Ontogenesis of Endangered Humpback Chub (Gila cypha) in the Little Colorado River, Arizona

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ABSTRACT.—The largest population of endangered humpback chub *Gila cypha* inhabits the Colorado River below Glen Canyon Dam and the lower 14 km of the Little Colorado River (LCR), Arizona. Currently, adults from both rivers spawn and their progenies grow and recruit to adulthood primarily within the LCR, where we studied *G. cypha*'s life history using hoop net capture data. Humpback chub undergo an ontogenesis from diurnally active, vulnerable, nearshore-reliant young-of-the-year (YOY; 30–90 mm total length) into nocturnally active, large-bodied adults (≥180 mm TL). During the day, adults primarily resided in deep midchannel pools; however, at night they dispersed inshore amongst the higher densities of YOY conspecifics. Many YOY *G. cypha* shifted to nocturnal habitats that provided greater cover, possibly, to avoid inshore invading adults. These findings mirror predator-prey scenarios described in other freshwater assemblages, but do not refute other plausible hypotheses. *Gila cypha* piscivorous activity may escalate in hoop nets, which can confine fish of disparate sizes together; adults were significantly associated with YOY conspecifics and small dead fish in hoop nets at night and eight *G. cypha* (156–372 mm TL) regurgitated and/or defecated other fish body parts during handling following capture. *Gila cypha* can definitely be piscivorous given the opportunity, but the magnitude of their piscivorous activity in the wild is debatable.

INTRODUCTION

The largest of six remnant populations of federally endangered humpback chub *Gila cypha* resides in the Colorado River below Glen Canyon Dam within Grand Canyon National Park and the lower 14 km of the Little Colorado River (LCR) on Navajo tribal lands, Arizona (USFWS, 1990; Douglas and Marsh, 1996). Historically, *G. cypha* spawned, matured and recruited throughout both rivers, but these activities have been largely curtailed in the mainstem Colorado River since its transformation into a regulated tailwater. Cold hypolimnetic water releases from Lake Powell have reduced the water temperature of the Colorado River to 8–10 C, inhibiting spawning and embryonic development of *G. cypha* (Hamman, 1982; Clarkson and Childs, 2000). Currently, the ichthyofauna of the Colorado River is dominated by introduced fishes that thrive in these modified river conditions and have become substantial competitors and predators of *G. cypha*, especially small young-of-the-year (YOY) that commonly migrate into the mainstem from the LCR (Minckley, 1991; Gorman *et al.*, 2005). As a result, the perpetuation of the entire humpback chub population currently depends on the lower LCR for spawning and juvenile rearing habitat and, ultimately, for recruitment to adulthood (Gorman and Stone, 1999).

The LCR flows intermittently throughout most of its 573 km corridor and is subject to episodic floods after spring thaws and summer rains throughout the 69,870 km^2 river basin (Johnson, 1975). Perennial springs located within the lower 21 km of the LCR maintain a mean base flow of 6.3 m^3/s (Cooley, 1976); however, *Gila cypha* only naturally inhabit the

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terminal 14 km below the Chute Falls travertine dam (Kaeding and Zimmerman, 1983). The lower LCR fish community is numerically dominated by native species, generally, *G. cypha* are most common, followed by speckled dace *Rhinichthys osculus*, bluehead sucker *Catostomus discobolus* and flannelmouth sucker *C. latipinnis* (Kaeding and Zimmerman, 1983; Gorman and Stone, 1999). The adult *G. cypha* population in the LCR peaks in the spring-summer months when the resident population is augmented with spawning migrants from the Colorado River (Douglas and Marsh, 1996; Gorman and Stone, 1999). The LCR contains a relatively depauperate invertebrate and plant food base, which likely limits its fish carrying capacity (Kaeding and Zimmerman, 1983; Oberlin *et al.*, 1999; Benenati *et al.*, 2002). To gain a better understanding of the life history of humpback chub, which is crucial to correctly identify which actions will best promote their recovery (USFWS, 1990), we examined the diel locomotor activity, habitat use and association patterns among different *G. cypha* life stages in the LCR.

METHODS

We studied humpback chub at two separate 1 km reaches within the lower LCR from 1991–1995. Powell reach was located from 2.4 to 3.4 km upstream of the confluence with the Colorado River and Salt reach from 10.4 to 11.4 km upstream of the confluence (Fig. 1a). These combined reaches constituted >14% of the LCR corridor occupied by *Gila cypha*. Compared to the Powell reach, the Salt reach contained an overall broader array of habitat types, such as perennial springs, larger travertine dams, deeper pools and more boulders.

To determine life history strategies under ecologically similar abiotic and biotic conditions, we focused our analyses on 12 data sets collected during six 1992–1994 summer sampling trips at both study reaches (Table 1). All 12 data sets were collected when the LCR discharge was at baseflow and adult *G. cypha* were not spawning (Gorman and Stone, 1999). Examination of water chemistry data, which was collected daily at both study reaches (Model 2100P Turbidimeter and Surveyor 3 Hydrolab, Hach Co., Loveland, CO), indicated that turbidity (mean $\pm$ SE = 6.1 $\pm$ 0.5 nephelometric turbidity units), water temperature (21.4 $\pm$ 0.2 C), dissolved oxygen (6.5 $\pm$ 0.1 mg/liter O_2), pH (7.7 $\pm$ 0.4 pH) and specific conductance (4820 $\pm$ 17.2 μS/cm) were relatively constant across data sets.

Sampling design.—Fifty cross-channel transects were permanently established at 20-m intervals throughout both 1 km study reaches. At each transect, unbaited hoop nets (50 cm diameter $\times$ 100 cm length, 10 cm throat, 6 mm nylon mesh) were deployed at 3–4 m intervals across the river by attaching them to ropes anchored to opposing stream banks. Half the transects were set with nets in the morning and half in the evening, whereby all nets were examined twice at fixed locations (within 2 h after sunrise and 2 h before nightfall) over a 24-h period and then relocated to the next upstream transect. This resulted in identical habitats being sampled for both diurnal and nocturnal periods. We only fished half of each study reach during a sampling trip and alternated the halves being sampled between sampling trips.

We usually measured (mm) all *Gila cypha* captured for total length (TL); however, to reduce handling stress at the Salt reach we only measured 731 (mean $\pm$ SD = 57 $\pm$ 5.3 mm TL) of 1425 YOY captured in July 1993 and 1419 (63 $\pm$ 7.5 mm TL) of 3444 YOY captured in August 1993. We measured all YOY *G. cypha* captured during both sampling periods across several full transects of nets to provide an unbiased representative sample for activity pattern comparisons, but mostly measured subsets from each net. Only *G. cypha* $\geq$30 mm TL were used for analyses because smaller ones could pass through the nets' 6 mm mesh.

We conducted habitat measurements concurrently with fish sampling. We measured distance (cm) from the center of each net to the nearest shoreline. Depth and current
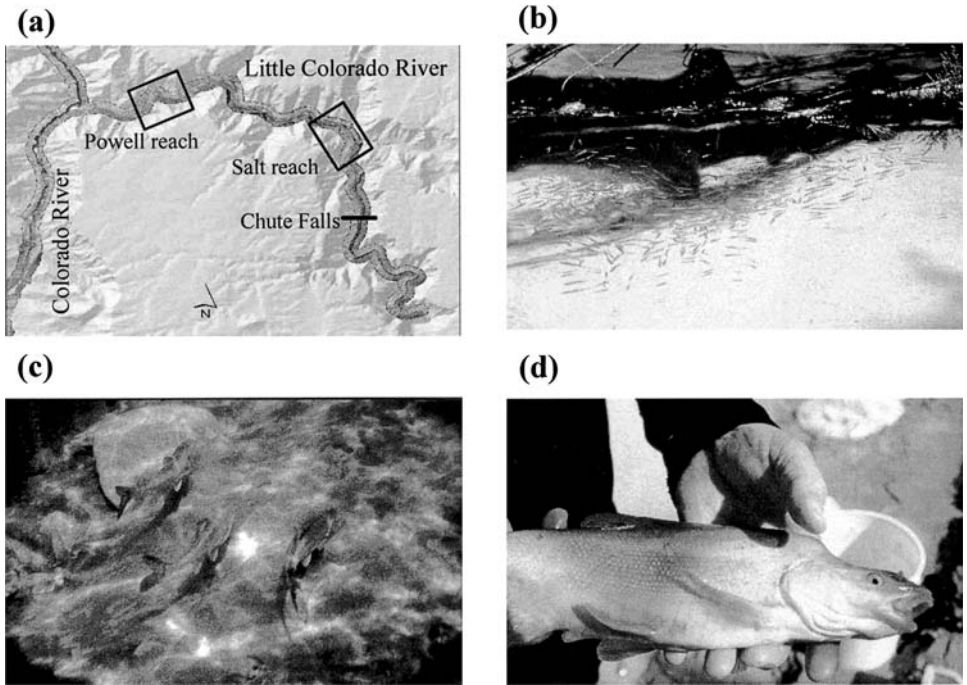
FIG. 1.—Map and photographs depicting humpback chub research in the Little Colorado River (LCR), Arizona (1991–1995). (a) *Gila cypha* naturally inhabit the lower 14 km of the LCR below the Chute Falls; this paper focuses on data collected concurrently at the Powell reach (2.4–3.4 km above mouth) and Salt reach (10.4–11.4 km) during six 1992–1994 summer sampling trips (12 data sets). (b) Young-of-the-year *G. cypha* schooling along a shoreline at the Salt reach in June 1993. (c) Underwater photo of adult *G. cypha* residing in a deep (>2 m) midchannel pool at Powell reach in June 1993. (d) A postspawned adult male *G. cypha* at the Salt reach in May 1995

velocity were quantified at 20 points, each spaced 50 cm from adjacent ones within a 1.5 × 2.0 m grid around each net, with a 25 mm diameter pole (Gorman and Stone, 1999). Point measurements for depths (cm) were analyzed as both mean depth and standard deviation of depth (hereafter, bottom profile "a 3-dimensional measure of structure heterogeneity", sensu Gore, 1978) for each net. Surface current at each point was identified to one of six categories that were defined by patterns of flow around the measuring pole and calibrated with a flow meter (Marsh-McBirney, Inc. Model 201, Frederick, Maryland) to calculate mean current velocity (m/s) for each net set (Gorman and Karr, 1978; Gorman and Stone, 1999). Points showing upstream flow were recorded as eddy currents, which were tabulated and analyzed as the frequency of eddies per net. The largest substrate existing within each net grid was identified to one of nine categories (ranging from silt ≤0.1 mm to large boulders >3 m) for each net. These six habitat variables were individually calculated for all 1310 day/ night net deployment sites. Habitat associations of 8871 *Gila cypha* were made by linking each individual fish to the corresponding net from which it was captured.

Diel locomotor activity.—The fact that fishes must be locomotory active to be captured by passive gears has been used to discern diel locomotor activity of fishes by comparing day vs. night catch rates (Mendelson, 1975; Magnan and FitzGerald, 1984; Tonn and Paszkowski,

TABLE 1.—Summary of humpback chub captured in hoop nets during six sampling trips at Powell and Salt study reaches (12 data sets) in the Little Colorado River, Arizona. Given for each data set are the sampling trip dates, study reach, number of hoop nets deployed and resulting captures of YOY (30–90 mm TL), juvenile (91–179 mm TL) and adult (180–410 mm TL) *Gila cypha* during the day and night sampling periods

Sampling trip	Reach	Nets	YOY		Juveniles		Adults	
			Day	night	day	night	day	night
15–23 Jun. 1992	Powell	90	28	13	57	50	6	18
	Salt	82	27	19	100	141	11	40
8–14 Jun. 1993	Powell	104	2	0	15	38	5	11
	Salt	118	33	25	5	40	4	34
12–19 Jul. 1993	Powell	133	375	248	8	17	2	9
	Salt	97	871	554	4	20	6	57
9–16 Aug. 1993	Powell	146	192	182	11	15	7	3
	Salt	110	1512	1932	4	21	4	48
6–13 Jun. 1994	Powell	99	122	86	72	74	4	5
	Salt	104	55	121	54	211	3	61
9–16 Aug. 1994	Powell	114	333	245	31	29	2	2
	Salt	113	195	172	80	119	10	21
Total		1310	3745	3597	441	775	64	309

1987; Reebs *et al.*, 1995). We assorted humpback chub into 10 size classes beginning with 30–50 mm TL *Gila cypha* and following in 20 mm TL increments until the final class, which contained all *G. cypha* >210 mm TL. As previously described, we only included a representative sample of YOY *G. cypha* (30–90 mm TL) captured at the Salt reach in July 1993 (295 of 1425 captured) and August 1993 (126 of 3444); this avoided biases related to comparing catch rates from nets set in disparate habitats and prevented overshadowing YOY diel patterns with two atypical data sets. All other *G. cypha* captured during the study were included in the analyses (Table 1). We then enumerated and calculated percentages of the day and night *G. cypha* captures for each size class.

Diel habitat use and intraspecific association patterns.—*Gila cypha* were separated into YOY (30–90 mm TL), juveniles (91–179 mm TL) and adults (180–410 mm TL) size classes for analyses (Figs. 1b–d). These separations were based on mean YOY growth in the first year and the lower lengths that some individuals, primarily males, expressed gametes upon manual stripping during the spring spawning season. We used nonparametric procedures to examine habitat use patterns because violations to the assumptions for parametric tests were both common and disparate among habitat variables within each data set. We compared mean ranks derived from monotonic data transformations within each data set, independent of the other data sets (Conover and Iman, 1981). Basically, mean ranks reflected habitat use information for each fish group relative to the other fish groups despite disparate sample sizes (Siegel and Castellan, 1988). We omitted the June 1993 Powell reach data set from all habitat use analyses involving YOY because none were captured at night.

Kendall's Coefficient of Concordance was used to separately compare the day and night mean ranks of differential habitat use among YOY, juvenile and adult *Gila cypha* for each habitat parameter across 11 data sets. Kendall's "W" coefficients can range from zero (none) to one (complete) and directly relates to the patterns of the mean ranks (Kendall, 1962). For example, *G. cypha* from size classes repeatedly captured closest to shore, at the shallowest depths and in the slowest currents across data sets would be lower ranked for those variables

than those from other groups, and vice versa. Thus, resulting habitat use patterns statistically represent the relative position of each group of fishes with respect to each other across all data sets.

Wilcoxon Signed Rank tests were used to unravel disparate day versus night Kendall's mean rank patterns that resulted from diel shifts in habitat use by one or more groups of *Gila cypha*. Comparisons were conducted between day and night monotonic mean ranks of each habitat variable for each group of *G. cypha* across data sets. Resulting diel shifts by YOY, juvenile or adult *G. cypha* with respect to each habitat variable would only reflect two-tailed significance if it was directionally repeated across a preponderance of data sets. Inspection between day and night mean ranks provided the direction of significant shifts in habitat use. We conducted Spearman correlation tests on sampled habitat data to examine for significant relationships between habitat variables. All statistical tests were conducted using SPSS for Windows, Release 9, 1998 (SPSS Inc., Chicago, IL) and those resulting in P-values <0.10 were considered significant.

Adult humpback chub were separately paired with YOY and juvenile conspecifics to examine for intraspecific associations during the day and night periods. We pooled data across all data sets to increase fish sample sizes and resulting power of the association tests (Zar, 1996). This was justifiable given that all data were collected under ecologically similar summer conditions (Mantel *et al.*, 1997). We calculated separate chi-square statistics with Yates correction for continuity for each fish pair during each sampling period from presence/absence data enumerated into 2×2 contingency tables (Cole, 1949; Ludwig and Reynolds, 1988). For example, the table cells for the nighttime adult-YOY paired association contained the number of nets that captured (a) adults and YOY, (b) only adults, (c) only YOY and (d) no fish. All 1310 net sets were included in each paired association and differences between the observed and expected number of co-occupied nets distinguished positive from negative associations. Probability values ($\alpha = 0.1$) were obtained from Rohlf and Sokal (1981) with 1 df. We also calculated the Dice index for each paired association following the recommendations by Janson and Vegelius (1981) and Hubálek (1982). This index ranges from zero (no association) to one (maximum association).

Indications of humpback chub piscivorous activity.—We provided accounts of *Gila cypha* that regurgitated other fishes and/or defecated fish body parts while we were handling them. We also occasionally found small dead fish in the nets and speculated that larger *G. cypha* may have killed many of these fish. Therefore, we conducted chi-square tests (described above) to examine whether small dead fishes (30–90 mm TL) were significantly associated to either adult or juvenile *G. cypha*. All 1310 nets sets were included for each paired association of each sampling period.

We examined catch rates between sequential sampling trips for patterns potentially indicative of piscivorous activity. Summer data were not used because only one sampling trip occurred in 1992, monthly catch rates of YOY *Gila cypha* increased from June through August in 1993 as new cohort fish emerged and grew to catchable sizes, and the two sampling trips in 1994 were separated by over a month (Table 1). Therefore, we compared catch rates between sequential April and May sampling trips from 1994 and 1995. All spring sampling trips occurred when LCR discharge was slightly above base flow but stable, large numbers of adult *G. cypha* were in the system to spawn, and before new cohort fishes were being captured. For each sampling trip, mean catch rates were calculated separately for YOY (11–12 mo old), juvenile and adult *G. cypha* and speckled dace (30–90 mm) from hourly catch rates of individual net sets; dace were included for insight of another small fish. Mean catch rates within two standard errors (± 2 SE) that did not overlap were considered significantly different.
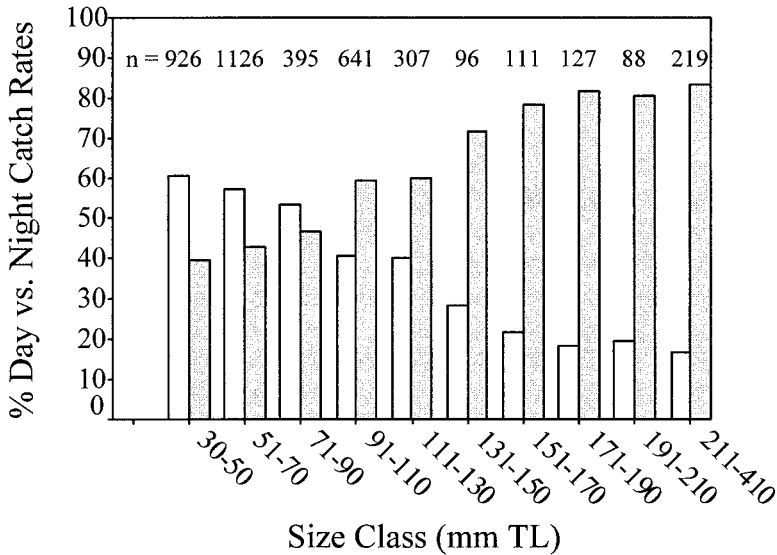
FIG. 2.—Proportions of day (clear bars) versus night (shaded bars) catch rates of humpback chub from ten different size classes during summers 1992–1994 in the Little Colorado River, Arizona

RESULTS

A total of 13,718 fishes ≥30 mm TL were captured in 2620 net sets during the summers 1992–1994. Native fishes (99.2% of total catch) included 8871 humpback chub (64.7%), 3761 speckled dace (27.4%), 763 bluehead sucker (5.6%) and 225 flannelmouth sucker (1.6%). Nonindigenous fishes (0.7%) included 87 fathead minnow *Pimephales promelas* (0.6%), 6 channel catfish *Ictalurus punctatus* (0.04%), 4 common carp *Cyprinus carpio* (0.03%) and 1 black bullhead *Ameiurus melas* (0.01%). The mean ± SD of humpback chub TL was 59 ± 11.6 mm for 4240 measured YOY (30–90 mm; 7342 were captured), 117 ± 23.8 mm for 1216 juveniles (91–179 mm) and 239 ± 56.1 mm for 373 adults (180–410 mm). Humpback chub captures and efforts for each data set are given in Table 1.

Diel locomotor activity.—Humpback chub catch rates progressively decreased during the day and increased at night with incrementally larger size class fish (Fig. 2). Overall, the catch rate pattern indicates that *Gila cypha* undergo an ontogenetic transition from diurnal to nocturnal locomotor activity. Hereafter, humpback chub classified as YOY should be considered generally diurnal (53–60% were captured during the day), juveniles mostly nocturnal (59–82% captured at night) and adults essentially nocturnal (81–84% captured at night). These diel activity designations agree with day versus night catch rates in 10 of 12 data sets for each size class (Table 1).

Diel habitat use and intraspecific association patterns.—Kendall's comparisons revealed that during the day, YOY, juvenile and adult humpback chub were sequentially captured further from shorelines, at greater depths, in faster current velocities and in fewer eddies (Table 2, Figs. 1b, c). At night, however, most adults resided between YOY and juveniles with respect to distance from shore, current velocity and bottom profile.

Wilcoxon signed rank tests reflected a reoccurring inshore shift by adults for the night that would explain much of the disparity between day and night habitat use patterns. For the night, adults repeatedly shifted closer to shorelines across all 12 data sets (Z = 3.059,

TABLE 2.—Kendall's Coefficient of Concordance results of relative habitat use patterns among YOY (30–90 mm), juvenile (91–179 mm) and adult (180–410 mm) humpback chub across 11 data sets collected in the Little Colorado River, AZ (Table 1). The chi-square (χ^2) statistic, P-value (2 df; P < 0.100 significant), Kendall's "W" coefficient and mean ranks ($\downarrow$ denotes the smallest, $\uparrow$ the largest) are given for the day and night diel period of each habitat parameter

					Mean Ranks		
Habitat parameter	Diel period	χ^2	P-value	W	YOY	Juvenile	Adult
Distance to shore	day	17.3	0.001	0.788	1.2 $\downarrow$	1.9	2.9 $\uparrow$
	night	7.1	0.029	0.322	1.4 $\downarrow$	2.4 $\uparrow$	2.2
Mean depth	day	13.3	0.001	0.603	1.3 $\downarrow$	1.9	2.8 $\uparrow$
	night	5.2	0.076	0.235	1.5 $\downarrow$	2.0	2.5 $\uparrow$
Bottom profile	day	0.9	0.643[NS]	0.040	1.8	2.1 $\uparrow$	2.1 $\downarrow$
	night	5.1	0.078	0.231	2.4 $\uparrow$	1.4 $\downarrow$	2.2
Mean current velocity	day	12.7	0.002	0.577	1.3 $\downarrow$	1.9	2.8 $\uparrow$
	night	11.5	0.003	0.521	1.2 $\downarrow$	2.5 $\uparrow$	2.3
Frequency of eddies	day	6.2	0.045	0.282	2.3 $\uparrow$	2.3 $\uparrow$	1.4 $\downarrow$
	night	6.1	0.046	0.279	2.6 $\uparrow$	1.8	1.6 $\downarrow$
Largest substrate	day	1.6	0.441[NS]	0.074	2.0	1.7 $\downarrow$	2.3 $\uparrow$
	night	1.6	0.441[NS]	0.074	2.3 $\uparrow$	2.0	1.7 $\downarrow$

P = 0.002), into slower current velocities in 10 of 12 data sets (Z = 2.275, P = 0.023) and more eddies in 8 of 10 data sets (2 other data sets had tied mean ranks, Z = 2.497, P = 0.013). Shifts by the adult population to shallower depths for the night were not significant (8 of 12 data sets, Z = 0.549, P = 0.583); however, adult individuals were significantly captured more in shallower depths at night in 11 of 12 data sets (Z = 2.903, P = 0.004). Distance to shore at the 1310 net deployment sites was positively correlated to mean current velocity ($r_s = 0.376$, P ≤ 0.001) and mean depth ($r_s = 0.206$, P ≤ 0.001), but negatively correlated to frequencies of eddies ($r_s = -0.106$, P ≤ 0.001). Thus, all significant habitat shifts by adults for the night were directed inshore.

Although YOY humpback chub remained in nearshore areas for the night (Table 2), many individuals shifted to habitats containing larger substrates (10 of 11 data sets; Z = 2.045, P = 0.041) and, as with adults, to more eddies (9 of 11 data sets; Z = 1.778, P = 0.075). For example, the proportions of YOY captured in nets deployed alongside large boulders (>3 m; only 3.8% of all net sets) increased from 8.7% during the day to 14% at night, and those caught in nets set entirely within eddies (only 0.7% of all net sets) increased from 3.6% during the day to 10.1% at night. Many juvenile *Gila cypha* shifted to more homogenous bottom habitats at night (9 of 12 data sets; Z = 2.134, P = 0.033), leaving adults and YOY to occupy the more heterogeneous bottoms (Table 2).

Adult humpback chub were not significantly associated with YOY conspecifics during the day ($\chi^2 = 0.179$, P > 0.5), but were at night ($\chi^2 = 11.569$, P < 0.001), and the Dice index was three fold lower during the day (0.08) than at night (0.25). The proportion of YOY *Gila cypha* captured in nets with adult conspecifics increased from 3% during the daytime to 28% at night. Although juvenile *G. cypha* were significantly associated with adults during both sampling periods, the chi-square statistic and Dice index were much lower during the day ($\chi^2 = 33.456$, P < 0.001; Dice index = 0.18) than at night ($\chi^2 = 111.186$, P < 0.001; Dice index = 0.40), indicating a greater nocturnal association. The proportion of juveniles captured in nets with adults increased from 17% during the daytime to 39% at night. The proportions of adults captured in daytime net sets with YOY (45%) and juveniles (48%) were only slightly lower than in nighttime net sets (51% with YOY; 62% with juveniles).
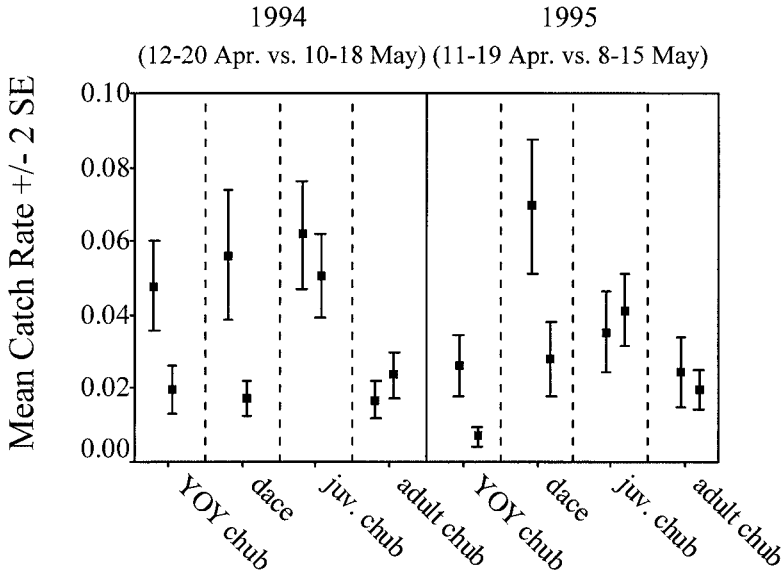
FIG. 3.—Mean hourly catch rates (± 2 SE) of YOY (30–90 mm TL), juvenile (91–179 mm TL) and adult (180–428 mm TL) humpback chub and speckled dace (30–90 mm TL) during April and May sampling trips of 1994 and 1995 in the Little Colorado River, Arizona

Indications of humpback chub piscivorous activity.—While handling humpback chub captured in nets set at night in 1993: (1) a 279 mm TL *Gila cypha* regurgitated a 47 mm TL conspecific and defecated large quantities of incompletely digested fish parts; (2) a 237 mm TL *G. cypha* regurgitated a speckled dace, parts of two unidentifiable fish and was bloated with other fish; (3) a 176 mm TL *G. cypha* regurgitated a 48 mm TL conspecific; and (4) a 280 mm TL and (5) a 187 mm TL *G. cypha* each defecated many fish bones and scales. During later LCR fishery investigations, a 166 mm TL *G. cypha* regurgitated a 64 mm TL speckled dace (1 May 1999), a 372 mm TL *G. cypha* regurgitated a 60 mm TL fathead minnow (3 May 2003) and a 156 mm TL *G. cypha* regurgitated a 57 mm TL conspecific (9 September 2004). The five 1993 observations occurred when small fishes were highly abundant, the three later observations occurred when small fishes were less available. The observations of 156, 166 and 176 mm TL juvenile *G. cypha* regurgitating whole fish provided evidence that piscivory is not restricted to adults.

During this study, we found 61 small fishes (30–90 mm TL) dead in the nets: 33 humpback chub, 23 speckled dace, 3 bluehead sucker, 1 flannelmouth sucker and 1 unidentifiable individual. Most mortalities (74%) occurred during the night when adult *Gila cypha* were most active, 23% of all carcasses were found in nets also containing live adults (13% for day vs. 27% for night), and many carcasses appeared masticated. Adult *G. cypha* were not significantly associated with mortalities during the day ($\chi^2 = 1.282$, P > 0.1) but were at night ($\chi^2 = 4.468$, P < 0.05). Juvenile *G. cypha* showed no association to small dead fish (day $\chi^2 = 0.173$, P > 0.5; night $\chi^2 = 0.600$, P > 0.1).

The April and May sampling trips examined for catch rate patterns were separated by only 19 d in 1994 and 18 d in 1995 (Fig. 3). Whereas the mean catch rates of both YOY humpback chub and speckled dace significantly declined from April to May in both years, the mean

catch rates of both juvenile and adult *Gila cypha* remained relatively stable between adjacent trips in both years.

DISCUSSION

Our findings on the diel activity, habitat use, and association patterns of humpback chub in the LCR mirror predator-prey scenarios described in other freshwater assemblages; however, alternative hypotheses exists that cannot be refuted. The argument that adult *Gila cypha* can be highly piscivorous deviates from the common perception of this species; for example, fish are not even mentioned as a potential food item in the Humpback Chub Recovery Plan (USFWS, 1990). Yet, if true, then this has important implications to future recovery activities (*e.g.,* translocations, exotic fish removals, food base issues) and, therefore, is integrated throughout the ensuing discussion. Several dietary studies were conducted on adult humpback chub in Grand Canyon that offer some pertinent background information. Dissections of adult *G. cypha* digestive tracts (excluding empty specimens) uncovered fish remains from 2 of 14 LCR specimens, but none from 13 Colorado River specimens in 1980–1981 (Kaeding and Zimmerman, 1983), and 1 of 12 LCR specimens in 1985–1986 (Kubly, 1990). Stable isotope analyses of *G. cypha* trophic links in 1998–1999 indicated a dietary shift that included piscivory by adults (via nitrogen enrichment) captured in both the LCR (Benenati *et al.*, 2002) and Colorado River (Shannon *et al.*, 2001). Conversely, nonlethal lavage of 168 Colorado River adults in 1991–1993 (Valdez and Ryel, 1997) and 45 in 1996 (Valdez and Hoffnagle, 1999) revealed no evidence of piscivory. All studies indicated that adult *G. cypha* are opportunistic generalist feeders; however, evidence of piscivory was more affiliated with *G. cypha* in the LCR than in the Colorado River.

The day vs. night catch rates of humpback chub revealed an ontogenetic diurnal-to-nocturnal transition in locomotor activity. However, it may be more accurate to consider this as an ontogenetic positive-to-negative transition in phototaxis because humpback chub show less diel periodicity under high turbidities when light penetration into the water column is reduced (Stone, 1999). Either way, YOY *Gila cypha* are more active during the day than at night. Perhaps this is solely related to undeveloped sensory abilities; however, many YOY *G. cypha* survive repeated flood events and successive months of extremely high turbidity, which suggests that they possess sensory abilities other than eyesight (*e.g.,* tactile, chemical and electrical) that should allow for nocturnal activity. Thus, the diurnal activity of many YOY *G. cypha* may be a behavioral response to avoid nocturnal encounters with adult conspecifics or other large-bodied fishes. Moreover, small-bodied speckled dace are also primarily diurnal in the LCR (Stone, 1999), but are considered nocturnal in other systems (Sigler and Sigler, 1987). Opposing activity patterns between predators and prey has been described in other freshwater assemblages (Schwassman, 1971; Helfman, 1981; Bourke *et al.*, 1996).

Subadult *Gila cypha* were most segregated from and least associated to adult conspecifics during the daytime. Humpback chub from consecutively larger size classes occupied diurnal habitats that were progressively further from shorelines, at greater depths and in faster current velocities (Figs. 1b, c). The diurnal residency of adults in deep midchannel pools is probably related to negative phototaxis (Stone, 1999), whereas the absence of smaller conspecifics from these habitats may have been a behavioral response to reduce encounters with adult *G. cypha* and other large fishes (Harvey and Stewart, 1991). Conversely, adult *G. cypha* became much more active at night and dispersed from their diurnal habitats, whereby many individuals shifted inshore amongst the higher densities of smaller conspecifics. Many YOY *G. cypha* shifted to larger substrates that provided greater cover for the night, possibly, to seek refuge from inshore invading adults and other fishes, while many larger juveniles shifted to more homogeneous bottom habitats, thereby leaving YOY and adults

together in the more heterogeneous habitats. In an analogous assemblage, juvenile eastern creek chub *Semotilus atromaculatus* and blacknose dace *Rhinichthys atratulus* used cover or moved to avoid nighttime encounters with piscivorous adult creek chub (Fraser and Cerri, 1982; Cerri, 1983; Fraser and Emmons, 1984). The diel occupancy of YOY *G. cypha* to nearshore habitats would allow them easy access of shallow depths and cover to seek refuge from larger fishes (Sogard, 1994). Alternatively, numerous other hypotheses could be generated to explain these patterns outside of any predator-prey framework.

Our findings from hoop nets indicate that *Gila cypha* can be piscivorous given opportunity, but provide little insight into the degree of occurrence in the wild. *Gila cypha* piscivorous activity may unnaturally escalate within hoop nets where fishes of different sizes are often confined together. Most fish carcasses regurgitated by *G. cypha* appeared more masticated than digested suggesting that they were consumed that night, probably while inside the nets. Adult *G. cypha* likely killed many of the 61 small fishes found dead in nets, especially at night, when they were most active and most mortalities occurred. Adults commonly escape these nets overnight (Stone, 2005), which may explain nets containing dead carcasses but no adults. During a different LCR investigation, we accrued no mortalities out of 9031 small fish captured in 1588 Gee's standard minnow traps, which excluded larger fishes. Conceivably, the presence of small fishes within hoop nets may lure foraging adult *G. cypha* into the nets; for example, hoop nets baited with processed hatchery feed (basically fish and meat byproducts) captured over two fold more *G. cypha* than unbaited nets (Stone, 2005).

Some evidence of *Gila cypha* piscivorous activity in the wild does exists and suggests that this may be a relatively common occurrence, especially in the LCR. The fish parts defecated by *G. cypha* after being pulled from hoop nets probably belonged to fish consumed before the nets were even deployed; for example, bonytail chub *G. elegans* retained fish material 45 h after ingestion (Stone, 2004). The dissection studies conducted on adult *G. cypha* were of individuals captured in gill and trammel nets, which exclude smaller fishes, yet fish remains were detected in 11% of nonempty specimens from the LCR (Kaeding and Zimmerman, 1983; Kubly, 1990). The stable isotope signatures of adult *G. cypha* indicated a trophic shift inclusive of piscivory from foods assimilated well before those adults were captured (Shannon *et al.*, 2001; Benenati *et al.*, 2002). Adult *G. cypha* were observed preying upon YOY conspecifics underneath an undercut bank in the LCR during 1994 (R. Van Haverbeke, pers. obs.). Large-scale piscivory by adult *G. cypha* could explain the significant catch rate declines of YOY conspecifics and speckled dace during the springs of 1994 and 1995 (Fig. 3). Those small fishes survived through winter flood events to steadier spring flow regimes, but declined when the greatest numbers of adult *G. cypha* were in the system to spawn. The LCR contains a relatively depauperate invertebrate food base (Kaeding and Zimmerman, 1983; Oberlin *et al.*, 1999; Benenati *et al.*, 2002) and insufficient food supply has been found to increase both piscivory (Starrett, 1950) and cannibalism (Smith and Reay, 1991) in other systems.

Conclusions and conservation implications.—The cumulative evidence indicates that humpback chub undergo an ontogenesis from diurnally active, vulnerable, nearshore-reliant YOY into nocturnally active, large-bodied adults. Though adults can definitely be piscivorous given the opportunity, the magnitude of their piscivorous activities is open for debate. Hoop net sampling may escalate *Gila cypha* piscivory on smaller fishes; however, it may still be the best gear to monitor and study fishes in the LCR. This gear is deployable in a wide range of habitats and different river conditions, collects data on the entire fish community and alleviates the potential of harming reproductively capable adult *G. cypha* with entanglement (Hopkins and Cech, 1992) or electroshocking devices (Ruppert and Muth, 1997).

We doubt that any remedial actions focused solely within the lower 14 km of the LCR could significantly improve humpback chub recruitment, especially while they continue to

numerically dominate the fish community. To reverse their population decline in Grand Canyon, recovery efforts should focus on improving Colorado River conditions for the survival and growth of YOY *G. cypha* that migrate there from the LCR. Their reliance on nearshore habitats elucidates the need to eliminate diel discharge fluctuations from Glen Canyon Dam. Otherwise, YOY *G. cypha* must continually vacate refuges, which increases their exposure to piscine predators, or become stranded. However, these efforts would likely be futile without modifying Glen Canyon Dam to release warmer water so that YOY *G. cypha* could grow, become less susceptible to piscivory and, ultimately, recruit to adulthood. This warmer water, stable flow regime should only be implemented in the late summer-early fall when YOY *G. cypha* are most abundant in the Colorado River.

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