA is in Table 1. Based upon a priori statistical contrasts, estimated populations within both Confluence and Salt Canyon reaches were statistically similar, but each was significantly larger than at Powell Canyon reach, irrespective of fishing effort (Table 1).

Population estimates by reach and river.—Population estimates, standard deviations, and lower/upper 95% confidence limits are presented by reach and month in Appendix 1, as are estimates normalized by river km. Three-dimensional plots of these estimates are in Figure 3. Monthly population estimates, with standard deviations and lower/upper 95% confidence limits are presented in Appendix 2, which also contains a summation of estimates by month over reaches (as recorded in Appendix 1). An ANOVA comparing these estimates (monthly vs summed by month over reaches; Appendix 2) was nonsignificant ($F = 1.15$; $df = 1,36$; $P > 0.7$; Proc GLM, SAS Institute, Inc., 1985). A plot of monthly vs summed monthly population estimates is provided in Figure 4. In 1991, highest estimates were recorded for early Aug. (3157 vs 5390; Appendix 2), whereas lowest were for Dec. (745 vs 1285). In 1992, highest estimates were for April (5555 vs 5683), whereas lowest (interestingly enough) were for Aug. (635 vs 408). A Dec. sampling trip in 1992 was cancelled due to inclement weather. Both techniques indicated elevated population estimates from early March through June of 1992 (Fig. 4). Both years demonstrated an upswing in estimated population size in autumn. Average monthly 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 Institute, Inc., 1985).

Five best-fitting population estimates were retained from analysis of a CH-matrix that included all 19 months of the study (Table 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–

TABLE 1. POPULATION ESTIMATES (NUMBER/RIVER KILOMETER) 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). Log_{10} fishing effort was used as ANCOVA covariate. Diagonal elements represent average least-squares population estimates (adjusted for log_{10} fishing effort) and have been converted from log_{10} values. Upper triangular cells represent F-values for pairwise a priori contrasts.

	Confluence	Powell	Salt
Confluence	263	6.2[a]	0.2[b]
Powell		110[c]	4.3[a]
Salt			222

[a] $P < 0.016$.
[b] $P > 0.657$.
[c] $F = 4.34$; $P < 0.019$; $df = 3,48$.
[d] $P < 0.044$.

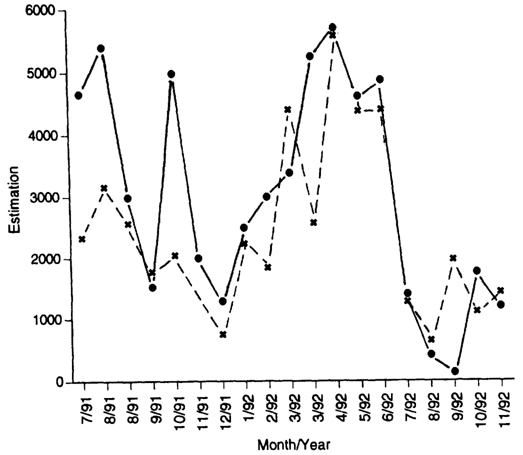

Fig. 4. Bivariate plot of population estimates for 1991–1992 by month (solid line) and by month summed over reach (dashed line).

50). The model with the second-highest criterion (i.e., the Null model; M_o) is also the simplest in that it presumes that all members of the population are equally at risk of capture on every trapping occasion. Burhnam'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_h) accept that capture probabilities vary by individual animal.

Movement by season within and between 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 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%. Direct measurements of upstream movement by some tagged fish are provided in Table 3. 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, whereas 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 Jan./Feb. of 1992 (Fig. 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. 3), 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 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 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, whereas 76% (n = 54) of

TABLE 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 (= SD), and 95% lower and upper confidence intervals (= LOWER CI; UPPER CI). Models are defined in text.

MODEL	CRITERION	ESTIMATE	SD	LOWER CI	UPPER CI
Pollock and 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	10,901
Jackknife (M_h)	0.42	10,444	329	9833	11,121
Chao's (M_h)	0.42	8039	210	7648	8472

TABLE 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	23 (11.9%)	37 (19.2%)	22 (11.4%)	82 (42.5%)
		Autumn	2 (01.0%)	6 (03.1%)	4 (02.1%)	12 (06.2%)
		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	5 (04.9%)	17 (16.5%)	1 (01.0%)	23 (22.4%)
		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	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	1 (01.7%)	0 (00.0%)	21 (35.0%)	22 (36.7%)
		Summer	0 (00.0%)	0 (00.0%)	21 (35.0%)	21 (35.0%)
		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	11 (05.3%)	7 (03.4%)	81 (39.3%)	99 (48.0%)
		Autumn	3 (01.5%)	0 (00.0%)	19 (09.2%)	22 (10.7%)
		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	0 (00.0%)	0 (00.0%)	54 (31.6%)	54 (31.6%)
		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	1 (03.7%)	1 (03.7%)	8 (29.6%)	10 (37.0%)

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, whereas 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 4). In 1991, 13 out of 3272 fish were recaptured during the same trip in a reach upstream from their initial capture, whereas 23 of 3272 were recaptured downstream from their initial capture reach (i.e., n = 36; 0.01% of total;

TABLE 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 1991/1991. 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 4). In 1992, only one of 4030 fishes was recaptured during the same trip in a reach upstream from their initial capture, whereas none was recaptured in downstream reaches (i.e., n = 1; 0.0003% of total; Table 4).

DISCUSSION

Colorado River as habitat.—During historic times, temperature and flow regimes of the Colorado River fluctuated greatly; seasonal flooding transported heavy sediment loads whereas 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, to include *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. 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 Lake Powell 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. Although terrestrial species in GCNP adapted to the post-dam Colorado River ecosystem (Carothers and Brown 1991:147; Johnson, 1991), indigenous fishes found it difficult or impossible (Kaeding and Zimmerman, 1983:592).

Little Colorado River as habitat.—Temperataure 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* hinged upon reproduction 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. Although 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 (Fig. 3) and on seasonal recaptures of tagged *G. cypha* (Table 3). Before each of these results is discussed, however, it is important to briefly 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). Although 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, unpubl.).

However, 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 (Table 4). Thus, closure both by reach/month and by month for the entire LCR is indeed supported, and the resulting population estimates appear robust.

Past and present population estimates in the LCR.—Population estimates for *G. cypha* in the LCR are presented in Table 5. In May of 1992 (Appendix 1), the confluence was estimated to contain 1320 adult *G. cypha*. This is a reduction of 27% and 54%, respectively, from estimates of 1800 and 2900 individuals in May of 1987 and 1988 (Table 5). An estimate for the entire 14.9 km length of the LCR during May of 1992 was 4346 (summed estimate for the three reaches = 4602; Appendix 2). This contrasts with the estimate of 25,000 chub in 1989 (Table 5).

The best-fitting population estimate for our entire 19-month study (4508 individuals; Table 2) 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., 2992 (monthly summed over reaches) and 2434

TABLE 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	7–8000	Kaeding and Zimmerman[a]
1987	May	Confl.	—	5783	C. O. Minckley[b]
1987	May	Confl.	Multiple Census	1800	Kubly[c]
1988	May	Confl.	—	7060	C. O. Minckley[b]
1988	May	Confl.	Multiple Census	2900	Kubly[c]
1989	May	All	Multiple Census	25000	Kubly[c]
1992	May	Confl.	Multiple Census	1320	Douglas and Marsh[d]
1992	May	All	Multiple Census	4346	Douglas and Marsh[d]
1992	May	All	Multiple Census	4602	Douglas and Marsh[e]

[a] L. R. Kaeding and M. A. Zimmerman, USFWS Final Report, 1982, unpubl. (Special Collections, Hayden Library, Arizona State University, Tempe).
[b] C. O. Minckley, AZ/NM Chapter, Amer. Fish. Soc. Proc., 1989, unpubl. (Special Collections, Hayden Library, Arizona State University, Tempe).
[c] D. M. Kubly, Bureau of Reclamation Draft Report, 1990, unpubl. (Special Collections, Hayden Library, Arizona State University, Tempe).
[d] Appendix 1.
[e] Appendix 2.

(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.—Results in Table 1 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. 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. Suttkus, G. H. Clemmer, C. Jones, and C. R. Shoop, GCNP report, 1976, unpubl.; C. O. Minckley, unpubl. field notes, 1977). Extent of its movement within the LCR was not clarified until Sept. 1977 when three large individuals (278–295 mm TL) were captured 12.8 RKM above the confluence (C. O. Minckley, field notes, 1977, unpubl.). 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. The fact that greater numbers of *G. cypha* were found at the confluence during spring of 1992 (Table 1; Fig. 3B) supports an hypothesis of staging prior to upstream movement. Downstream (i.e,, postreproductive) movement also clearly occurred (Table 3) but spanned a long period and was diffuse. Movements between LCR reaches during a given sampling period were negligible (Table 4), suggesting temporal closure during periods of sampling. No evidence of explosive or extensive reproductive movements was noted (Table 3; Fig. 3B).

Table 3 primarily reflects population stasis within reaches, particularly summer through winter. These data suggest *G. cypha* is more of a resident component of the LCR than previously imagined. Our observations of stasis by *G. cypha* within the LCR 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 is instead the 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. 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.).

Greater numbers of *G. cypha* were found in the Salt Canyon reach (Table 1) when compared to Powell Canyon reach. These data 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 to a chemical one produced by high CO_2, or to other chemical content.

Glen Canyon Dam and Gila cypha.—There is long-term residency by *G. cypha* within the LCR, particularly summer through winter (Table 3). 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 mainstream 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). Second, larvae and juvenile *G. cypha* are often transported via flood into the mainstem, but adults smaller 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 enhance long-term survival of *G. cypha* (and may allow upriver movement of other 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. POPULATION ESTIMATES (= ESTIMATE) FOR *Gila cypha* IN THE LITTLE COLORADO RIVER BY REACH AND MONTH, WITH STANDARD DEVIATION OF THE ESTIMATE (= SD), AND 95% LOWER AND UPPER CONFIDENCE INTERVALS (= L.CI; U.CI), AND ESTIMATES RELATIVE TO RIVER KILOMETER (= EST./RKM). TRIP = month/year; C = Confluence; P = Powell; S = Salt.

REACH	TRIP	ESTIMATE	SD	L.CI	U.CI	EST./RKM
C	07/91[a]	0	0	0	0	0
P	07/91	643	218	356	1264	113
S	07/91	4007	1521	2001	8315	581
C	08/91[b]	1034	366	552	2071	862
P	08/91[b]	939	123	738	1239	165
S	08/91[b]	3417	620	2430	4901	495
C	08/91[c]	276	56	192	434	230
P	08/91[c]	773	127	576	1084	136
S	08/91[c]	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	13,744	690
C	11/91[d]	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[b]	1944	728	1067	6240	1620
P	03/92[b]	1428	777	585	5720	251
S	03/92[b,d]	0	0	0	0	0
C	03/92[c]	1173	440	602	2434	978
P	03/92[c]	2585	773	1491	4642	454
S	03/92[c]	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[e]	670	103	507	931	558
P	06/92[e]	1102	251	730	1741	193
S	06/92[e]	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

APPENDIX 1. CONTINUED.

REACH	TRIP	ESTIMATE	SD	L.CI	U.CI	EST./RKM
P	09/92[d]	0	0	0	0	0
S	09/92[d]	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] No net set at confluence.
[b] Early month sampling.
[c] Late month sampling.
[d] No recaptures.
[e] In flood.

APPENDIX 2. POPULATION ESTIMATES FOR *Gila cypha* IN THE LITTLE COLORADO RIVER BY MONTH (= TRIP), WITH STANDARD DEVIATION OF THE ESTIMATE (= SD), AND 95% LOWER AND UPPER CONFIDENCE INTERVALS (= L.CI; U.CI). Σ (Estimate) = monthly population estimates summed over the three reaches (data recorded in Appendix 1).

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

[a] Summation for two of three reaches only.
[b] Early month sampling.
[c] Late month sampling.
[d] In flood.
[e] Summation for one of three reaches only.