

Ecology of Humpback Chub (*Gila cypha*)
in the Little Colorado River,
near Grand Canyon, Arizona

by Dennis Marshall Stone

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ABSTRACT

Ecology of Humpback Chub (*Gila cypha*) in the Little Colorado River, near Grand Canyon, Arizona

Dennis Marshall Stone

Within the Colorado River and its major tributaries, a unique assemblage of fish species began to evolve during the Miocene that were morphologically and physiologically capable of surviving periods of drought intermingled with stochastic flood events, high sediment loads, and fluctuations in the types and quantity of food resources. Within the last century, anthropogenic disturbances have decimated much of this original ichthyofauna. The lower 14 km of the Little Colorado River (LCR) is the last holdout where humpback chub (*Gila cypha*) numerically dominate over other piscine species. Moreover, the other most common fishes are native species and include speckled dace (*Rhinichthys osculus*), bluehead sucker (*Catostomus discobolus*), and flannelmouth sucker (*C. latipinnis*). We found evidence that adult HBC, which are considered opportunistic feeders, can be highly piscivorous and may structure the life history of smaller fish in the LCR. Regardless of water clarity, all small native fish in this

system were diurnally active including dace and all young-of-the-year (YOY) fish; whether this was a result of undeveloped sensory abilities or a behavioral response is unknown. In contrast, adult humpback chubs (≥ 180 mm TL) were predominately nocturnally active. During nighttime, adult chubs shifted habitat use to nearshore areas where they could forage on small fish. Piscivory by adult chubs is supported by observations of dead small fish being found in miniature hoopnets during the nighttime and cases where adults regurgitated or defecated undigested fish while being handled. Also, in clear water conditions (< 30 NTUs), when adults moved inshore at night, YOY chubs (≤ 90 mm TL) shifted to areas of greater cover, while juvenile chubs (110-160 mm TL) and dace shifted to midchannel habitats. At night in turbid water conditions (≥ 30 NTUs), the two smaller size classes of chubs and dace appeared to avoid habitats occupied by adult chub spawning aggregations. During daytime irrespective of water clarity, habitats used by chubs were delineated by fish size, such that increasingly larger chubs were captured progressively further midchannel, at greater depths, and in faster currents. Patterns of diel activity and habitat use documented in this study are consistent with predator-prey interactions found in other freshwater fish assemblages.

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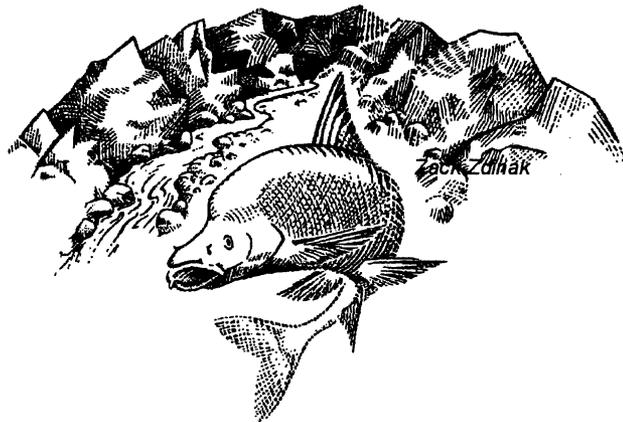


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CHAPTER 1

INTRODUCTION

In a letter by Robert R. Miller (Associate Curator of Fishes, U.S. National Museum, Washington D.C.) to Louis Schellbach (Grand Canyon National Park Naturalist) on August 28, 1944, Miller wrote "You will note that the large minnow originally identified as a hump-back sucker, is regarded as an undetermined species of the genus Gila. I feel quite sure that this fish is new and, with your permission, would like to retain it for further study. In the event that it should be described, we would like very much to retain it here permanently since it is the only specimen known."

(Grand Canyon National Park Archives). Later, this fish not only became the holotype for *Gila cypha* (humpback chub; U.S.N.M. no. 131839; Miller 1946), it also represented an additional endemic species of the morphologically unique and depauperate ichthyofauna from the predammed era of the Colorado River and its tributaries (Minckley 1991).

The endangered status of *Gila cypha* (Federal Register 32:4001) represent one of the many casualties caused by anthropogenic disturbances of the Colorado River ecosystem. Efforts to eradicate native fish ("trash fish") hit an unprecedented high with the poisoning of the Green River and its tributaries above Flaming Gorge Dam (Binns 1967); this resulted in the decimation of the upper most range of *G.*

cypha in the Colorado River Basin (Holden 1991; Bosley 1960). Generally, habitat alteration and nonnative fish introductions are considered the two most critical elements in the reduction or extirpation of native fish fauna in the western United States (Minckley and Meffe 1987; Deacon 1979; Minckley 1991). Major habitat alterations of the Colorado River ecosystem were initiated with the construction of large dams such as Flaming Gorge and Glen Canyon Dams. Native fish are often at a competitive disadvantage to species more adapted to modified systems (Minckley and Meffe 1987; Deacon 1979; Miller 1961; Moyle et al. 1987). For example, the cold, clear hypolimnetic releases from Glen Canyon Dam (6-13° C) are believed to have impaired *G. cypha* recruitment in the mainstem Colorado River in Grand Canyon (Hamman 1984; Schmidt et al. 1998), and allowed for their replacements by coldwater species (Minckley 1991). Presently, only six populations of *G. cypha* are known, all of which are restricted to the largest rivers and major tributaries of the Colorado River system (Minckley 1996; Minckley 1991; USFWS 1990).

The largest and only known self-sustaining *G. cypha* aggregation in the lower Colorado River basin below Glen Canyon Dam resides in the lower 14 km of the Little Colorado River (LCR) (USFWS 1990; Douglas and Marsh 1996; Valdez and Ryel 1995). Because the LCR represents the largest and least disturbed tributary of the Colorado River in the Lower

Basin and is dominated by native fish, it serves as a model system to study native fish ecology under near natural conditions.

The LCR is ~573 km long with the source located in the reservation lands of the White Mountain Apache tribe (Johnson 1975). This intermittent river drains a 69,870 km² river basin and is subject to floods carrying high sediment loads following Spring thaws in March and April and after Summer rains in August and September (Johnson 1975). Although the LCR contains no major hydroelectric dams regulating the discharge, it is not an untouched pristine river. Water is impounded throughout the basin in small reservoirs for recreation, irrigation, and livestock purposes (U.S. Department of Agriculture 1981). Colton (1937) believed that the LCR was perennial throughout much of northern Arizona prior to overgrazing of range vegetation by introduced livestock.

During periods of no runoff, discharges from springs maintain perennial flow in the terminal 21 km. The initial discharge of 2.547 m³/sec from Blue Spring (Cooley 1976) is supplemented by other springs resulting in a final discharge between 6.14 to 6.57 m³/sec near the mouth (Johnson and Sanderson 1968). At baseflow, pronounced travertine deposition occurs, forming sluices, terraces, cascades and dams, among other features. The bulk of this deposition occurs 12-16 km upriver of the confluence (Cooley 1976).

Gila cypha, along with native bluehead (*Catostomus discobolus*) and flannelmouth (*C. latipinnis*) suckers are restricted to below Chute Falls, a travertine dam located ~14.2 km upstream of the mouth (Kaeding and Zimmerman 1983; Mattes 1993; Minckley 1996). Speckled dace, *Rhinichthys osculus*, are the only native species found above this barrier.

Although not pristine, the LCR maintains many characteristics of an unregulated riverine system. It is a relatively harsh Southwestern river ecosystem in terms of fluctuation in discharge (from baseflow ~6.36 m³/s to relatively recent extremes of 705 m³/s on 1/21/52 and 515 m³/s on 1/12/93), sediment loads (>2,000,000 metric tons/day were reported on 1/12/93), conductivity (ranging from ~620- >4,000 μ S/cm) and temperatures (2-26.3 C^o) (Rote et al. 1997). When Kolb and Kolb (1914) visited the LCR in the early 1900s they drank from the muddy Colorado River over the clear LCR because of the high mineral content; Kubly and Cole (1979) found the LCR contains one of the highest salt concentrations (especially NaCl) of waters entering the Colorado River. These harsh conditions may have allowed the ichthyofauna of the lower 14 km to be dominated by native rather than introduced fish species (Kaeding and Zimmerman 1983; Minckley and Meffe 1987), with *G. cypha* being the most abundant fish captured (Minckley 1991; Kaeding and Zimmerman 1983; Gorman 1994).

This thesis focuses primarily on the life history of *G. cypha* in the LCR, but also addresses the ecology of the other three resident native fishes including *R. osculus*, *C. latipinnis* and *C. discobolus*. Chapter 2 examines diel activity patterns of different size classes from all four native species under both high and low water clarities. In Chapter 3 ontogenetic shifts in habitat use by *G. cypha* are examined during different periods within the diel cycle and under both clear and turbid water clarities. The hypothesis that piscivory by adult *G. cypha* may structure much of the habitat use patterns within the small fish community is examined in Chapter 4. A more complete knowledge of the ecology of *G. cypha* in the LCR may lead to a better understanding to their decline in more regulated systems.

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CHAPTER 2

Diel Activity Patterns of Four Native Fish Species in the Little Colorado River, Arizona

Abstract.-Research was conducted in the Little Colorado River, AZ from 1991-1995 to investigate ontogenetic differences in diel activities among four native fish species. Passive capture devices (miniature hoopnets and minnow traps) were deployed to systematically sample the majority of available habitat types. They were checked for fish on a scheduled rotation of dawn and dusk. Although some fish were collected in the Fall (October-December), the majority of collections occurred during the Spring (April-June) and Summer (July-September). Activity patterns were not significantly influenced by seasonality. However, activity patterns of all species, except for speckled dace (*Rhinichthys osculus*), were effected by water clarity. All sizes of *R. osculus* were diurnally active in both clear (<30 nephelometric turbidity units; NTUs) and turbid water (≥ 30 NTUs) conditions. In clear water, the smaller ontogenetic stages of humpback chub (*Gila cypha*; ≤ 90 mm TL), bluehead sucker (*Catostomus discobolus*; ≤ 110 mm TL) and flannelmouth sucker (*C. latipinnis*; ≤ 70 mm TL) were diurnally active. In contrast, fish from larger size classes of *G. cypha* (>130 mm TL) and *C. latipinnis* (>150 mm TL) were nocturnally active under clear water, while *C.*

discobolus >110 mm TL were active both day and night. In turbid water the diel periodicity of *G. cypha* and *C. latipinnis* was less distinct than in clear water, however the pattern of increasing nocturnal activity with increasing fish size was maintained. In contrast, *C. discobolus* >110 mm were more diurnally active in turbid than clear water. Additional "midnight" investigations under clear water found that *G. cypha* >150 mm were predominately captured during the first half of the night (1800-0100), while smaller *G. cypha* size classes and all other species were predominately captured either in the second half of the night (0100-0800) or during the day (0800-1800). These patterns may be the result of differences in degree of ontogenetic sensory development, food selection and predator-prey interactions. Our sampling design was unique in that an assessment of diel activity patterns of an entire native fish assemblage, including different ontogenetic stages, was conducted simultaneously.

Key Words: activity patterns; ontogenetic shifts; diel; nocturnal; diurnal; water clarity; seasonality; *Gila cypha*; *Rhinichthys osculus*; *Catostomus discobolus*; *C. latipinnis*

INTRODUCTION

Though historically recognized, periods of heightened fish activity have been largely neglected because of the difficulty in developing appropriate study designs coupled with the need for intensive field research. Carlander and Cleary (1949) pioneered techniques aimed at delineating diel activity patterns in fishes. They assessed different activity patterns for a variety of lacustrine fish species by periodic sampling over a diel cycle with gill nets. This method worked well for species that remained in the same general habitats throughout a diel cycle. However, they found that periods of elevated activity for some species with pronounced diel habitat shifts were confusing or difficult to assess.

At the present time, some fifty years after Carlander and Cleary's initial investigations, activity patterns of most fish are still largely unknown. Most of the literature concerning activity patterns of fishes is from coral reef and lacustrine communities, while activity patterns for the majority of riverine species are, for the most part, unstudied (Helfman 1993).

Active sampling techniques, such as seining or electroshocking, may provide data on habitat use, but do not provide measures of diel activity. Gill and trammel netting are often restricted to certain habitats and are size

selective. Volumetric determinations of food items in fish' stomachs have been used to establish optimum foraging periods (Cerri 1983; Starrett 1950). However, the back-calculations required to establish when foods were consumed require knowledge of the digestive rates for the particular food items, which may vary depending on the fish species, the fullness of the stomach, and the water temperature.

Helfman (1981) used visual observations to assess specific activity patterns associated with crepuscular changeover periods for various lacustrine fish species, but diminishing light levels precluded nocturnal observations. Both underwater lighting and visual observations may also alter fish behavior, because of disturbance (Spoor 1941). Electronic devices have been used with some success. Radiotelemetry has been used to assess diel activity on *Salvelinus fontinalis* (Bourke et al. 1996) and *Esox lucius* (Cook and Bergersen 1988), but this technique is restricted to larger fish. Hydroacoustic studies have been used in lakes (Imbrock et al. 1996; Gliwicz and Warsaw 1992), but both species and quantity are usually difficult to quantify.

Passive capture devices have been used to quantitatively assess fish activity. To be captured in a passive device, a fish must be active and voluntarily enter a trap. Magnan and FitzGerald (1984) detected ontogenetic shifts in diel activity of *Semotilus atromaculatus* in baited minnow traps set perpendicular to a lake's shoreline. The

use of bait in passive capture devices was not recommended by Reeb et al. (1995); they found that baiting 'dampened' differences in diel activity levels. Mendelson (1975) detected differences in activity periods among different species of *Notropis* using unbaited fish traps set at varying heights and locations in pools of a Wisconsin stream. In two Wisconsin lakes, unbaited minnow traps and fyke nets were set in a stratified random design to monitor the activities of *Umbra limi* and *Perca flavescens* (Tonn and Paszkowski 1987).

We developed an improved saturation technique to quantify diel activity patterns of the native fish assemblage in the Little Colorado River (LCR). Passive capture devices were systematically placed to sample the majority of available habitats and were checked for fish within two hours of sunrise and sunset. In this manner, diel activities were quantified for the entire fish assemblage within their selected habitats, and observer disturbance was avoided.

Our objective was to describe diel activity patterns for various size classes of native fishes inhabiting the lower LCR in the vicinity of Grand Canyon, Arizona. We also wanted to test whether changes in turbidity alter these activity patterns. Our investigations were conducted at two study reaches located within the terminal 14 km of the LCR over the period 1991-1995.

METHODS

Study areas.-The Little Colorado River (LCR) is the largest tributary of the Colorado River in the lower Colorado River Basin. During Spring thaws and occasionally after prolonged Summer rains, the river is subject to severe floods. During periods of no runoff, baseflow (6.14 to 6.57 m³/sec) in the lower 21 km is maintained by perennial discharge from springs (Johnson and Sanderson 1968).

During baseflow periods, high bicarbonate levels result in travertine deposition that form dams and reefs throughout this lower portion of the river. The alkalinities during these periods measured >500 mg/L CaCO₃ at 14.2 km upstream from the mouth (Mattes 1993; Allen Haden pers. comm.). Water clarity was usually highest during baseflow periods following Winter and Spring floods; Secchi depths were typically >200 cm during these periods. Following periods of prolonged baseflow, turbidity becomes slightly elevated because of CaCO₃ precipitation in the system. During periods of high run-off, the turbidity often measures in hundreds to thousands of nephelometric turbidity units (NTUs) because of the elevated sediment loads.

Fish sampling.-Three native fish species, humpback chub (*Gila cypha*), bluehead sucker (*Catostomus discobolus*) and flannelmouth sucker (*C. latipinnis*) were found downstream of Chute Falls, a travertine dam located 14.2 km upstream of

the mouth (Kaeding and Zimmerman 1983; Mattes 1993; Minckley 1996; Figure 1). Speckled dace (*Rhinichthys osculus*) was the only native fish captured above this dam. In both biomass and numbers, these four native species dominate the fish community of the lower 14 km of the LCR; typically *G. cypha* is most common, followed by *R. osculus*, *C. discobolus*, and *C. latipinnis* (Gorman 1994; Kaeding and Zimmerman 1983).

Two 1-km study reaches were established within the lower 14 km of the perennially flowing portion of the LCR (Figure 1). The Powell Canyon study reach was located ~2.3-3.8 km upstream of the confluence with the Colorado River (36°11'45"N, 111°46'0"W) and the Salt Canyon study reach was located further upriver at ~10.5-11.9 km (36°10'42"N, 111°42'16"W). These study reaches were representative of the range of habitats found in the lower 14 km of the LCR (Gorman et al. 1993). Fish capture data used in this paper were the result of an extensive effort that took place over numerous sampling trips during a 5 year period (1991-1995) (Table 1). These data were separated by season and water clarity, which will be discussed subsequently.

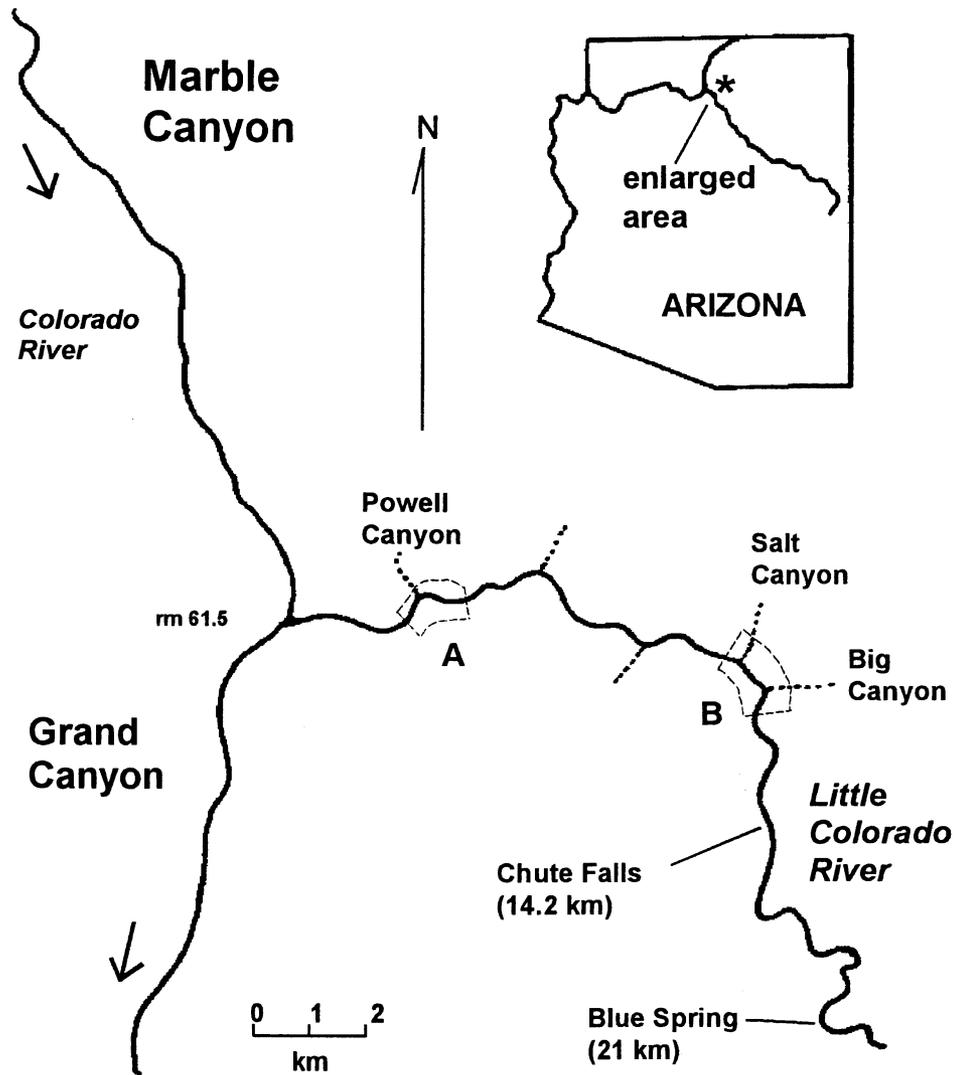


Figure.1. Map of the lower Little Colorado River (LCR) from Blue Spring to the confluence with the Colorado River (CR), Coconino County, Arizona. The perennial flows in this lower portion of the LCR are maintained by Blue Spring. Powell Canyon study reach (A) was located ~2.3-3.8 km upstream of the confluence with the CR and Salt Canyon study reach (B) was located further upriver at ~10.5-11.9 km. In the majority of ~10 day duration research trips, both study reaches were worked simultaneously. *Gila cypha*, *Catostomus discobolus* and *C. latipinnis* were restricted to below the travertine dam, Chute Falls.

Table 1. Fish sampling trips used in analyses from the Little Colorado River, Arizona. Each trip includes the season of the year, water clarity (WC) delineated as clear (C <30 NTUs) or turbid (T ≥30 NTUs), river reaches sampled (Powell, Salt, or both), actual fishing days, and # of miniature hoopnets (Nets) and minnow traps (Traps) deployed.

Sampling Trip (Season)	WC	Reach	Days	Nets	Traps
Dec 1991 1st half (Fall)	C	Both	4	54	16
Dec 1991 2nd half (Fall)	T	Both	3	34	22
June 1992 (Spring)	C	Both	9	162	148
July 1992 (Summer)	T	Pow	8	65	47
Aug 1992 (Summer)	T	Both	4	53	30
Sept 1992 (Summer)	T	Both	7	66	38
Nov 1992 (Fall)	T	Both	9	91	53
April 1993 (Spring)	T	Both	9	183	107
May 1993 (Spring)	C	Both	9	177	103
June 1993 (Spring)	C	Both	7	222	174
July 1993 (Summer)	C	Both	8	230	117
Aug 1993 (Summer)	C	Both	8	256	177
Sept 1993 (Summer)	T	Both	6	150	87
Nov 1993 (Fall)	C	Salt	4	46	24
April 1994 (Spring)	T	Both	9	219	96
May 1994 (Spring)	T	Both	9	254	102
June 1994 (Spring)	C	Both	8	203	94
Aug 1994 (Summer)	C	Both	8	227	113
April 1995 (Spring)	T	Salt	9	191	28
May 1995 (Spring)	T	Salt	8	185	4
<hr/>					
Total clear water effort			65	1,577	966
Total Turbid water effort			81	1,491	614
Total effort			146	3,068	1,580

Each study reach was divided into two 500 m study sites. Permanent cross-channel transects were established at 20 m intervals throughout all four study sites. Within each study reach, the 500 m sites were sampled alternately between sampling trips. During a sampling trip, fish were sampled in a systematic manner along transects moving in an upstream direction. Transects selected for sampling were staggered (eg., fish two, skip one etc.) to cover each site in 10 days. On subsequent trips, transects that were not selected previously were sampled by offsetting the starting transects. Ropes were tied to opposite stream banks at transects selected for sampling. Miniature hoopnets (nets; 50 cm diameter X 100 cm length, 10 cm throat, 6 mm nylon mesh) were deployed at 3-4 m intervals across the river along these ropes; Standard Gee's minnow traps (traps; 23 cm diameter X 45 cm length, 2.5 cm double entrance openings, 6 mm galvanized steel mesh) were placed along the shallow (<25 cm) stream edges (Figure 2).

Nets and traps sampled day and night periods within a 24h cycle, then were relocated to the next upstream transect. All capture devices were checked during daylight within 2 h of sunrise and sunset to assess diel activity patterns. Because nets and traps were sampled on the same schedule, capture data from these sources were pooled. All fish were identified, measured (TL in mm), weighed (to nearest g), and when possible, sexed.

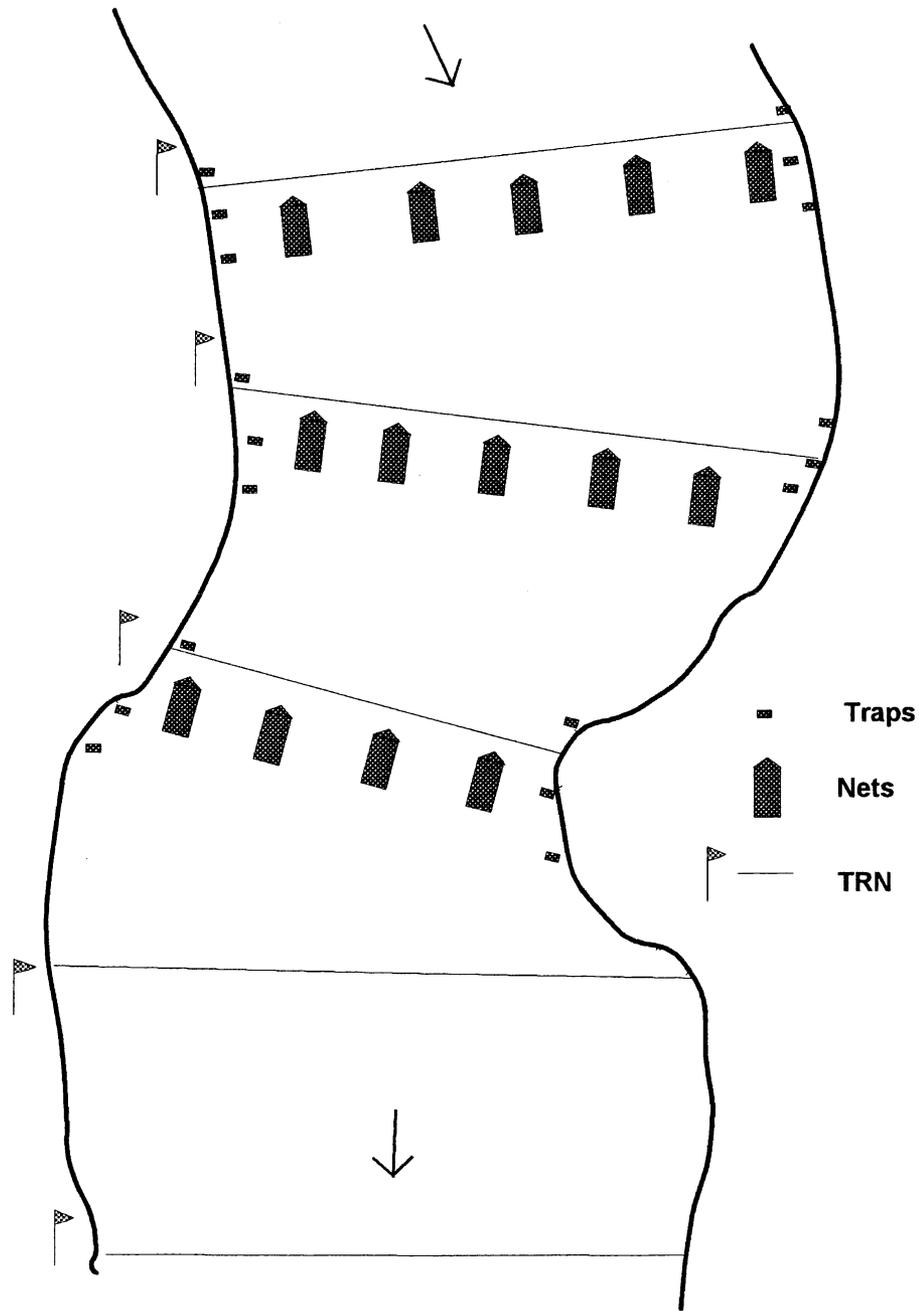


Figure 2. Fish sampling grid used in the Little Colorado River, Arizona from 1991-1995. Cross-channel transects (TRN) were spaced 20 m apart. Transects selected for fish sampling were staggered to cover each 500 m study site in 10 days. Miniature hoopnets (Nets) were fastened at 3-4 m intervals along ropes located at the selected transects. Minnow traps (Traps) were deployed along the shallow stream edges at each selected transect.

Water clarity.-Turbidities above and below 30 NTUs have been found to alter diel movements of smaller *G. cypha* (≤ 180 mm) and *R. osculus* (Chapter 4); daytime use of nearshore habitats of *R. osculus*, and smaller *G. cypha* and *C. latipinnis* (< 150 mm) (Tim Hoffnagle, AZ Game and Fish Dept., unpub. data); relative position in the water column and use of shoreline habitat by adult *G. cypha* (Valdez and Ryel 1995); and foraging success of *Oncorhynchus mykiss* (Barrett et al. 1992). Thus, we divided our sets of data into those sampling trips with low turbidity, clear water conditions (< 30 NTUs; "clear water") and those with high turbidity conditions (≥ 30 NTUs; "turbid water"). Turbidity was measured initially with a Hach Model 16800 Portalab turbidimeter and after June 1993 with a Hach Model 2100P turbidimeter. We restricted turbid water analyses to data that were collected in sufficiently reduced flows (< 19 m³/s) that allowed nets to be deployed across the full width of the river.

Size classes.-In order to assess size-related differences in activity, we assigned individual fish to size classes for analyses. Between the first and last size classes, the fish lengths were in intervals of 20 mm for *G. cypha*, 10 mm for *R. osculus*, 40 mm for *C. discobolus*, and 80 mm for *C. latipinnis* (Table 2). These intervals allowed adequate sample sizes for analyses of young-of-the-year (YOY) through mature adult stages of the life cycle.

YOY *Gila cypha* were especially abundant in the Salt study reach during July 1993 (N=2,132) and August 1993 (N=4,053). Because of the large numbers captured, we were unable to measure all YOY in each capture device (>90% of 3,120 measured YOY *G. cypha* were ≤ 70 mm). In these cases, we first removed and processed the larger fish from each capture device. Then, for each separate capture device, we measured subsamples (~50%) of the total YOY catch and counted the rest. Later, the percentages from each size class were computed separately for each capture device. The corresponding proportions of unmeasured YOY from each device were then added to the measured fish. In addition, both day and night capture data from entire transects of capture devices that were run outside of our scheduled sampling periods were omitted from the analyses. These omissions from the Salt study reach only slightly reduced the length of river corridor sampled yet retained relatively large samples; all data collected at the Powell reach were included in the analyses.

Table 2. Species size classes and numbers of captures of native fishes used in the analyses from the Little Colorado River, AZ. Between 1st and last size classes, the fish lengths (TL) were grouped in 20 mm for *Gila cypha*, 10 mm for *Rhinichthys osculus*, 40 mm for *Catostomus discobolus*, and 80 mm for *C. latipinnis*. Samples were separated between clear (CLR) and turbid (TUR) water conditions. Fish size classes with insufficient samples for comparison were bracketed {#}.

<u>Gila cypha</u>			<u>Rhinichthys osculus</u>			<u>Catostomus discobolus</u>			<u>C. latipinnis</u>		
TL	CLR	TUR	TL	CLR	TUR	TL	CLR	TUR	TL	CLR	TUR
≤50	1868	93	≤40	155	12	≤70	659	{3}	≤70	58	{1}
51-70	3802	444	41-50	429	28	71-110	214	8	71-150	106	{5}
71-90	838	690	51-60	1476	167	111-150	27	23	151-230	44	10
91-110	718	658	61-70	1041	336	151-190	35	104	231-310	51	11
111-130	335	267	71-80	1446	501	191-230	47	161	>310	26	17
131-150	132	105	81-90	1275	228	>230	37	88			
151-170	153	70	91-100	463	72						
171-190	157	66	>100	141	26						
191-210	101	79									
>210	318	404									
# Used	8422	2876		6426	1370		1019	384		285	38

Capture comparisons.-Sample sizes varied greatly between species, size classes, and water clarity (Table 2). For subsequent comparisons, these data were further stratified into different sampling periods and season. Because the same deployment of capture devices were used to compare captures between different sampling periods, effort between sampling periods differed only by deployment times. Using methods similar Staples (1978, 1975), Magnan and FitzGerald (1984), and Tonn and Paszkowski (1987), the mean catch/h for

different sampling periods were expressed as a percentage of the total catch rate throughout the diel cycle. Thus percent captures for any particular sampling period account for differences in time between sampling periods.

Seasonal comparisons.-Fish samples were primarily collected in three different seasons: Spring (April-June), Summer (July-September), and Fall (October-December) (Table 1). Winter data were not used because flooding reduced sampling efficiency. Most fish were collected during the Spring and Summer, however larger size classes of all species were more common in the Spring than Summer, while smaller size classes were more common in the Summer than Spring. Although Fall contained insufficient samples (<3% of the total captures) for statistical comparisons with the Spring and Summer, many night and day captures patterns appeared consistent with those of Spring and Summer (See Results). Spring sampling differed from the later seasons, in that Spring contained the majority of turbid water sampling trips, adult fish (but fewer YOY), and spawning activity; Spring trips usually followed floods of greater magnitude than later seasons. Therefore, diel captures from Spring were compared against those from Summer-Fall to test for seasonal influences.

During the Spring and Summer Months, nets and traps were set for an average of 14 h during the night and 10 h during the day portion of the diel cycle. Catch/h for both night and day sampling periods were calculated for each size

class within each species by dividing the night captures by 14 and day by 10. Capture data from the Fall months were treated similarly except night effort consisted of 16 h and day of 10 h. Percent night captures for Spring were then calculated by dividing the night catch/h by the combined night and day catch/h. Percent night captures for Summer-Fall were calculated by dividing the sum of Summer and Fall night catch/h by the total of all catch/h during the Summer and Fall. Because % day captures were the reciprocal of night, only % night captures were compared.

The patterns of % night captures for each species between Spring and Summer-Fall were compared separately for the clear and turbid water periods using the Wilcoxon Signed Ranks Test in SPSS version 6.1.2 (1995). This test was selected because it incorporates both direction and magnitude of the differences. Only those size classes that contained ≥ 8 fish during both Spring and Summer-Fall periods were used. Tests resulting in $P < 0.1$ were considered significantly different.

Water clarity comparisons.-To investigate whether water clarity affected the diel captures, the % night captures for the different size classes within each species were compared between clear and turbid water conditions, irrespective of season. As previously described, the catch/h during the Fall used efforts of 16 h for night and 8 h for day, while both Spring and Summer catch/h used efforts of 14h for night

and 10 h for day. Percent night captures were computed separately for clear and turbid water clarity periods by dividing the summed Fall and Spring-Summer night catch/h by their summed day and night catch/h. Wilcoxon Signed Ranks Tests were used to compare each species distribution between the two water clarities (SPSS 1995), whereby tests resulting in $P < 0.1$ were considered significantly different.

Comparisons within the day and night.-Because our daytime sampling period also included the earlier part of dusk, while our nighttime sampling period also included the later part of dusk and all of dawn, we needed to determine whether captures occurred throughout the day and night periods, or merely during crepuscular periods. We addressed this by supplementing our daytime and nighttime fish sampling routines with noon and midnight runs. These additional sampling periods were conducted, when possible, during selected clear water sampling trips.

Midnight runs were conducted during May 1993, June 1992, 1993, 1994, and August 1994 using a total of 355 nets and 253 traps set in transects. The diel cycle was separated into three fish sampling periods: the "day" period (~0800-1800; 10h) encompassed all of daytime period from after dawn to the beginning of dusk, the "dusk-midnight" period (~1800-0100; 7h) included the later part of evening twilight and first half of the night, while the "midnight-

dawn" (~0100-0800; 7h) period encompassed from midnight through dawn.

During June and July 1993, 191 nets and 137 traps were examined during noon as well as the normal morning and evening periods. The diel cycle was again divided into three sampling periods: the "night" period (~1800-0800; 14h) encompassed the latter portion of evening twilight, through night, until after dawn; the "morning" period (0800-1300; 5h) ran from after sunrise into the afternoon; while "afternoon" period (~1300-1800; 5h) ran from noon to the beginning of dusk.

As previously described, species were subdivided into size classes and % captures for each sampling period were calculated from the mean hours sampled in each subdiel period. To establish reasonable sample sizes from this portion of our study, *G. cypha*, *C. discobolus* and *C. latipinnis* were subdivided into three size classes: Fish ≤ 70 mm included all young-of-the-year (YOY); fish 71-150 mm contained YOY and subadults, and fish >150 mm contained older subadults and adults. Because *R. osculus* were more plentiful than the other species, % captures were calculated on size classes divided into 10 mm increments.

RESULTS

Seasonal and water clarity comparisons.-Water clarity appeared to have a greater influence on % night captures than seasonal differences under similar water clarities (Table 3). Comparisons of % night captures between the Spring (April-June) and Summer-Fall (July-September) sampling periods resulted in no significant seasonal differences. Under clear water conditions, all size classes were represented. Under turbid water conditions, tests could not be conducted on *C. latipinnis* (N=3) and *C. discobolus* (N=18) because of insufficient Summer-Fall fish captures. In addition, the analysis of *G. cypha* did not include the smallest size class (≤ 50 mm), while analysis of *R. osculus* did not include either the smallest (≤ 40 mm) or the largest (>100 mm) size classes because of insufficient samples.

In cases where Fall samples were of sufficient size to visually compare with Spring and Summer we could detect no distinct differences. Few turbid water comparisons could be made because Fall samples constituted only 1.6% of all data collected on *G. cypha* (N=45), 1.3% for *C. discobolus* (N=5), and zero for *C. latipinnis* and *R. osculus*. Patterns for *G. cypha* under both water clarities and *C. latipinnis* under clear water conditions showed similar trends of increasing night captures with increasing size during all three

seasons. Also in clear water, the smaller size classes of *C. discobolus* (≤ 110) and *R. osculus* (≤ 60 mm) were captured primarily during the day in all three seasons.

Table 3. Wilcoxon Signed Ranks Test results of seasonal and water clarity influences on night fish captures in the Little Colorado River, AZ. Analyses compared the variation of % night captures of different size classes for each of *G. cypha*, *R. osculus*, *C. discobolus* and *C. latipinnis*. Seasonal comparisons were conducted separately for clear and turbid water clarities between the Spring (April-June) and the Summer-Fall (July-December). Water clarity comparisons were conducted between clear and turbid water clarities, irrespective of season. Included are the # size classes tested and sum of ranks ($\bar{}$ signs were Summer-Fall < Spring or turbid < clear; $\bar{}$ signs were vice versa), Z-score and two-tailed P values ($P < 0.1$ are significant). Only size classes that contained ≥ 8 fish in both categories were compared.

Species	Wilcoxon Test Comparison	Size Classes	Sum of Ranks	Z-Score	2-Tailed P
<u><i>G. cypha</i></u>	Seasonal in Clear Water	10 (4 $\bar{}$ 6 $\bar{}$)	25 $\bar{}$ 30 $\bar{}$	0.2548	0.7989
	Seasonal in Turbid Water	9 (3 $\bar{}$ 6 $\bar{}$)	18 $\bar{}$ 27 $\bar{}$	0.5331	0.5940
	Water Clarity	10 (7 $\bar{}$ 3 $\bar{}$)	49 $\bar{}$ 6 $\bar{}$	2.1958	0.0281*
<u><i>R. osculus</i></u>	Seasonal in Clear Water	8 (3 $\bar{}$ 5 $\bar{}$)	16 $\bar{}$ 20 $\bar{}$	0.2801	0.7794
	Seasonal in Turbid Water	6 (2 $\bar{}$ 4 $\bar{}$)	6 $\bar{}$ 15 $\bar{}$	0.9435	0.3454
	Water Clarity	8 (5 $\bar{}$ 3 $\bar{}$)	16.5 $\bar{}$ 19.5 $\bar{}$	0.2113	0.8326
<u><i>C. discobolus</i></u>	Seasonal in Clear Water	6 (2 $\bar{}$ 4 $\bar{}$)	7 $\bar{}$ 14 $\bar{}$	0.7338	0.4631
	Water Clarity	5 (4 $\bar{}$ 1 $\bar{}$)	14 $\bar{}$ 1 $\bar{}$	1.7529	0.0796*
<u><i>C. latipinnis</i></u>	Seasonal in Clear Water	5 (4 $\bar{}$ 1 $\bar{}$)	12 $\bar{}$ 3 $\bar{}$	1.2136	0.2249
	Water Clarity	3 (3 $\bar{}$ 0 $\bar{}$)	6 $\bar{}$ 0 $\bar{}$	1.6036	0.1088

Water clarity influenced % night captures of all native species, except *R. osculus* (Table 3). Both *G. cypha* and *C. discobolus* were significantly different between clear and turbid water conditions. Although *C. latipinnis* were only borderline significant ($P < 0.1088$), this was the lowest

probability value that could be achieved with only 3 cases available from turbid water conditions for comparison. *Rhinichthys osculus* were the only species whose diel captures were not influenced by water clarity. Because water clarity often influenced the % night captures, whereas no seasonal effects were detected, graphs showing the % night captures for both clear and turbid water conditions were separately generated for each species using all available capture data (see Table 2 in Methods).

Humpback chub.-A progressive increase in % night captures was evident from small to large adult *G. cypha* (Figure 3). Percent captures did not appear to be linear, consecutive size classes were often captured in similar percentages between sampling periods. In clear water: 65-69% of small *G. cypha* (≤ 90 mm) were captured during the day; *G. cypha* (91-130 mm) showed equal day-night captures; 64% of *G. cypha* (131-170 mm) were captured at night; and 74-77% of *G. cypha* (>170 mm) were night captures.

Compared to clear water, turbid water analyses showed a reduction in nocturnal captures for size classes >90 mm. Similar captures between day and night sampling periods occurred for larger juvenile and small adult *G. cypha* (131-210 mm), while the largest adult size class (>210 mm) remained the most frequently captured in nocturnal samples (63%). Although smaller *G. cypha* (<91 mm) were captured predominately during the day, the proportion of daytime

catch was reduced compared to clear water conditions.

Overall, differences in % night captures were less distinct in turbid, than in clear water conditions.

Speckled dace.-*Rhinichthys osculus* were captured mostly during the day, whether in clear or turbid water conditions (Figure 4). The mean of % daytime captures for all size classes combined was 70% in clear water and 69% in turbid water.

Bluehead suckers.-In clear water, captures of small *C. discobolus* (≤ 110 mm) were most frequent in the daytime (Figure 5). *Catostomus discobolus* between 110-190 mm appeared to be captured equally between day and night. Larger *C. discobolus* (191-230 mm) were captured slightly more at night.

In turbid water, fish from all size classes represented were captured more during the day than at night (Figure 5). Because of insufficient samples, the smallest size class (≤ 70 mm: N=3) were not analyzed. The four larger *C. discobolus* size classes (>110 mm) were captured ~15% more frequently during daytime periods compared to clear water conditions. Also, these four size classes maintained similar percentages of daytime captures (62-65%). The slightly greater % night captures of *C. discobolus* (N=8) between 71-110 mm may be related to low sample size.

Flannelmouth suckers.-Capture patterns for *C. latipinnis* (Figure 6) closely resembled those for *G. cypha* (Figure 3).

Under clear water conditions, most small *C. latipinnis* (≤ 70 mm) were captured during the daytime sampling periods (66% of captures). As with *G. cypha*, nearly equal proportions of juvenile *C. latipinnis* (71-150 mm) were captured in day and night periods. Larger *C. latipinnis* size classes (>150 mm) were captured mostly during the nighttime (68-75% of captures).

During turbid water, most captures for the three larger size classes (>150 mm) occurred at night (Figure 6). Like *G. cypha* (Figure 3), nighttime captures were fewer during turbid than clear water. During turbid water, captures of *C. latipinnis* 151-310 mm were nearly evenly divided between day and night periods, while adults >310 mm were captured during nighttime periods as was observed during clear water. Because of insufficient samples, the two smallest size classes were not analyzed (≤ 70 : N=1; 71-110: N=5).

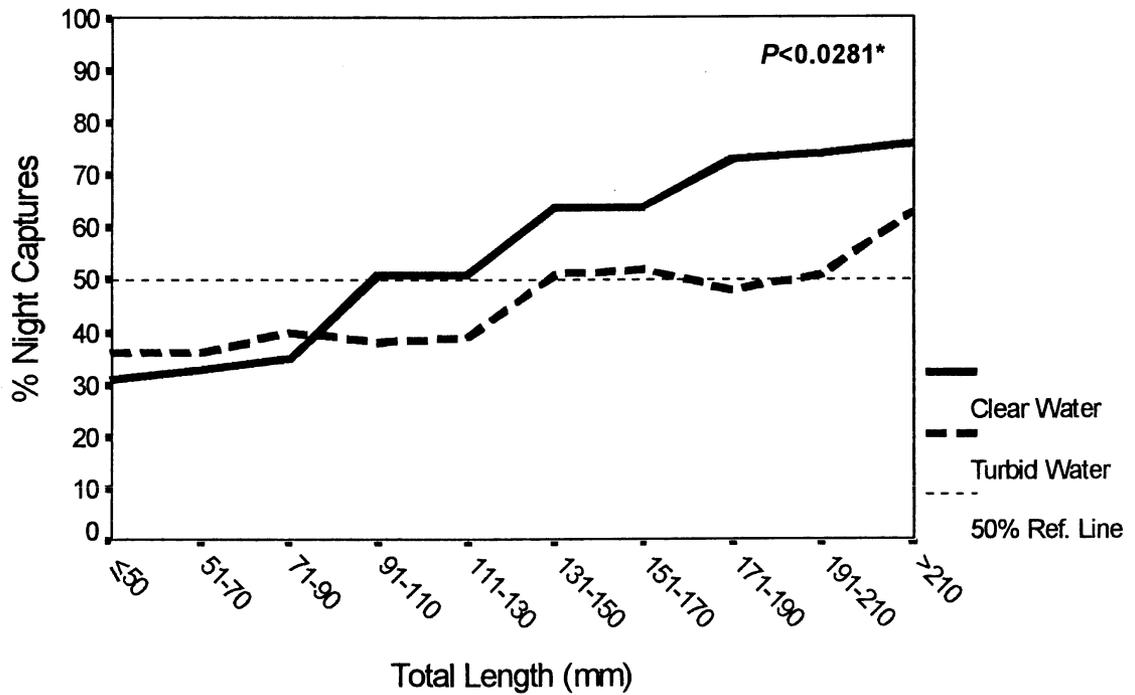


Figure 3. Percent night captures of *Gila cypha* in the Little Colorado River, Grand Canyon, AZ from 1991-1995. Percent day captures represents the reciprocal of % night captures. Size classes whose % captures were close to the 50% reference line were captured in similar proportions between night and day, those with % captures above the line were captured more frequently at night, while those with % captures below the line were captured more often during the day. Fish capture data were divided on the basis of water clarity: "clear water" contains data collected when turbidities were <30 nephelometric turbidity units (NTUs) and "turbid water" contains data collected when turbidities were ≥ 30 NTUs. Wilcoxon Signed Ranks 2-tailed Test (P -value) compared % night captures between water clarities. See Table 2 in Methods for sample sizes.

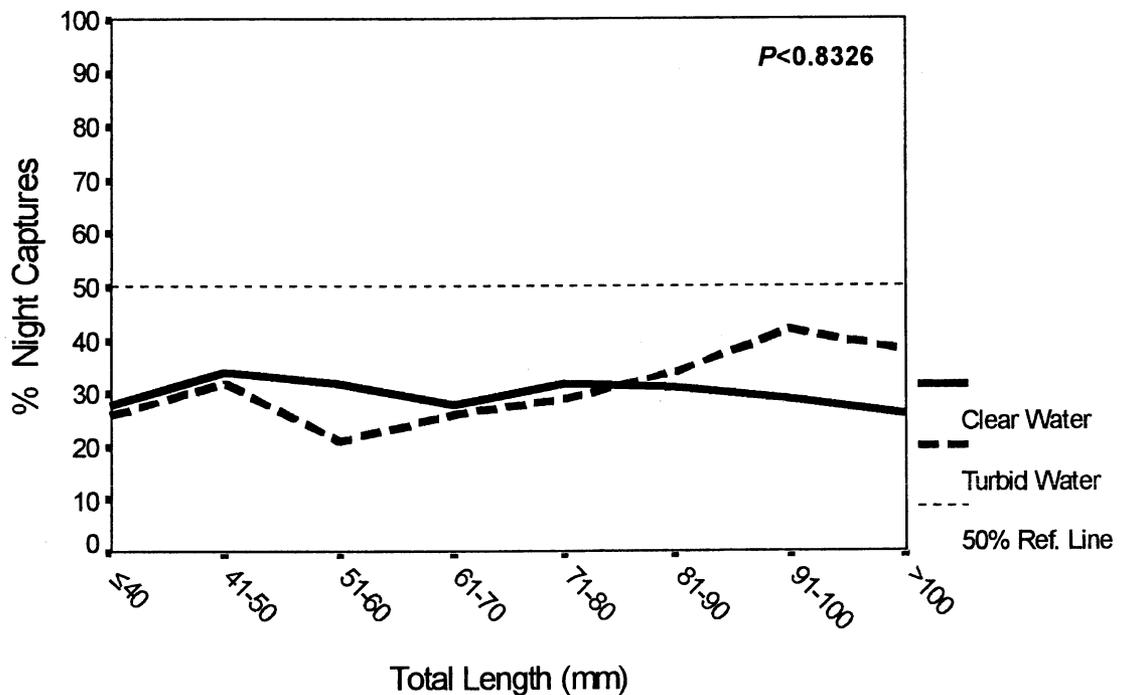


Figure 4. Percent night captures of *Rhinichthys osculus* in the Little Colorado River, Grand Canyon, AZ from 1991-1995. Percent day captures represents the reciprocal of % night captures. Size classes whose % captures were close to the 50% reference line were captured in similar proportions between night and day, those with % captures above the line were captured more frequently at night, while those with % captures below the line were captured more often during the day. Fish capture data were divided on the basis of water clarity: "clear water" contains data collected when turbidities were <math>< 30</math> nephelometric turbidity units (NTUs) and "turbid water" contains data collected when turbidities were ≥ 30 NTUs. Wilcoxon Signed Ranks 2-tailed Test (P -value) compared % night captures between water clarities. See Table 2 in Methods for sample sizes.

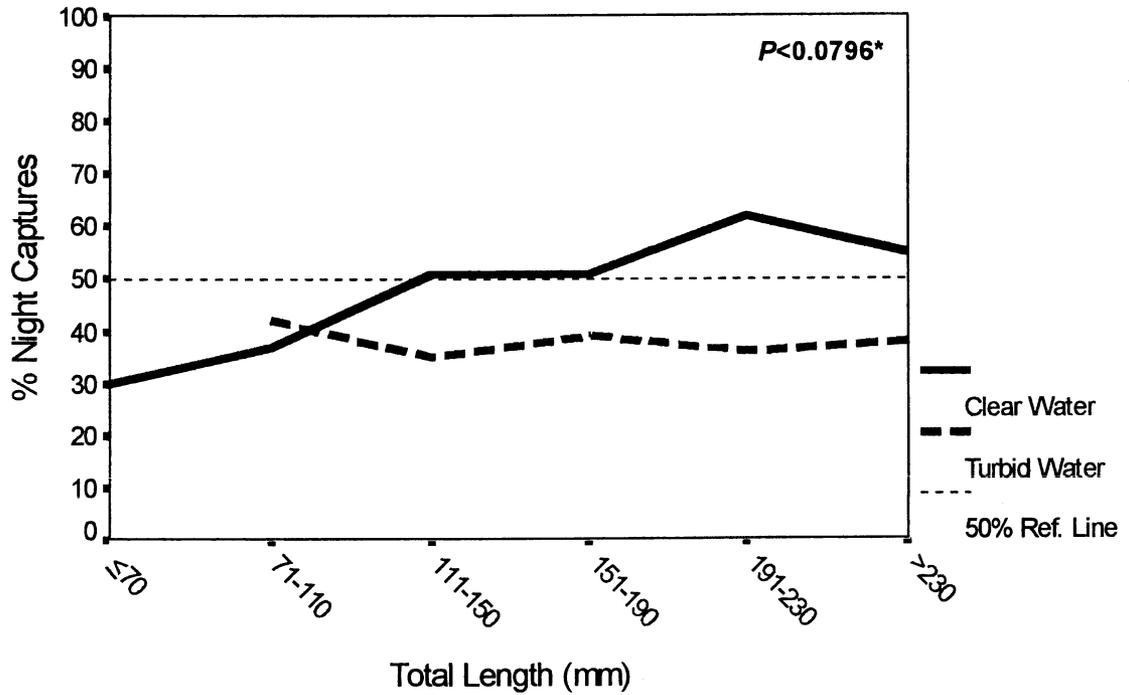


Figure 5. Percent night captures of *Catostomus discobolus* in the Little Colorado River, Grand Canyon, AZ from 1991-1995. Percent day captures represents the reciprocal of % night captures. Size classes whose % captures were close to the 50% reference line were captured in similar proportions between night and day, those with % captures above the line were captured more frequently at night, while those with % captures below the line were captured more often during the day. Fish capture data were divided on the basis of water clarity: "clear water" contains data collected when turbidities were < 30 nephelometric turbidity units (NTUs) and "turbid water" contains data collected when turbidities were ≥ 30 NTUs. Wilcoxon Signed Ranks 2-tailed Test (P -value) compared % night captures between water clarities. See Table 2 in Methods for sample size.

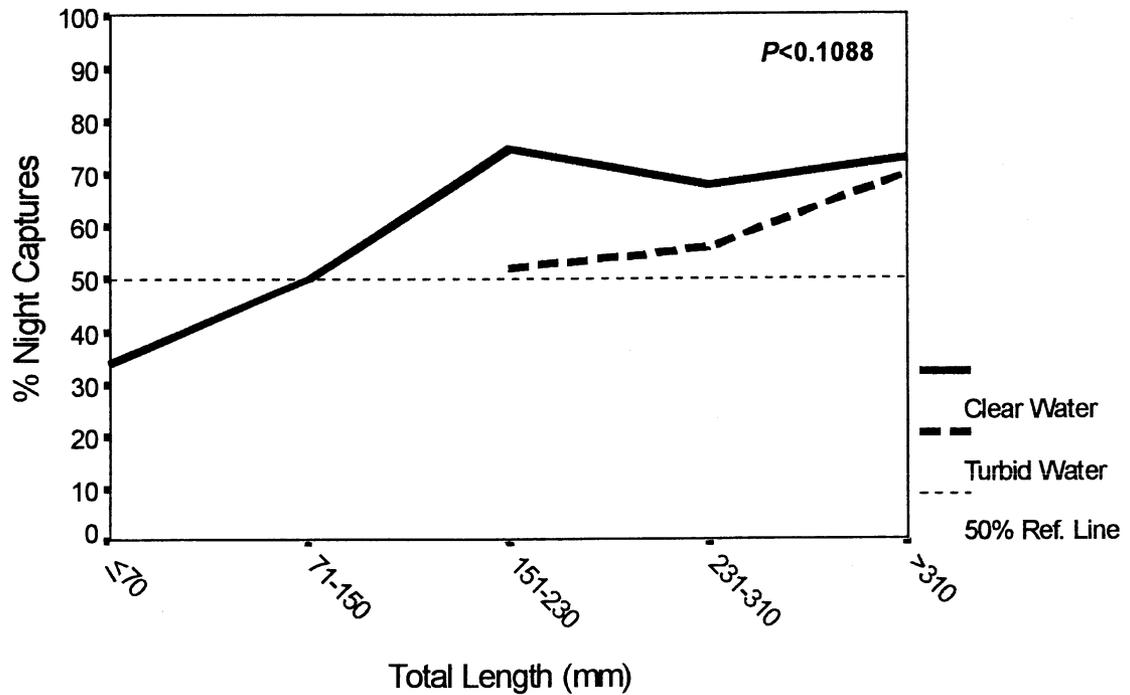


Figure 6. Percent night captures of *Catostomus latipinnis* in the Little Colorado River, Grand Canyon, AZ from 1991-1995. Percent day captures represents the reciprocal of % night captures. Size classes whose % captures were close to the 50% reference line were captured in similar proportions between night and day, those with % captures above the line were captured more frequently at night, while those with % captures below the line were captured more often during the day. Fish capture data were divided on the basis of water clarity: "clear water" contains data collected when turbidities were < 30 nephelometric turbidity units (NTUs) and "turbid water" contains data collected when turbidities were ≥ 30 NTUs. Wilcoxon Signed Ranks 2-tailed Test (P -value) compared % night captures between water clarities. See Table 2 in Methods for sample sizes.

Comparisons within the day and night.-The additional noon and midnight sampling indicated that captures were not evenly distributed throughout day or night. Percent fish captures from the smallest size classes (≤ 70 mm) of *G. cypha*, *C. latipinnis*, *C. discobolus* (≤ 110 mm), and all size classes of *R. osculus*, were greater during the day than night (Tables 4&5). Because all size classes of *R. osculus* demonstrated similar capture patterns (data not shown), all size classes were pooled for presentation. Generally, except for *C. discobolus*, greater captures of small fish (≤ 70 mm) occurred during the latter portion of the day (Table 4). The two larger size classes of *Gila cypha* (>70 mm), when captured during the day, were also captured more in the afternoon, whereas intermediate size classes of *C. latipinnis* (71-150 mm) were captured more in the earlier portion of the day. Because of small samples of *C. discobolus* >70 mm (n=7) and *C. latipinnis* >150 mm (n=2), daytime comparisons were not addressed.

Table 4. Comparisons of % captures between two daytime and one nighttime consecutive subdiel sampling periods in the Little Colorado River, AZ. Percent captures for each subdiel represent the proportion of total captures/hr for a given species and size class. Species (Spp) include *G. cypha* (HBC), *C. discobolus* (BHS), and *C. latipinnis* (FMS), each of which were subdivided into three contiguous size classes and, *R. osculus* (SPD), which were pooled. Percent captures were generated separately for Day (~0800-1800) vs. Night (~1800-0800), and also for Morning-Noon (~0800-1300) vs. Afternoon (~1300-1800) vs. Night (~1800-0800). Total fish captures were given following % captures (). Total sampling effort included 191 net/days and 137 trap/days that were deployed over multiple clear water sampling trips (<30 NTUs) in June and July 1993.

Spp	Size class	# Fish Captured	Percent Captures during different subdiel periods				
			Day : Night		Morning-Noon : Afternoon : Night		
			(10 h) :	(14 h)	(5 h) :	(5 h) :	(14 h)
HBC	≤70 mm TL	551	70 (347) :	30 (204)	39 (163) :	44 (184) :	17 (204)
HBC	71-150 mm TL	31	25 (6) :	75 (25)	0 (0) :	40 (6) :	60 (25)
HBC	>150 mm TL	66	12 (6) :	88 (60)	4 (1) :	18 (5) :	78 (60)
BHS	≤70 mm TL	26	79 (19) :	21 (7)	51 (11) :	37 (8) :	12 (7)
BHS	71-150 mm TL	3	41 (1) :	59 (2)	58 (1) :	0 (0) :	42 (2)
BHS	>150 mm TL	4	58 (2) :	42 (2)	0 (0) :	74 (2) :	26 (2)
FMS	≤70 mm TL	19	66 (11) :	34 (8)	22 (3) :	58 (8) :	20 (8)
FMS	71-150 mm TL	19	45 (7) :	55 (12)	44 (5) :	18 (2) :	38 (12)
FMS	>150 mm TL	2	0 (0) :	100 (2)	0 (0) :	0 (0) :	100 (2)
SPD	All lengths	457	69 (283) :	31 (174)	34 (116) :	48 (167) :	18 (174)

Nighttime captures of all fish categories, except *G. cypha* > 150 mm, were highest during the 2nd half of the night (Table 5). Of all fish categories, only *G. cypha* >150 mm were captured more during the 1st half of night than any other subdiel period. Captures during this period were lowest for all other fish categories, except *C. latipinnis* >150 mm. These disproportionate captures within the night resulted in the greatest captures of *G. cypha* 70-150 mm, *C.*

discobolus >70 mm, and *C. latipinnis* ≤70 mm occurring during the 2nd half of the night (which also included dawn), while their overall captures were higher during the day than night. The smaller *G. cypha* and *C. discobolus* (≤70 mm), and *R. osculus* were consistently captured more during the day, while the largest *G. cypha* (>150 mm) and *C. latipinnis* (>70 mm) were consistently captured at night.

Table 5. Comparisons of % captures between two nighttime and one daytime consecutive subdiel sampling periods in the Little Colorado River, AZ. Percent captures for each subdiel represent the proportion of total captures/hr for a given species and size class. Species (Spp) include *G. cypha* (HBC), *C. discobolus* (BHS), and *C. latipinnis* (FMS), each of which were subdivided into three contiguous size classes and, *R. osculus* (SPD), which were pooled. Percent captures were generated separately for Day (~0800-1800) vs. Night (~1800-0800), and also for Day (~0800-1800) vs. Dusk-Midnight (~1800-0100) vs. Midnight-Dawn (~0100-0800). Total fish captures were given following % captures (). Total sampling effort included 362 net/days and 261 trap/days that were deployed over multiple clear water sampling trips (<30 NTUs) in May 1993, June 1992, 1993 and 1994, and August 1993.

Spp	Size class	# Fish Captured	Percent Captures during different subdiel periods				
			Day : Night		Day : Dusk-Midnight : Midnight-Dawn		
			(10 h)	(14 h)	(10 h)	(7 h)	(7 h)
HBC	≤70 mm TL	448	71 (284)	: 29 (164)	55 (284)	: 15 (56)	: 30 (108)
HBC	71-150 mm TL	432	53 (193)	: 47 (239)	36 (193)	: 24 (89)	: 40 (150)
HBC	>150 mm TL	208	27 (44)	: 73 (164)	16 (44)	: 48 (94)	: 36 (70)
BHS	≤70 mm TL	85	73 (56)	: 27 (29)	57 (56)	: 12 (8)	: 31 (21)
BHS	71-150 mm TL	52	64 (29)	: 36 (23)	47 (29)	: 5 (2)	: 48 (21)
BHS	>150 mm TL	24	54 (11)	: 46 (13)	37 (11)	: 24 (5)	: 39 (8)
FMS	≤70 mm TL	22	58 (11)	: 42 (11)	41 (11)	: 5 (1)	: 54 (10)
FMS	71-150 mm TL	28	48 (11)	: 52 (17)	31 (11)	: 28 (7)	: 41 (10)
FMS	>150 mm TL	23	28 (5)	: 72 (18)	16 (5)	: 37 (8)	: 47 (10)
SPD	All lengths	1,527	71 (965)	: 29 (562)	54 (965)	: 12 (146)	: 34 (416)

DISCUSSION

The use of passive capture devices as an indicator of fish activity was suggested by Stott (1970) and used in a variety of studies (Staples 1975, 1978; Magnan and FitzGerald 1984; Tonn and Paszkowski 1987; Mendelson 1975; Reeb et al. 1995). For fish to be captured in a passive sampling device they must be actively moving, whereby they voluntarily enter the trap. Thus percent captures is a measure of locomotor activity and can be used to describe diel activity patterns. Also, because our traps were deployed across a broad range of habitats, increased fish movements were detectable in both inshore and offshore habitats.

Our analyses suggests that water clarity was more influential on diel activity patterns of most LCR fish, than seasonal differences. Müller (1978a, b) stated that the majority of fish species whose diel activity patterns are seasonally influenced are found in high latitudes (beginning $\sim 60^{\circ}$ N. latitude in the Northern Hemisphere), while activity patterns of lower latitudes (our study was 36° N), where the photoperiod fluctuates less between seasons, are usually more synchronized with day and night. However, because seasonal influences of various midlatitude species have been observed in laboratory (Eriksson 1978; Spencer 1939) and field investigations (Staples 1978, 1975; Tonn and

Paszkowski 1987), we should emphasize that our study was essentially depicting activity patterns during the Spring and Summer, with some comparisons from the Fall.

Nocturnal, diurnal and crepuscular activity.-Whether it is a time of activity cessation or elevation, the twilight periods play a major role in the daily life of many fish species (Helfman 1981, 1993). Our noon sampling defined the only sampling period (~0800-1300) completely isolated from the crepuscular periods. Captures during this morning sampling period showed that *R. osculus* and all smaller size classes of *G. cypha* (≤ 90 mm), *C. latipinnis* (≤ 70 mm) and *C. discobolus* (≤ 110 mm) were active during that period. However, the afternoon sampling period, which encompassed the onset of dusk, resulted in higher captures of all smaller fish except for *C. discobolus*. Whether the higher capture rates were related to a shelter seeking behavior associated with evening twilight is unknown. We also remain unsure, if the majority of small fish captured during the night sampling effort entered the nets and traps during morning twilight or were captured throughout the night. In any event, greater proportions of small fish were captured during daylight or crepuscular periods than at night.

The high percentages of captures during midnight sampling suggested that many fish from larger size classes of *G. cypha* (>170 mm), *C. latipinnis* (>150 mm), and *C. discobolus* (>110 mm) were active throughout the night.

Although it is possible that most fish swam into the traps during the later portion of dusk, it is unlikely, for illumination does not appear to be necessary for these fish to be active. Nocturnal activity of adult *G. cypha*, *C. latipinnis* and *C. discobolus* was indicated by our frequent captures of these fish in trammel nets set in the Colorado River during very dark, cloudy nights (USFWS unpub.data). BIO/WEST, Inc. also captured many adult *G. cypha*, *C. latipinnis* and *C. discobolus* in trammel nets set late at night in the Colorado River, often under heavy cloud cover and high turbidities (Richard Valdez, pers. comm.) Elevated nocturnal activity of adult *G. cypha* was also reported from other trammel netting efforts (Kaeding and Zimmerman 1983), radiotelemetry results (Valdez and Ryel 1995), and our late-night visual observations of adult *G. cypha* movements along shorelines (USFWS unpub. data).

Although nocturnal activity is substantiated for adult *G. cypha*, *C. latipinnis*, and *C. discobolus*, their activity during crepuscular periods is not well known. Radiotelemetry results on 69 adult *G. cypha* in the Colorado River found that their activity rapidly increased around dusk, started to wane prior to midnight (2200-2300), and rose again between 0430-0630 in the morning (Richard Valdez pers. comm.). Similarly, we captured the greatest number of large *G. cypha* (>170 mm) during dusk-midnight, followed by midnight-dawn, and the fewest during the day sampling

period. Under clear water conditions larger *C. latipinnis* (>150 mm) were predominately active from dusk through dawn, while *C. discobolus* (>110 mm) were active during both night and day, so the role of the crepuscular periods on their activity is also unclear.

Of the four native fishes we studied, adult *G. cypha* and *C. latipinnis* exhibited the highest degree of nocturnal activity in both clear and turbid water clarities. This activity corresponds to periods of movement between habitats. In the LCR, adult *G. cypha* (≥ 180 mm) migrated at night to nearshore habitats in both clear and turbid water (Chapter 4). Although diel movements of adult *C. latipinnis* have not been quantified in the LCR, nocturnal shifts to nearshore habitat have been observed at the confluence of the Paria and Colorado Rivers (Weiss 1993). Like *G. cypha*, adult *C. latipinnis* were captured more frequently in shallower water during the night.

Increased nocturnal activity of adult *G. cypha* and *C. latipinnis* suggests that they can shift from primary reliance of eyesight to other sensory modes at night. Nocturnal species rely more on tactile, chemical, and/or electrical senses than diurnally active species (Schwassmann 1971). The development of many of these senses may also correspond to growth. For example, the olfactory lamellae increase in number and size until a certain juvenile or adult body size is attained (Noakes and Godin 1988).

Fishes that inhabit chronically turbid waters often have degenerate eyes, while their other senses become more highly developed (Evans 1952). The relatively small eyes found in adult *G. cypha* may represent a degeneration correlated with the reduced light in turbid waters and/or it may have been a response to the scouring action of suspended matter (Miller 1946; Minckley 1973). Because the LCR has prolonged periods of both extremes in water clarity, the ability to shift to alternate sensory mechanisms may be critical to the survival of these native fish.

The cover provided by high turbidity may allow larger *G. cypha* and *C. latipinnis* to be more active during the daytime. In the mainstem Colorado River, radiotelemetry studies conducted on adult *G. cypha* found less pronounced diel patterns, but significantly higher movements during periods of high turbidity (Valdez and Ryel 1995). Adult *C. latipinnis* may follow this general pattern: we captured significantly more *C. latipinnis* during the daytime under high turbidity than in clear water in both the LCR and mainstem Colorado River.

Activity of small fishes.-Under clear water, smaller *G. cypha* (≤ 90 mm) were predominately diurnally active; these diurnal tendencies extended to *G. cypha* ≤ 130 mm in turbid water. Smaller *C. latipinnis* (≤ 70 mm) and *C. discobolus* (≤ 110 mm) were also diurnally active in clear water, but this conclusion could not be extended to turbid water

because only a few small suckers were captured. However, because fish from the five larger size classes of *C. discobolus* were predominately captured during the day and *C. latipinnis* displayed a pattern where consecutively smaller size class fish were captured more frequently during the daytime, we assume that the smallest size class fish of both suckers were also diurnal. The smallest species, *R. osculus*, was diurnally active across all life stages/size classes regardless of water clarity.

Development of sensory organs may affect diel activity patterns in smaller fish. One of the first senses to develop in larval fish is eyesight, which often occurs during the yolk sac period (Blaxter 1988). Most teleost species examined by Blaxter and Staines (1970) had a pure-cone retina upon first feeding. These findings suggest that light is a requirement for feeding in many early larval stages of fish (Blaxter 1986). Noakes and Godin (1988) stated that the relative rate of eye growth is generally dependent on the rate of body growth and because most teleosts have indeterminate growth, eye growth is often a continuous process. As retinal growth continues, the ratio of rods to cones increases, while the cones expand. Increasing scotopic sensitivities to lower ambient light intensities may allow an expansion and/or shift of activity to periods with much lower light levels. Bulkowski and Meade (1983) found that the shift from positive to negative

phototaxis in walleyes (*Stizostedion vitreum*) was more closely related to fish size than to age.

The LCR presently contains only two commonly occurring piscine predators, adult *G. cypha* (Chapter 4) and channel catfish (Marsh and Douglas 1997; Kaeding and Zimmerman 1983). *Gila cypha* go through a period of metamorphosis, whereby they shift from being possible prey to being a potential predator (Chapter 4). Because adult *G. cypha* and channel catfish are generally nocturnally active (Kaeding and Zimmerman 1983; Hara 1993), diurnal activity in smaller fish would reduce encounters with both predators. The LCR is not unique in this respect. Segregation of activity periods between predators and smaller prey has been observed in other freshwater fish assemblages (Helfman 1981; Frazer and Cerri 1982; Schwassmann 1971; Bourke et al. 1996; Tonn and Paszkowski 1987; Magnan and Fitzgerald 1984).

Whether the diurnal activities of small fish are because of physiological constraints or behavioral responses requires further examination. For example, Sigler and Sigler (1987, 1996) reported *R. osculus* to be nocturnally active, whereas our results found this species to be diurnally active. If nocturnally active *R. osculus*, described by Sigler and Sigler (1987, 1996) inhabited systems where the principal predators were diurnally active, then this represents a remarkable behavioral plasticity within this species in response to predation pressure.

Unlike *R. osculus*, diurnal activity in the other three species is highest among the youngest life stages, suggesting that sensory development could be important factor.

Lacking diurnal periodicity.-Bourke et al. (1996), reported ontogenetic shifts in activity patterns of brook charr (*Salvelinus fontinalis*) in Quebec, Canada that were similar to our finding with *G. cypha* and *C. latipinnis*. YOY brook charr were mostly diurnally active, adults were mostly nocturnally active, while juveniles were equally active both day and night.

Both *G. cypha* and *C. latipinnis* undergo a transition from diurnal to nocturnal activity as they grow. Intermediate size class fish of both species were equally active between day and night. These fish may have grown to lengths where the threat of intra- and interspecific predation is relaxed because much of fish predation is directed towards smaller fish that are easier to capture (Juanes 1994). However, the higher captures of juvenile *G. cypha* and *C. latipinnis* during the second half of the night, when larger *G. cypha* were less active, may suggest an avoidance of larger *G. cypha*.

Under clear water conditions, captures of *C. discobolus* (>110 mm) were similar between day and night. These fish have modified, cartilaginous jaws for scraping harder bottoms for algae and incidental macroinvertebrates living

within these algal communities (Sigler and Sigler 1996, 1987; Minckley and Rinne 1991). Because both young and adult *C. discobolus* eat mostly the same epilithic food items (Sigler and Sigler 1996, 1987), *C. discobolus* (>110 mm) can feed throughout the diel cycle when this food source is available. Because epilithic growth is both reduced and scoured away in turbid water, the increased diurnal activity of *C. discobolus* may be related to feeding shifts to alternate food resources.

Conclusion.-The LCR is subject to prolonged periods of elevated turbidities and flood conditions. The resident native fish assemblage has likely evolved under these conditions. These fish species may have evolved sensory and behavioral abilities to withstand months of negligible visibility. Although all native fish were predominately diurnally active during their younger life stages, only *R. osculus* maintained this pattern throughout its life. However, even *R. osculus* may rely on sensory abilities other than eyesight to survive prolonged periods of stochastic river conditions. Though we have suggested possible explanations for activity patterns in these native fish species (sensory development, optimizing foraging abilities, and reducing predation risks), the biological and environmental conditions under which these patterns evolved is hidden by eons of time. Darwin's perception "Though nature grants vast periods of time for the work of natural

selection, she does not grant an indefinite period; for as all organic beings are striving, it may be said, to seize on each place in the economy of nature, if any species does not become modified and improved in a corresponding degree with its competitors, it will soon be exterminated (1859:147)" may be the only explanation for these patterns.

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CHAPTER 3

Ontogenetic shifts in habitat use of humpback chub (*Gila cypha*) in the Little Colorado River

Abstract.-Investigations of habitat use by different ontogenetic stages of humpback chub (*Gila cypha*) were conducted in the Little Colorado River from 1992-1995. Twelve habitat variables were used to quantify the habitats where each of 2,495 miniature hoopnets were deployed. Habitats used by 11,406 *G. cypha* were established by linking each fish to the corresponding hoopnet it was captured in. Analyses were divided between day and night sampling periods, and clear and turbid water clarities (<30 NTUs and ≥ 30 NTUs respectively). Stepwise multiple linear regressions of fish lengths against the 12 habitat variables were conducted separately for young-of-the-year (YOY; ≤ 90 mm TL) *G. cypha* and chubs across all lifestages, except larval (30-445 mm TL). Concordance of habitat use patterns by three ontogenetic stages of *G. cypha* were examined between different sampling trips and two river reaches, when water clarities and sampling periods were similar. Habitat use varied with ontogenetic stage, portion of diel cycle, and water clarity. Shifts in habitat use apparently begin at early lifestages. YOY regressions showed that as the range of fish lengths expanded during the Summer, the habitat differences became more pronounced. Shifts in habitat used

by *G. cypha* (all lifestages) usually followed a generalized pattern, whereby increasingly larger *G. cypha* occupied habitats that were progressively further from shore and/or emergent edges, in faster current velocities, and at greater depths. Departures from this generalized pattern occurred during all periods and river clarities, but were most pronounced during nights. During nighttime in clear water, adults (≥ 180 mm TL) were often captured in nearshore habitats with YOY, while juveniles (91-179 mm TL) moved to midchannel habitats. In contrast, during nighttime in turbid water, juveniles and YOY often co-occupied nearshore habitats; although adults moved inshore at night, they remained further from shoreline habitats than smaller conspecifics. Similar habitat use patterns for *G. cypha* were described in a separate study conducted in the highly regulated mainstem Colorado River, below Glen Canyon Dam. Because these rivers are very different with respect to hydrology, water chemistry, and other piscine species, these habitat use patterns may be evolutionarily derived, rather than learned behavioral traits.

Key Words: *Gila cypha*; young-of-the-year; predation, competition; Cyprinidae; habitat; ontogenetic shifts; Little Colorado River

INTRODUCTION

On March 11, 1967, humpback chub (*Gila cypha*) were designated as an endangered species on the original list of "Endangered and Threatened Wildlife and Plants" (U.S. Federal Register 32:4001). This listing prompted studies and surveys for this minnow in both the upper and lower Colorado River Basin. Surveys were originally implemented to locate remnant populations of this species; only six known populations have been reported to date and are all located in the Colorado River or its major tributaries (Converse et al. 1998, Valdez and Ryel 1995; Douglas and Marsh 1996).

The difficulties encountered in studying *G. cypha* in the remote, canyon bound, riverine systems where they reside, restricted advancements of biological knowledge concerning this species (Minckley 1973). An attempt to development habitat suitability index curves for four ontogenetic stages of *G. cypha*, by combining data from nearly 100 investigations, collected over a 22 year period, by 17 different principal investigators, was only marginally successful (Valdez et al. 1990). To date much of our perception of the general life history of *Gila cypha* has resulted from observations and remains highly speculative.

The largest known *G. cypha* aggregation occurs within the terminal 14 km of the Little Colorado River (LCR) on

Navajo tribal lands (USFWS 1990) and Colorado River near the LCR inflow, within Grand Canyon National Park (Douglas and Marsh 1996; Valdez and Ryel 1995). Recruitment of *G. cypha* is dependent on the LCR, where the vast majority of reproduction occurs (Valdez and Ryel 1995; Gorman and Stone 1999; USFWS 1990). Our native fish research in the LCR (1992-1995) allowed for a more quantitative investigation of *G. cypha* habitat utilization than obtained in prior studies. This paper examines whether or not *G. cypha* undergo ontogenetic shifts in habitat usage. If ontogenetic shifts in habitat use were evident, then follow-up questions that are to be addressed include: 1) Which habitat variables showed a consistent pattern of predicting the presence of different ontogenetic stages of *G. cypha*? 2) Are the patterns of habitat use consistent between day and night periods? 3) How are these patterns affected by differences in water clarities. A better understanding of how different ontogenetic stages of *G. cypha* use habitats could greatly enhance future recovery efforts in this species.

METHODS

Study area.-The Little Colorado River (LCR) is an unregulated river system subject to periodic flooding interspersed with baseflow conditions. During periods of no runoff, baseflow between 6.1 to 6.6 m³/sec is maintained in the lower 21 km by perennial springs (Johnson and Sanderson 1968). At baseflow, both heavy precipitation of unconsolidated CaCO₃ (marl) and travertine deposition occur. Along with *G. cypha*, the LCR fish assemblage is dominated by three other native species, speckled dace (*Rhinichthys osculus*), flannelmouth (*Catostomus latipinnis*) and bluehead sucker (*C. discobolus*). Although Kaeding and Zimmerman (1983) collected specimens from ten nonnative species in the LCR, they reported that only the four native species were found in large numbers. We found that many of these nonnative fish were mainly restricted to the mouth or were extremely rare, while the others appeared and disappeared in cyclic patterns in this unpredictable river system. *Gila cypha* and the two native suckers were restricted to below Chute Falls, a travertine dam located ~14.2 km upstream of the mouth (Kaeding and Zimmerman 1983; Mattes 1993; Minckley 1996).

Two separate study reaches, each divided into two 500 m study sites, were established within the terminal 14 km of the LCR (Figure 1). The Powell Canyon reach was located

approximately 2.3-3.8 km upstream of the confluence with the Colorado River (36°11'45"N, 111°46'0"W) and the Salt Canyon reach was located further upriver at approximately 10.5-11.9 km (36°10'42"N, 111°42'16"W). These combined reaches constituted 14% of the LCR corridor occupied by *G. cypha*. Because of greater travertine deposition in upriver locations (Cooley 1976), the Salt reach contained a greater abundance of large travertine dams, deeper pools, and a broader array of habitat types than the Powell reach.

Fish sampling.-Cross-channel transects were permanently established at 20 m intervals throughout the study reaches. In each study reach, the 500 m sites were sampled alternately between sampling trips. Transects selected for sampling were staggered (eg., fish two, skip one etc.) to cover each site in 10 days; on subsequent trips, transects that were not selected previously were sampled by offsetting the starting transects. Ropes were tied to opposite stream banks at selected transect locations. Miniature hoopnets (50 cm diameter X 100 cm length, 10 cm throat, 6 mm nylon mesh) were fastened to transect ropes at 3-4 m lateral intervals (Figure 2).

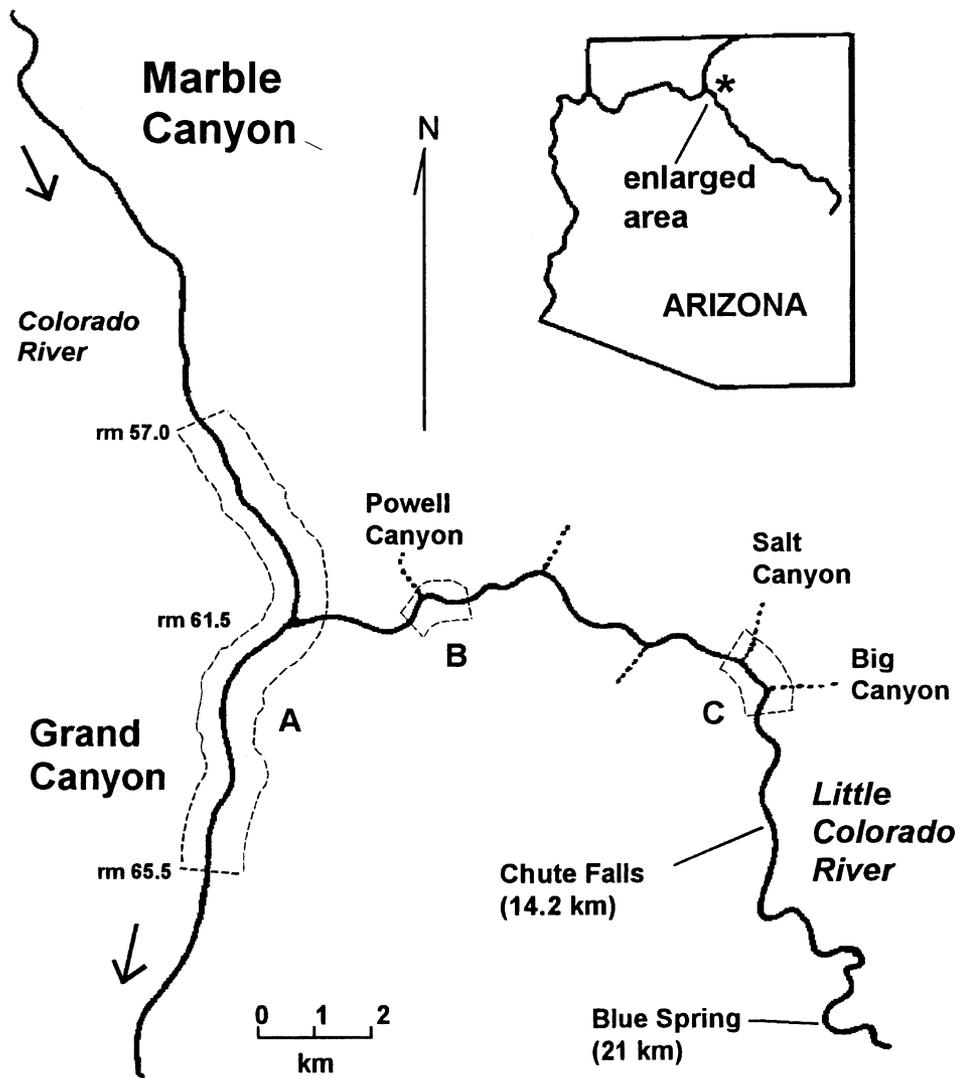


Figure 1. Map of the lower Little Colorado River (LCR) from Blue Spring to the confluence with the Colorado River (CR), Coconino County, Arizona. The perennial flows in this lower portion of the LCR are maintained by Blue Spring. Powell Canyon study reach (A) was located ~2.3-3.8 km upstream of the confluence with the CR and Salt Canyon study reach (B) was located further upriver at ~10.5-11.9 km. In the majority of ~10 day duration research trips, both study reaches were worked simultaneously. *Gila cypha*, *Catostomus discobolus* and *C. latipinnis* were restricted to below the travertine dam, Chute Falls. The CR reach between 57-65.5 river miles (rm) downstream from Lees Ferry is where 87% of adult *G. cypha* were captured in a separate CR research project; smaller ontogenetic stages were most frequently captured in the section below the LCR (see Valdez and Ryel 1995).

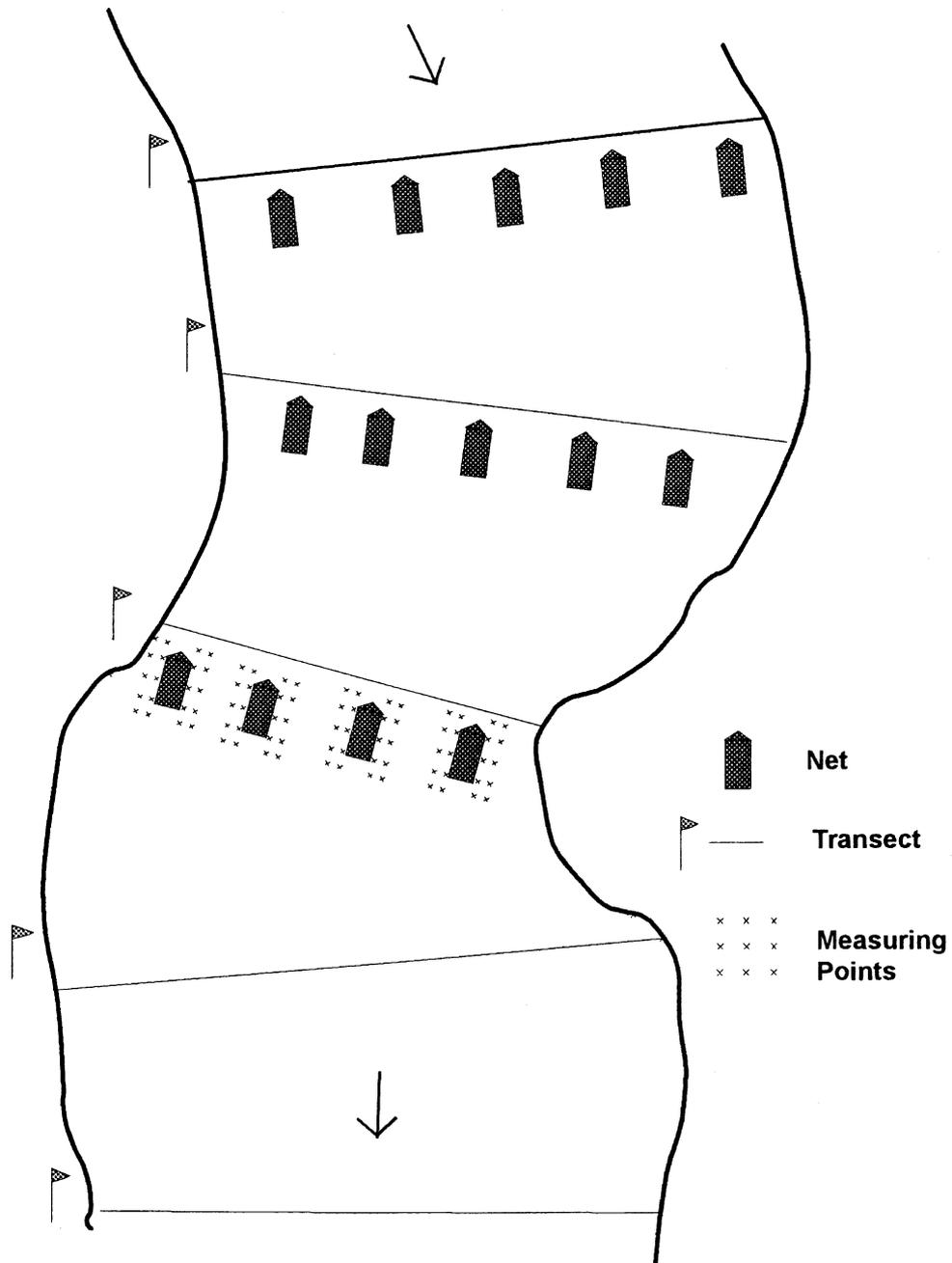


Figure 2. Fish sampling grid used in the Little Colorado River, Arizona from 1991-1995. Cross-channel transects were spaced 20 m apart. Transects selected for fish sampling were staggered to cover each 500 m study site in 10 days. Miniature hoopnets (Net) were fastened at 3-4 m intervals along ropes located at the selected transects. Habitat measurements were made at 20 points located over a 1.5 X 2.0 meter grid around each net.

Nets were set to sample day and night over a 24h period and then relocated to the next upstream transect. To assess fish habitat use during the day and night, nets were checked during daylight within two hours of sunset and sunrise. All fish captured were identified to species, measured to total length (TL) in mm, weighed to nearest g, and sexed when possible. The physical condition of each fish was noted by recording scars, parasites, abrasions, and reproductive condition. The *G. cypha* capture data used in this paper were collected during twelve separate sampling trips between 1992-1995 (Table 1). During each ~10 d sampling trip, data were collected from both study reaches simultaneously, except for the trips of 4/95 & 5/95 when only the Salt reach was sampled.

Habitat measurements.-Habitat measurements were conducted at 20 points, each spaced 50 cm from the adjacent points, located over a 1.5 X 2.0 m grid around each net (Figure 2; Gorman and Stone 1999). Depth, velocity, and substrate were measured at these points using the method of Gorman and Karr (1978). The measuring pole was constructed with 1.9 cm diameter PVC pipe and marked at 5 cm increments. The pole was placed at each point and habitat variables were measured. Later, net statistics were calculated for habitat variables using data collected from the 20 sampling point grid.

Depth was measured directly. Point measurements for depths were analyzed as mean depth (cm) per net set (MDPH). Standard deviation of depths (cm) (SDDPH) per net provided a measure of bottom roughness profile for each net set, sensu Gore (1978). The angle from each point to the next highest point, located adjacent to it on the sampling grid or to an emergent edge located <100 cm away, were calculated and summarized as mean positive vertical angles (MPVA; Gorman and Stone 1999). In this manner, MPVA could use information from points not confined to the net grid and provided a measure of angular variation associated with bottom contours underlying each net set.

Current meters were only indirectly used because they were time consuming, difficult to use in deep habitats, and were subject to malfunction. Instead, current velocity was quantified by observing the flow of water around the measuring pole. Six major categories of current velocity were recognized (0-5), each of which, except zero, was subdivided into three subcategories. By simultaneously comparing the velocity readings (m/s) from a Marsh-McBirney (Model 201) portable water flow meter to all 16 current categories, we developed conversion factors. All current flow categorical data collected in the field were later translated to (m/s) velocities using these conversions. Mean current velocity (MCURV) and standard deviation of current velocity (SDCURV) surrounding each net were

calculated. SDCURV measures the degree of current velocity variation around the net. Points where the direction of flow was upstream were recorded as eddy currents. Eddy frequency (FEDDY) was tabulated as the number of eddy points per net.

Substrates were categorized at each of the 20 sampling points as fines (≤ 0.1 mm) which contained predominately silt but also fine precipitate of CaCO_3 (marl); sand (0.11-2.0 mm); gravel and small rocks (2.1-100 mm); cobble (101-256 mm); and boulders (>256 mm). Substrate frequencies (FFINES, FGRAVL, FCOBBL, FBOULD) for each net represented the number of points each substrate category occurred within the 20 point grid.

Mean lateral position (MLATP) of each net set was calculated as the mean distance (cm) of the sample points to the nearest emergent edge (boulder, shoreline, travertine dam, sand bars). Lateral distance (LATDS) was the distance (cm) of the net to the nearest shoreline. MLATP and LATDS were viewed as separate variables because the LCR contained many large boulders and travertine dams in the midsection of the river.

The 12 habitat variables just described were calculated for each of 2,495 net sets. Habitat associations of 11,406 *G. cypha* were generated by linking each individual fish to the corresponding net from which it was captured.

Sampling periods and river conditions.-Turbidities above and below 30 nephelometric turbidity units (NTUs) have been found to alter *G. cypha* diel activity patterns (Chapter 2; Valdez and Ryel 1995), diel movements (Chapter 4), and utilization of shoreline habitats (Valdez and Ryel 1995; Tim Hoffnagle AZGFD, unpub. data). Therefore, data collected in different sampling trips were divided between those where the median water turbidities were <30 NTUs (clear water) and ≥30 NTUs (turbid water; Table 1). During each sampling trip, except June 1992, turbidity was measured with a Hach Model 16800 Portalab Turbidimeter or a Hach 2100P Turbidimeter. The June 1992 trip contained clear water conditions based on observations in trip reports and photographs. Because of reduced sampling efficiency during floods, data from trips with discharges >19 m³/s were omitted from the analyses.

Univariate Analyses.-To determine if different *G. cypha* ontogenetic stages used habitat randomly or showed shifts in habitat use, Friedman Test Statistic-Kendall's Coefficient of Concordance (FTS and KCC, respectively) were conducted with SYSTAT V 7.0 (1997). *Gila cypha* were divided into three different size classes based on total length. Fish ≤90 mm were classified as young-of-the-year (YOY), although some were actually yearlings. *Gila cypha* between 91-179 mm were classified as juveniles and those ≥180 mm were classified as adults. All previously described habitat

variables were examined. Medians for each habitat variable used by each size class (YOY, juveniles and adults) were calculated separately from capture data collected during day and night sampling periods, at each study reach, during each sampling trip. Because the two study reaches were separated by ~seven km, they were treated independently. This not only increased the number of sampling blocks, but it tested concordance using different areas in which *G. cypha* reside. The habitat use data were separated into four categories depending on the river condition and sampling period.

During May and June 1993, captures of small *G. cypha* (≤ 90 mm) were negligible because of low survivorship of 1992 cohort fish (USFWS unpub. data), while 1993 cohort fish were too small to be contained by the nets' 6 mm mesh. Therefore, data collected during May 1993 at both study reaches and during the nighttime of June 1993 at Powell study reach were not included in the FTS-KCC clear water analyses, but were used in the "all" *G. cypha* regressions, described subsequently. Because FTS-KCC cannot compensate for missing groups, we omitted any data set containing a missing size class from our analyses. Thus, each test consisted of three treatments (3 size classes), while the number of blocks varied, depending on the number of sampling trips, which study reaches were occupied, and if all three size classes contained capture data. In clear water, the

Table 1: Numbers of young-of-the-year (YOY), juvenile, and adult *G. cypha* captured in nets. Data are divided by sampling reaches (Salt vs Powell), sampling periods (night vs day) & water clarity (clear vs turbid). Because no YOY size class fish were captured during 5/93 or the nighttime period during 6/93 at Powell study reach, these data could not be used in the Friedman test-Kendall's Coefficient of Concordance (FTS-KCC) analyses, but were included in the "all" *G. cypha* multiple regression. Total *G. cypha* used in the FTS-KCC analyses is broken down for the diel sampling periods in clear and turbid water clarities.

DATE	REACH	# NETS	TURB (NTUs)	# YOY (≤90mm TL)		# JUVENILE (91-179mm TL)		# ADULT (≥180mm TL)	
				night	day	night	day	night	day
0692	SALT	82	-	19	27	141	100	40	11
0692	POWELL	90	-	13	28	50	57	18	6
0593	SALT	75	17	0	0	13	9	52	13
0593	POWELL	103	17	0	0	42	39	22	11
0693	SALT	118	3	48	34	40	5	34	4
0693	POWELL	104	3	0	2	38	15	11	5
0793	SALT	97	4	554	871	20	4	57	6
0793	POWELL	133	4	248	375	17	8	9	2
0893	SALT	110	5	1932	1512	21	4	48	4
0893	POWELL	146	5	182	192	15	11	3	7
0694	SALT	104	3	122	55	211	54	61	3
0694	POWELL	99	3	86	122	74	72	5	4
0894	SALT	113	13	172	195	119	80	21	10
0894	POWELL	114	13	245	333	29	31	2	2
TOTAL		1488	CLEAR	3621	3746	830	489	383	88
USED	FTS-KCC	1310	CLEAR	3621	3746	737	441	298	64
0993	SALT	69	967	109	84	4	2	16	12
0993	POWELL	88	967	69	81	5	2	4	3
0494	SALT	125	180	76	122	126	164	36	26
0494	POWELL	94	180	29	16	15	8	10	13
0594	SALT	130	379	24	40	100	130	47	34
0594	POWELL	124	379	27	23	41	25	44	11
0495	SALT	191	37	46	65	65	89	89	18
0595	SALT	186	129	11	20	95	87	60	26
TOTAL		1007	TURB	391	451	451	507	306	143
USED	FTS-KCC	1007	TURB	391	451	451	507	306	143

total sampling effort included 1,488 net sets, of which 1,310 were used in the FTS-KCC analyses. In turbid water, all data collected from a total sampling effort of 1,007 net sets were used in the FTS-KCC analyses (Table 1).

Stepwise multiple regressions on "all" *G. cypha*.-In addition to the univariate FTS-KCC analyses, multivariate stepwise multiple regression analyses were used to model habitat associations by different sizes of *G. cypha*. Data collected from both Powell and Salt study reaches during May 1993, June 1993, and June 1994 were pooled to increase sample size. All three sampling trips occurred in clear water conditions, following Spring floods, and prior to the greatest influx of young-of-the-year (YOY) resulting from the Spring *G. cypha* spawn. Stepwise multiple regressions (SPSS 1995) were conducted separately for both the daytime and nighttime sampling periods. Stepwise procedures were chosen for consistency in comparing the different regressions represented in this paper. A $\log_{(10)}$ transformation of *G. cypha* total length was used as the dependent variable to normalize the residuals from the regression. Independent variables examined included all previously described habitat variables. The entry of the probability of F was set at $\alpha=0.05$ and removal was set at $\alpha=0.10$.

Stepwise multiple regressions on YOY.-A similar multiple regression was devised to test whether shifts in habitat use

could be detected within the same cohort of YOY. Because of frequent flood conditions during 1992, few or no YOY from 1992 survived into 1993 (USFWS unpub. data). During 1993 stable flow regimes led to an extremely large cohort. Length frequency histograms showed a bimodal distribution between 1993 cohort *G. cypha* and the progeny prior to 1992, therefore the regressions could be conducted solely on 1993 YOY by restricting the analyses to smaller fish represented in the lower distribution of the histogram.

Fish habitat data for Salt and Powell study reaches were combined. We were unable to measure all YOY captured at the Salt study reach during July and August of 1993, therefore any nets that contained unmeasured YOY had the entire transect of nets deleted from the analyses. All capture data from the Powell reach were included in the analyses. Regressions were conducted separately for the daytime and nighttime sampling periods for July, August, and September 1993. Both July and August were clear water periods while the river water was turbid during September. The main difference between these YOY regressions and "all" *G. cypha* regressions was that the total length dependent variable did not require a log transformation to normalize the regression error terms.

RESULTS

Habitat use between different sampling trips and sites.-

Different size classes of *Gila cypha* not only use habitat differently, but habitat use patterns were also concordant between different sampling trips and study sites. Thus, habitat use is predictable to a certain degree. The daytime habitat association patterns of different size classes of *G. cypha* were often similar between clear (Table 2) and turbid water (Table 3) conditions. During the day in both water clarities, consecutively larger size class fish were further from shoreline and emergent edges, at greater depths and in faster currents than smaller fish. Except for current velocity, which showed higher concordance during turbid water, these patterns contained higher significance and concordance in clear than turbid water conditions. In clear water, larger size classes were also significantly associated with habitats containing greater variations in current velocities.

During the night, habitat association patterns by different size classes were more variable than during the day. During night in clear water, YOY fish were most often captured closer to shorelines, emergent edges and in shallower water than larger fish (Table 4). However, adults also use shoreline habitats at night in clear water (see rank sums). Compared to both YOY and juveniles, adults were

captured closer to shores and emergent edges in 27% of the sampling trips and in shallower water in 18% of sampling the sampling trips. In contrast, during the night in turbid water, adults were usually captured further from shorelines, at greater depths and in faster currents than either YOY or juveniles (Table 5). Adults were also captured more frequently around cobble and boulder substrates, while YOY were collected least around these substrates.

Nighttime habitat use by juveniles also varied between clear and turbid water conditions. During the night in clear water, juveniles were associated further midchannel than adults in 54.5% of sampling trips, a pattern also evident in the rank sums (Table 4). In contrast, during the night in turbid water, juveniles were usually captured more inshore than adults (Table 5). In fact, the data showed that 37.5% of the sampling trips captured the majority of juveniles at shallower depths and closer to shorelines and emergent edges than even the YOY.

Table 2: Friedman Tests (FTS) and Kendall's Coefficient of Concordance (W) results of *G. cypha* (HBC) habitat usage during daytime in clear water conditions. These tests compared medians for each habitat variable (HV) where YOY (≤ 90 mm TL), JUV (91-179mm TL) & A (≥ 180 mm TL) were captured (treatments=3, df=2) in each of twelve separate sampling efforts (# blocks). Sampling efforts included six from both Powell and Salt study reaches during 6/92, 6/93, 7/93, 8/93, 6/94 & 8/94. Habitat variables are defined in methods. The number of fish captured in each size class during each sampling effort are given in Table 1.

HV	#	W	FTS	PROB	RANK SUM OF HBC SIZE CLASSES
LATDS	12	0.924	22.167	0.000	YOY(13.0):JUV(23.0):A(36.0)
MLATP	12	0.606	14.542	0.001	YOY(15.5):JUV(22.5):A(34.0)
MDPH	12	0.533	12.792	0.002	YOY(15.5):JUV(23.5):A(33.0)
MCURV	12	0.595	14.292	0.001	YOY(14.5):JUV(24.5):A(33.0)
SDCURV	12	0.231	5.542	0.063	YOY(18.0):JUV(24.5):A(29.5)
FCOBBL	12	0.090	2.167	0.338	YOY(21.0):JUV(23.0):A(28.0)
FBOULD	12	0.090	2.167	0.338	YOY(21.0):JUV(23.0):A(28.0)

Table 3: Friedman Tests (FTS) and Kendall's Coefficient of Concordance (W) results of *G. cypha* (HBC) habitat usage during daytime in turbid water conditions. These tests compared medians of each habitat variable (HV) where YOY (≤ 90 mm TL), JUV (91-179mm TL) & A (≥ 180 mm TL) were captured (treatments=3, df=2) in each of eight separate sampling efforts (# blocks). Sampling efforts included three from both Powell and Salt study reaches during 9/93, 4/94 & 5/94 and two from the Salt reach during 4/95 & 5/95. Habitat variables are defined in methods. The number of fish captured in each size class during each sampling effort are given in Table 1.

HV	#	W	FTS	PROB	RANK SUM OF HBC SIZE CLASSES
LATDS	8	0.824	13.188	0.001	YOY(8.50):JUV(16.5):A(23.0)
MLATP	8	0.562	9.000	0.011	YOY(10.0):JUV(16.0):A(22.0)
MDPH	8	0.484	7.750	0.021	YOY(11.0):JUV(15.0):A(22.0)
MCURV	8	0.754	12.063	0.002	YOY(11.5):JUV(12.5):A(24.0)
SDCURV	8	0.027	0.438	0.804	YOY(14.5):JUV(17.0):A(16.5)
FCOBBL	8	0.082	1.312	0.519	YOY(13.5):JUV(18.0):A(16.5)
FBOULD	8	0.141	2.250	0.325	YOY(13.0):JUV(19.0):A(16.0)

Table 4: Friedman Tests (FTS) and Kendall's Coefficient of Concordance (W) results of *G. cypha* (HBC) habitat usage during nighttime in clear water conditions. These tests compared medians for each habitat variable (HV) where YOY (≤ 90 mm TL), JUV (91-179mm TL) & A (≥ 180 mm TL) were captured (treatments=3, df=2) in each of eleven separate sampling efforts (# blocks). Sampling efforts included five from both Powell and Salt study reaches during 6/92, 7/93, 8/93, 6/94 & 8/94 and one from the Salt reach during 6/93. Habitat variables are defined in methods. The number of fish captured in each size class during each sampling effort are given in Table 1.

HV	#	W	FTS	PROB	RANK SUM OF HBC SIZE CLASSES
LATDS	11	0.390	8.591	0.014	YOY(14.5):JUV(28.0):A(23.5)
MLATP	11	0.231	5.091	0.078	YOY(16.0):JUV(26.0):A(24.0)
MDPH	11	0.256	5.636	0.060	YOY(16.0):JUV(23.0):A(27.0)
MCURV	11	0.163	3.591	0.166	YOY(17.0):JUV(23.5):A(25.5)
SDCURV	11	0.025	0.545	0.761	YOY(21.0):JUV(21.0):A(24.0)
FCOBBL	11	0.099	2.182	0.336	YOY(26.0):JUV(20.0):A(20.0)
FBOULD	11	0.107	2.364	0.307	YOY(21.0):JUV(19.0):A(26.0)

Table 5: Friedman Tests (FTS) and Kendall's Coefficient of Concordance (W) results of *G. cypha* (HBC) habitat usage during nighttime in turbid water conditions. These tests compared medians for each habitat variable (HV) where YOY (≤ 90 mm TL), JUV (91-179mm TL) & A (≥ 180 mm TL) were captured (treatments=3, df=2) in each of eight separate sampling efforts (# blocks). Sampling efforts included three from both Powell and Salt study reaches during 9/93, 4/94 & 5/94 and two from the Salt reach during 4/95 & 5/95. Habitat variables are defined in methods. The number of fish captured in each size class during each sampling effort are given in Table 1.

HV	#	W	FTS	PROB	RANK SUM OF HBC SIZE CLASSES
LATDS	8	0.328	5.250	0.072	YOY(12.0):JUV(15.0):A(21.0)
MLATP	8	0.109	1.750	0.417	YOY(13.0):JUV(17.0):A(18.0)
MDPH	8	0.293	4.687	0.096	YOY(13.5):JUV(13.5):A(21.0)
MCURV	8	0.473	7.562	0.023	YOY(10.5):JUV(16.0):A(21.5)
SDCURV	8	0.109	1.750	0.417	YOY(13.0):JUV(18.0):A(17.0)
FCOBBL	8	0.543	8.688	0.013	YOY(11.0):JUV(14.5):A(22.5)
FBOULD	8	0.402	6.437	0.040	YOY(10.5):JUV(17.0):A(20.5)

Habitat use across all size classes.-Linear relationships modelled in the separate daytime and nighttime stepwise multiple regressions (Table 6) support the habitat use patterns depicted by the FTS-KCC analyses (Tables 2-5). Both regressions met the assumptions of normality, linearity, homoscedasticity, and independence that are required to conduct parametric tests (See Appendix 1).

The daytime regression modelled a linear progression further from emergent edges, to greater depths, and more variable current velocities with increasing fish length. This regression also found smaller fish associated with habitats containing significantly more boulder, fine, and gravel substrates than adults. The nighttime regression showed smaller fish in slower currents, shallower depths, and areas containing higher bottom angular variation, but less cobble than larger fish.

The adjusted coefficient of multiple determination (adj. R^2) during the daytime was more than twice the nighttime regression's, indicating a much stronger linear relationship. When considered, along with the higher significance and concordance found during the daytime than nighttime FTS-KCC analyses, seems to suggest that different sizes of *G. cypha* were more segregated during the day than at night.

Table 6. Stepwise multiple regression analyses for both daytime and nighttime habitat use by "all" lengths of *G. cypha*. \log_{10} of total fish lengths for *G. cypha* is used as the dependent variable from combined Powell and Salt Canyon study reaches in the Little Colorado River during combined 5/93, 6/93 & 6/94 clear water research trips. Included is the number of *G. cypha* and their corresponding means, standard deviations, coefficient of variation and range of total lengths used in each analysis. All habitat variables defined in methods were tested as independent "predictor" variables. Only habitat variables that were chosen in either the daytime or nighttime regressions were shown. The partial regression coefficients and Student's *t* significance levels of the independent variables included are numbered (#) in the order that they were selected up until the next variable entered would increase the coefficient of multiple determination (R^2) less than 1%. The values of R^2 at the first step, final adj. R^2 and first variable entered are given. Lilliefors Kolmogorov-Smirnov (K-S) tests and number of residual outliers are given for diagnostics of assumptions.

SAMPLING PERIOD	Daytime	Nighttime
# <i>G. cypha</i>	422	792
MEAN LENGTH	106.128	141.090
SD LENGTH	66.992	83.844
CV	63.1%	59.4%
LENGTH RANGE (mm)	27-401	22-445
ADJ. R^2	0.42593	0.19618
F	53.05983	49.26230
SIG F	0.0000	0.0000
# OUTLIERS	2	1
K-S (Lilliefors)	>0.2000	0.0009
1ST Variable entered	MLATP	MLATP (Dropped after MDPH)
R^2 at first step	0.1724	0.1081
Independent Variables		
Y-INTERCEPT	1.873409	2.014310
MLATP	2.02072E-04 P=0.0000 (1)	*
MDPH	8.15078E-04 P=0.0000 (4)	6.70786E-04 P=0.0000 (3)
MPVA	*	-0.005859 P=0.0000 (2)
MCURV	*	0.469883 P=0.0000 (1)
SDCURV	0.968192 P=0.0000 (6)	*
FFINES	-0.018834 P=0.0000 (2)	*
FGRAVL	-0.026007 P=0.0000 (3)	*
FCOBBL	*	0.010650 P=0.0000 (4)
FBOULD	-0.010312 P=0.0000 (5)	*

Habitat use across YOY size classes.-Regressions on the 1993 YOY cohort detected size related differences in habitat use. The regression results for 7/93, 8/93 and 9/93 are presented separately for the daytime (Table 7) and nighttime (Table 8) sampling period results. All YOY regressions appeared to have met the assumptions of normality, linearity, homoscedasticity, and independence (See Appendix 2).

In both daytime and nighttime YOY regressions, the standard deviation of YOY TL, coefficient of variation, and adjusted R^2 increased during each subsequent month from July through September 1993. The adj. R^2 increase from July to September was elevenfold during the daytime and threefold during the nighttime regressions. Whether the adj. R^2 was influenced by elevated turbidities during 9/93 is unknown. However, in similar clear water clarities, both August regressions resulted in higher adj. R^2 's than those from July; this pattern suggest that adj. R^2 's would have increased irrespective of water clarity.

There were many similarities between the daytime and nighttime regressions that may suggest YOY remain in the same general habitats throughout the diel cycle. Although the first variable to enter the regression model differed between the different months, it was the same for day and night sampling periods within each month. In all regressions the most frequently selected predictor variables were related to current and substrate. A difference in

lateral distance from shoreline was only found in the September daytime regression, while differences in depth and lateral distances from emergent edges were never selected.

All regressions showed a pattern of increasing associations with increasing YOY length to areas containing either larger and/or more heterogeneous substrates. For example, both July regressions showed a linear reduction in the use of sandy habitats by increasingly larger fish. Patterns of increasing use of cobble substrates with increasing fish size were found in the July nighttime and September daytime regressions. During the daytime of August, and both periods of September, larger YOY showed higher associations to areas of gravel. All August and September regressions showed an increasing use of boulder substrates by larger YOY.

During the nighttime of July and both periods during August, smaller YOY showed greater associations to eddies than larger YOY. Increasing associations of larger fish to more variable current velocities were found during the daytime of July and nighttime of September. A switch in habitat use was found whereby larger YOY used faster current velocities than smaller fish during both day (it later dropped out) and night sampling periods in August, then slower currents during both September periods.

Table 7. Stepwise multiple regression analyses for daytime habitat use by YOY *G. cypha*. Total lengths for YOY *G. cypha* is used as the dependent variable from combined Powell and Salt Canyon study reaches in the Little Colorado River during daytime sampling periods for each of the 7/93, 8/93 clear water & 9/93 turbid water research trips. Included is the number of *G. cypha* and their corresponding means, standard deviations, coefficient of variation and range of total lengths used in each analysis. All habitat variables defined in methods were tested as independent "predictor" variables. Only habitat variables that were chosen in either the nighttime (Table 8) or daytime regressions are shown. The partial regression coefficients and Student's *t* significance levels of the independent variables included are numbered (#) in the order that they were selected up until the next variable entered would increase the coefficient of multiple determination (R^2) less than 1%. The values of R^2 at the first step, final adj. R^2 and first variable entered are given. Lilliefors Kolmogorov-Smirnov (K-S) tests and number of residual outliers are given for diagnostics of assumptions.

	CLEAR WATER	CLEAR WATER	TURBID WATER
SAMPLING DATES	JULY 12-21, 1993	AUGUST 9-17, 1993	SEPTEMBER 10-18, 1993
# <i>G. cypha</i>	436	240	166
MEAN LENGTH	49.394	54.042	62.199
SD LENGTH	5.630	8.694	10.960
CV	11.4%	16.1%	17.6%
LENGTH RANGE (mm)	32-66	35-91	39-93
ADJ. R^2	0.03755	0.13805	0.42147
F	9.48502	13.75918	25.04132
SIG F	0.0001	0.0000	0.0000
# OUTLIERS	2	1	0
K-S (Lilliefors)	0.1244	>0.2000	>0.2000
1ST Variable entered	FSAND	MCURV (DROPPED OUT)	FBOULD
R^2 at first step	0.0308	0.0763	0.2690
Independent Variables			
Y-INTERCEPT	49.643238	51.965873	55.464263
LATDS	*	*	0.008071 P=0.0000 (2)
MCURV	*	*	-23.425351 P=0.0040 (4)
SDCURV	12.819453 P=0.0254 (2)	*	*
FEDDY	*	-0.260736 P=0.0109 (3)	*
FSAND	-0.101725 P=0.0029 (1)	*	*
FGRAVL	*	1.125882 P=0.0001 (1)	0.499843 P=0.0210 (5)
FCOBBL	*	*	0.654532 P=0.0000 (3)
FBOULD	*	0.309436 P=0.0009 (2)	0.850845 P=0.0000 (1)

Table 8. Stepwise multiple regression analyses for nighttime habitat use by YOY *G. cypha*. Total lengths for YOY *G. cypha* is used as the dependent variable from combined Powell and Salt Canyon study reaches in the Little Colorado River during nighttime sampling periods for each of the 7/93, 8/93, clear water & 9/93 turbid water research trips. Included is the number of *G. cypha* and their corresponding means, standard deviations, coefficient of variation and range of total lengths used in each analysis. All habitat variables defined in methods were tested as independent "predictor" variables. Only habitat variables that were chosen in either the nighttime or daytime (table 7) regressions are shown. The partial regression coefficients and Student's *t* significance levels of the independent variables included are numbered (#) in the order that they were selected up until the next variable entered would increase the coefficient of multiple determination (R^2) less than 1%. The values of R^2 at the first step, final adj. R^2 and first variable entered are given. Lilliefors Kolmogorov-Smirnov (K-S) tests and number of residual outliers are given for diagnostics of assumptions.

	CLEAR WATER	CLEAR WATER	TURBID WATER
SAMPLING DATES	JULY 12-21, 1993	AUGUST 9-17, 1993	SEPTEMBER 10-18, 1993
# <i>G. cypha</i>	333	271	178
MEAN LENGTH	51.174	54.764	64.208
SD LENGTH	6.170	9.202	10.922
CV	12.1%	16.8%	17.0%
LENGTH RANGE (mm)	32-67	36-92	37-89
ADJ. R^2	0.07221	0.18839	0.24876
F	9.61359	21.89082	15.65259
SIG F	0.0000	0.0000	0.0000
# OUTLIERS	3	2	0
K-S (Lilliefors)	0.0150	0.0044	>.2000
1ST Variable entered	FSAND	MCURV	FBOULD
R^2 at first step	0.0456	0.1410	0.1808
Independent Variables			
Y-INTERCEPT	51.724233	50.657632	62.240998
LATDS	*	*	*
MCURV	*	17.081679 P=0.0000 (1)	-33.338725 P=0.0019 (3)
SDCURV	*	*	55.225696 P=0.0126 (4)
FEDDY	-0.200479 P=0.0330 (3)	-0.310285 P=0.0034 (2)	*
FSAND	-0.181556 P=0.0002 (1)	*	*
FGRAVL	*	*	0.899431 P=0.0013 (2)
FCOBBL	0.122248 P=0.0250 (2)	*	*
FBOULD	*	0.232121 P=0.0075 (3)	1.045018 P=0.0000 (1)

DISCUSSION

In the Little Colorado River (LCR), *G. cypha* demonstrated a general pattern of habitat use where consecutively larger fish were associated with greater depths, faster current velocities, and areas further from shorelines and emergent edges. This pattern was most significant and concordant during the daytime in clear water, followed by the daytime in turbid water, and least distinctive during the nighttime irrespective of different water clarities.

Both the general habitat use pattern and departures from this pattern may be driven by competitive and predatory interaction between larger and smaller *G. cypha*. Piscivory by adult *G. cypha* has been documented and may be a major component of their feeding ecology (Chapter 4). Other than adult *G. cypha*, the LCR contains only one fairly common predatory fish, the channel catfish (*Ictalurus punctatus*). However, of fish resident to the LCR, *G. cypha* are the numerically dominant species and make up the greatest fish biomass. Thus *G. cypha* habitat use patterns may be highly influenced by intraspecific competition and predator-prey interactions.

Sogard (1994) listed physical limitations, competitive interactions, and predator avoidance as major factors in the restriction of smaller fish to specific habitats. Adult *G.*

cypba used wider ranges of lateral distances, depths, and current velocities than the smaller conspecifics. In contrast, the FTS-KCC analyses showed that the majority of YOY *G. cypba* were in nearshore habitats. We found that shoreline occupancy by YOY fish was maintained even at extremely high fish densities. For example, in spite of the large numbers of YOY captured in nets (N=3,444) during August 1993 in the Salt study reach, the majority of YOY were still located closer to shorelines than larger conspecifics. In other analyses YOY demonstrated various diel movements, but shifts away from shorelines were never significant (see Chapter 4). Nearshore habitats often contain shallow depths or cover that may function as refuges from predators (Sogard 1994).

The range of habitats used by YOY and juvenile *G. cypba* may have been restricted during periods when adult *G. cypba* were active. The majority of fish from each of the three size classes were sequentially further from shorelines during the daytime in clear water, compared to turbid water conditions. When considering that adults were least diurnally active in clear water (Chapter 2; Valdez and Ryel 1995), these patterns may suggest that smaller, diurnally active *G. cypba* may venture further midchannel when adult activity levels are most reduced. Harvey and Stewart (1991) found a similar linear relationship between the length of fish and the depth of pools; they speculated that the

deepest pools allowed the inhabitants to avoid predation from terrestrial predators, but a certain size had to be attained to not be vulnerable to other fish. In this manner, adults may have maintained the optimal midchannel deep habitats, while a competitive "pecking order" may have allowed juveniles to maintain intermediate habitats between the adults and YOY. Similar patterns were also observed in a minnow assemblage in an Ozark stream (Gorman 1987).

Adult *G. cypha* show a distinctive inshore movement at night (Chapter 4) which departs sharply from the general habitat use pattern. The FTS-KCC analyses showed lower significance and concordance, and the "all" *G. cypha* regression resulted in a much lower adj. R^2 during the nighttime than daytime sampling periods. At night in clear water, as adults moved into nearshore habitats, juveniles moved further into midchannel habitats, and YOY moved closer to emergent edges and areas containing greater mean positive vertical angles within the nearshore habitats (Chapter 4). The nighttime "all" *G. cypha* regression also showed a greater association of smaller fish to areas containing higher mean positive vertical angles. Because high mean positive vertical angles result from undercut stream banks, large boulders, or very heterogeneous bottom substrates, these areas provide cover for fish. During the night in clear water, adults were often closer to shorelines than YOY, while juveniles were often captured in midchannel

habitats. In contrast, during the night in turbid water, juveniles were often captured closer inshore than YOY; although adults shifted into nearshore habitats, they were captured further from shorelines than smaller conspecifics. These patterns suggest an avoidance of adults by YOY and juveniles.

In a study of two small Michigan lakes, Werner et al. (1977) found that predation pressure confined small fish to particular habitat types, while competition determines spatial relations among species within these habitat types. In our study, although YOY appear to be restricted to nearshore habitats, they still demonstrated differences in habitat use within the same YOY cohort. The YOY regressions showed a predictable range of habitat use patterns as the range of lengths of YOY fish expanded in the late Summer. Whether the linear relationships reflected a noncompetitive habitat expansion resulting from morphological and dietary changes, or from a sequential "pecking order" of *G. cypha* competing for more optimal habitats, needs further investigation.

Regardless of the cause, differential habitat use by *G. cypha* apparently begins in very early life stages. Childs et al. (1998) found that *G. cypha* metalarvae (16-26 mm TL) used slower current velocities than mesolarvae stages (10-15 mm TL), a pattern consistent with our September 1993 YOY regressions. Regressions of habitat association showed that

larger YOY used areas containing larger and/or more heterogeneous substrates, more variable water velocities, but fewer eddies than smaller conspecifics. It is unclear if these habitats were selected because of food resources, predator refuge, or some other purpose.

These patterns of ontogenetic shifts in habitat use observed in *G. cypha* are not restricted to the LCR. Valdez and Ryel (1995) observed similar transitions of habitat use by different size classes of *G. cypha* in the mainstem Colorado River in Grand Canyon National Park. They found subadult *G. cypha* <200 mm TL used shorelines while adults \geq 200 mm TL utilized offshore habitats; *G. cypha* <100 mm TL were never captured offshore. They perceived the transition from shoreline to offshore taking place after the fish were one year old (~100 mm) and ending at 3 years old (\geq 200mm). They also found that adults used shorelines during the night or in the daytime in elevated turbidities (>30 NTU). Also during the nighttime, significantly higher densities of subadult *G. cypha* (<200 mm) were located near shoreline habitats that contained cover, including vegetated banks, talus and debris fans (Valdez and Ryel 1995; Converse et al. 1998). Although the *G. cypha* habitat use patterns between the LCR and Colorado River were very similar, the systems were very different with respect to discharge, water chemistry, and fish fauna. Therefore, the similarities of *G. cypha* habitat use between the two systems may be

evolutionarily derived rather than learned behavioral traits.

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Appendix 1A.-Diagnostics summary of assumptions for the

"all" G. cypha multiple regressions.-Both the nighttime and daytime regressions for "all" *G. cypha* (Table 6) appears to meet all the major assumptions of normality, linearity, homoscedasticity, and independence. Although the Lilliefors modified K-S test for the nighttime sampling period ($P=0.0009$) brings the assumption of normality into question (Table 6), both the frequency histogram and normal P-P plot of regression standardized residuals (Appendix 1B) show the error terms to be very close to a normal distribution. Because perfectly normal distributions are exceedingly rare, when the sample sizes are large almost any goodness-of-fit test will result in rejection of the null hypothesis (SPSS 1995). The sample size ($n=792$) included in the nighttime sampling period would be considered a large sample. The question of normality for the daytime sampling period should not arise as the large sample size ($n=422$) passed the Lilliefors test with $p>0.2000$.

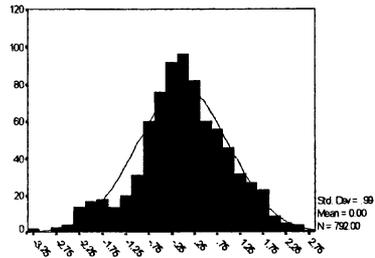
Though both scatterplots show the standardized residuals randomly scattered, there is an apparent downward trend (Appendix 1B). Rather than a violation homoscedasticity or linearity, this is more likely to be a result of an important variable missing from the model (Zar 1984). Certainly there are many more variables that are not included in this model, such as biotic components of aquatic and terrestrial vegetation types, macroinvertebrates, and

other possible food items. Also, the adj. R^2 of <0.50 show that there is still much variation that is not accounted for by the model (Table 6).

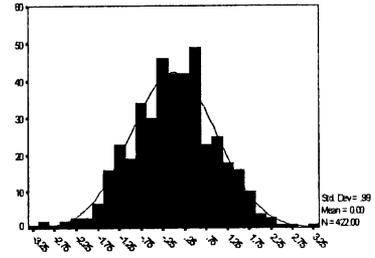
The time sequence plots do not seem to show any major violations of independence (Appendix 1B). Both nighttime and daytime plots appear to be highly random with no apparent pattern. The 5/93 portion of the nighttime sampling period shows reduced numbers of negative residuals. This pattern may reflect the inability of nets to catch very small YOY during that time.

Nighttime Frequency Histograms

Frequency



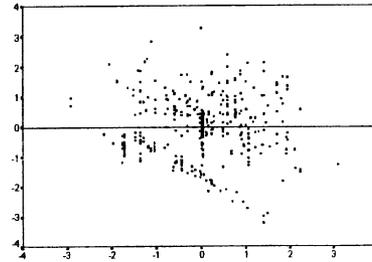
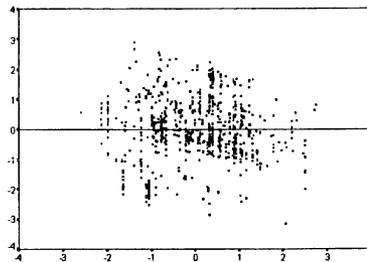
Daytime



Regression Standardized Residual

Scatterplots

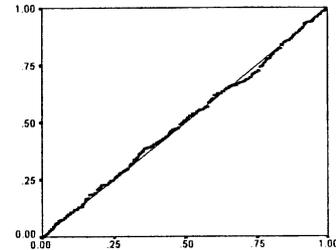
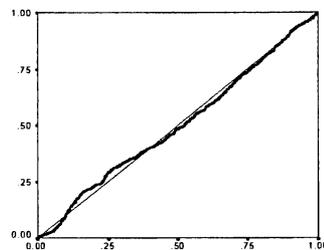
Regression
Standardized
Residual



Regression Standardized Predicted Value

Normal P-P Plots of Regression Standardized Residuals

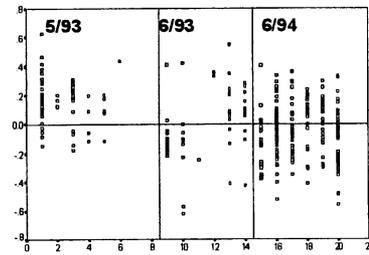
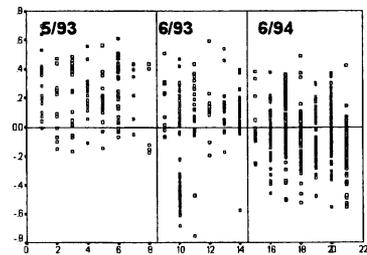
Expected
Cumulative
Probabilities



Observed Cumulative Probabilities

Time Sequences of Unstandardized Residuals

Residuals



Time Sequences

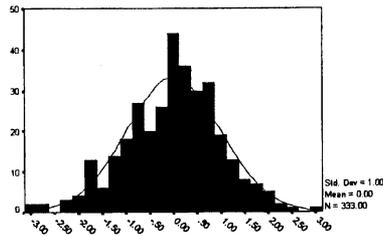
Appendix 1B. Graphic Diagnostics for Multiple Regressions of all HBC log(10) total lengths (mm) captured from both Powell and Salt Canyon study reaches of the Little Colorado River during 5/93, 6/93 & 6/94. Diagrams are separated between nighttime and daytime sampling periods and include: 1) frequency histograms of regression standardized residuals, 2) scatter plots of regression standardized residuals vs. predicted values, 3) normal P-P plots of expected vs observed cumulative probabilities of regression standardized residuals, & 4) time sequences of unstandardized residuals.

Appendix 2A.-Diagnostic summary of assumptions for multiple regressions on YOY.

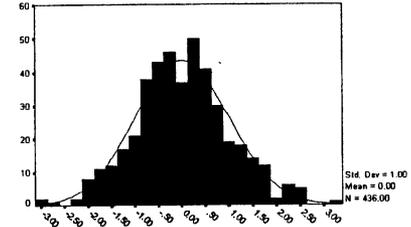
Overall, it appears that there were no major violations of the assumptions of normality, linearity, homoscedasticity, and independence for the three daytime (Table 7) and three nighttime (Table 8) YOY regressions. The assumption of independence is not relevant because regressions were conducted separately for each consecutive sampling trip. The histograms (Appendix 2B), scatter plots (Appendix 2C), and P-P plots (Appendix 2D) of the standardized residuals for each of these regressions do not reflect any major violations of normality, linearity, or homoscedasticity. Of these six regressions, only the nighttime analyses during July ($P=0.0150$) and August ($P=0.0044$) failed the Lilliefors modified K-S test (Table 8). Both of these regressions had high sample sizes, therefore making it difficult to pass any test of normality (SPSS 1995). The July regression just barely failed the Lilliefors modified K-S test and both the frequency histogram and normal P-P plot for this regression appear quite normal. The nighttime histogram from August was the least normal appearing regression of the group, but it still contains the basic shape of normality. In support, the residuals in the normal P-P plot for August resided closely to the line.

Frequency Histograms Nighttime

July 1993

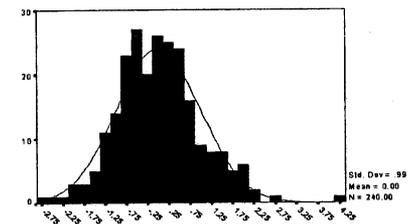
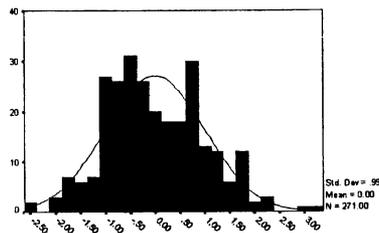


Daytime

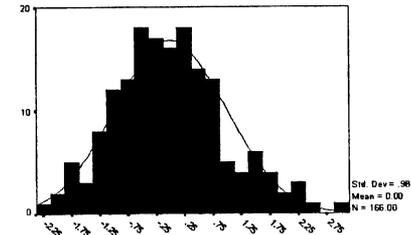
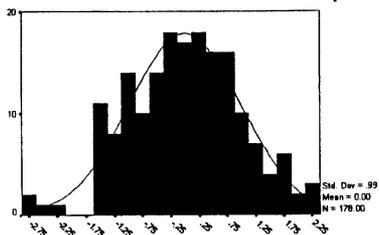


August 1993

Frequency



September 1993



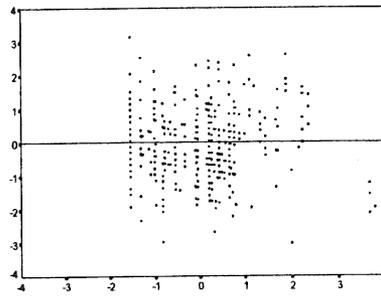
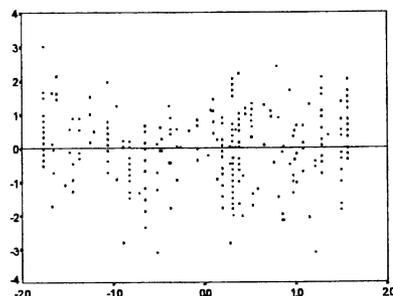
Regression Standardized Residuals

Appendix 2B. Frequency histogram diagnostics from multiple regressions of YOY HBC captured at both the Powell and Salt Canyon Study Reaches in the Little Colorado River. Figures are separated between nighttime and daytime sampling periods for each of the 7/93, 8/93 & 9/93 research trips. Axes represent frequency vs the standardized residuals of total fish lengths (mm).

Scatterplots
Nighttime

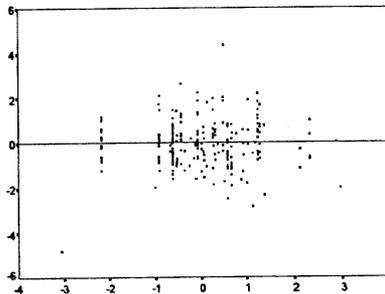
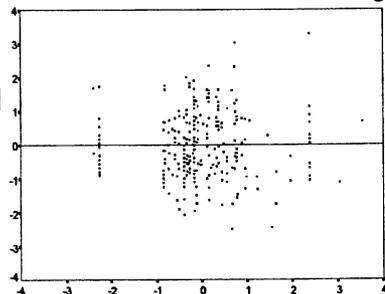
Daytime

July 1993

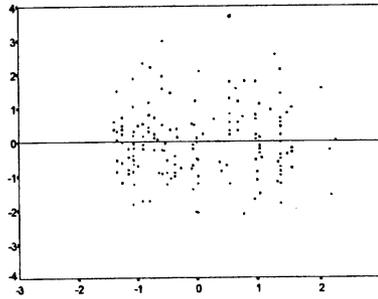
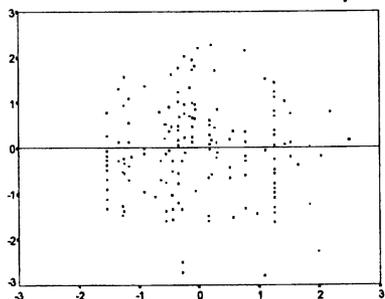


August 1993

**Regression
Standardized
Residuals**



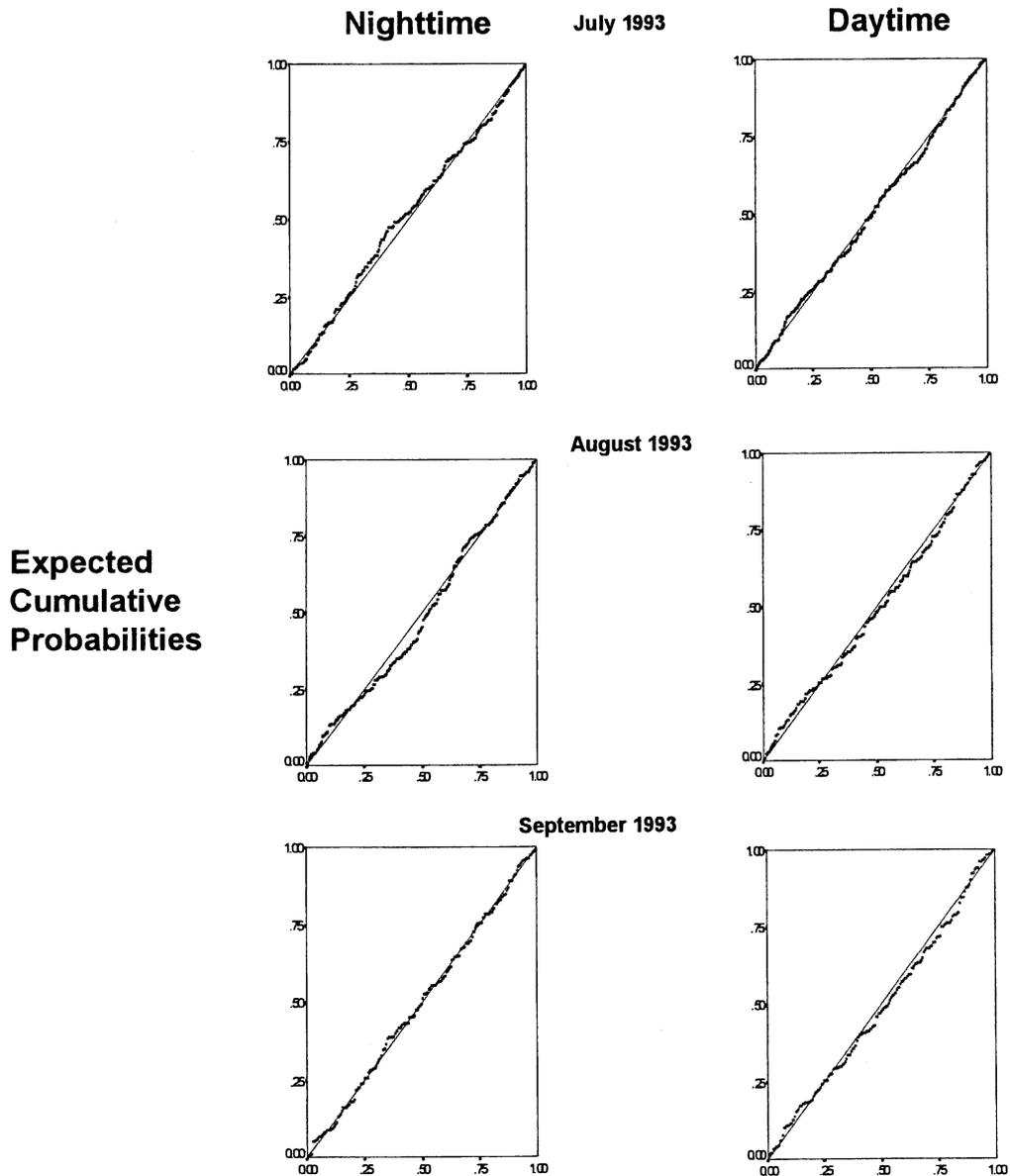
September 1993



Regression Standardized Predicted Values

Appendix 2C. Scatterplot diagnostics from multiple regressions of YOY HBC captured at both the Powell and Salt Canyon Study Reaches in the Little Colorado River. Figures are separated between nighttime and daytime sampling periods for each of the 7/93, 8/93 & 9/93 research trips. Axes represent the regression vs. predicted standardized residuals of total fish lengths (mm).

Normal P-P Plots of Regression Standardized Residuals



Observed Cumulative Probabilities

Appendix 2D. Normal P-P plot diagnostics from multiple regressions of YOY HBC captured at both the Powell and Salt Canyon Study Reaches in the Little Colorado River. Figures are separated between nighttime and daytime sampling periods for each of the 7/93, 8/93 & 9/93 research trips. Axes represent the expected vs. observed cumulative probabilities of the regression standardized residuals of total fish lengths (mm).

CHAPTER 4

Diel Shifts in Habitat Use by Speckled Dace and Three Different Size Classes of Humpback Chub in the Little Colorado River, AZ: Evidence of Predator-Prey Interactions?

Abstract.—Our investigations, conducted in the lower 14 km of Little Colorado River (1992-1995), showed that piscivory by adult humpback chub (*Gila cypha*; ≥ 180 mm TL) may be more than incidental, and in fact may structure the life history traits of smaller fish in that system. Although this was a habitat and not a dietary study, we observed six cases of chubs between 166-280 mm TL either regurgitating whole fish or defecating fish scales and bones while being lightly handled. In addition we found day/night shifts in habitat use that were consistent with predator-prey interactions reported from other fish assemblages. During the night in clear water (< 30 NTU), adult *G. cypha* shifted from relatively deep channels to shallow nearshore habitats. Young-of-the-year *G. cypha* (YOY; ≤ 90 mm TL) stayed near shore but shifted from exposed sandy areas to edge habitats with greater cover, characterized by high angular structure and heterogenous bottoms of boulders and cobble. In contrast to YOY, both juvenile *G. cypha* (110-160 mm) and speckled dace (*Rhinichthys osculus*) shifted away from shorelines to more midchannel habitats. During the night in turbid water (≥ 30 NTU), adult *G. cypha* were again inshore

and *R. osculus* offshore, but the juvenile chubs occupied nearshore habitats with YOY *G. cypha*. The inshore shifts at night of adult chubs may reflect a predator search behavior, while potential prey seem to be shifting either away from adults or to cover. Also at night in turbid water, YOY and juvenile chubs, and *R. osculus* showed similar shifts away from areas containing high angular structure, variable current velocities, and gravel deposition. Because these habitats contained significantly higher densities of ripe adults, especially during crepuscular or nighttime periods, these shifts may reflect an avoidance of adult chub spawning aggregations. Other evidence supporting high adult *G. cypha* piscivory includes: 1) opposing diel activity patterns between adult chubs and smaller fish, 2) mortalities of small fish, many which appeared partially digested, in nets which often contained adult chubs, and 3) declines in the densities of small fish during Spring sampling periods (1993-1995) when densities of adult *G. cypha* were greatest. Furthermore, our analyses suggests that piscivory by adult chubs is highest during the night in clear water, but may occur throughout the diel cycle in turbid water.

Key Words: Cyprinidae; *Gila cypha*; *Rhinichthys osculus*; piscivory; ecology; habitat; endangered species; Grand Canyon; Little Colorado River; Arizona

INTRODUCTION

In 1967, only 21 years after Miller (1946) described humpback chub (*Gila cypha*) as a species, *G. cypha* were listed as endangered (Federal Register 32:4001) by the U.S. Fish and Wildlife Service (USFWS). This listing prompted surveys and studies of *G. cypha* in both the upper and lower Colorado River basins. The largest *G. cypha* population exists in the Colorado River within Grand Canyon National Park and lower 14 km of the Little Colorado River (LCR) (Valdez and Ryel 1995; USFWS 1990).

The LCR is very different from the Colorado River in respect to discharge, water chemistry, and the biotic components (Cole and Kubly 1976). Unlike the Colorado River, the LCR contains no major dams controlling discharge, modifying the water temperature, and sediment load. High turbidities during elevated flows reduce photosynthesis in this system. During baseflow and high water clarity periods, rapid travertine deposition encrusts plants and invertebrates. The LCR's annual macroinvertebrate biomass is usually much lower than the mainstem Colorado River within Grand Canyon National Park (Dean Blinn, Northern Arizona University, pers.comm.; Larry Stevens, US Bureau of Reclamation, pers.comm.) and among the lowest of its tributaries (Oberlin et al. 1999).

Within the LCR, the number of invertebrate taxa, the total invertebrate biomass, and Chlorophyll a biomass were significantly lower downstream, than upstream of Chute Falls, a travertine dam located 14.2 km upstream from the mouth (Robinson et al. 1996). This difference may have resulted from greater foraging pressure generated by a larger fish biomass below the dam. Whereas only speckled dace (*Rhinichthys osculus*) and a few nonnative fish are resident above Chute Falls, the ichthyofauna below Chute includes all lifestages of native *G. cypha*, *R. osculus*, bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*C. latipinnis*), along with other nonnative fish species (Kaeding and Zimmerman 1983; Mattes 1993; Minckley 1996; Gorman and Stone 1999). In addition, the Spring spawning migrations of large adult *G. cypha* up the LCR from the Colorado River must put substantial pressure on this already limited food base (Gorman and Stone 1999).

Gila cypha are considered food generalists consuming such diverse foods as terrestrial and aquatic invertebrates, snails, filamentous algae, seeds (Valdez and Ryel 1995; Kaeding and Zimmerman 1983; Kubly 1990), lizards (Valdez and Hoffnagle 1999), and *Centroides* scorpions (Dennis Stone pers. obs.). They also eat a variety of discarded human foods; Minckley (1996) reported that they voraciously attacked his prepared sandwich spread, while we have observed them consuming assorted pasta, cheeses, and meats.

Valdez and Hoffnagle (1999) suggested that their food consumption is dictated by what is most available.

Because the diet of *G. cypha* is mostly constrained by availability and the LCR food reserves is considered relatively poor, we questioned what *G. cypha* were primarily eating in this system. Piscivory is not uncommon for large, long-lived stream cyprinids, such as the eastern creek chub (*Semotilus atromaculatus*; Fraser and Cerri 1982; Magnan and FitzGerald 1984), and species of squawfish (*Ptychocheilus lucius*, Vanicek and Kramer 1969; *P. oregonensis*, Thompson 1959; *P. grandis*, Vondracek 1987). In addition, Starrett (1950) found higher levels of piscivory by the river shiner (*Notropis blennioides*), northern common shiner (*N. cornutus*) and eastern creek chub when aquatic nymphs and larvae decrease. In the LCR, small fishes are common, however only two previous studies mentioned any evidence of piscivory by *G. cypha*. Kaeding and Zimmerman (1983) found fish in 2 of 44 (4.5%) *G. cypha* digestive tracts collected from the confluence of the LCR and Colorado Rivers. Kubly (1990) reported 1 of 17 (6%) digestive tracts from adult *G. cypha* (248-494 mm TL) collected at the mouth of the LCR contained fish remains. Currently, fish are not considered a major component of the *G. cypha* diet and were not mentioned in the latest Humpback Chub Recovery Plan (USFWS 1990).

To investigate the possibility that fishes contribute significantly to the diet of adult *G. cypha* in the LCR, we

examined habitat use patterns, diel activity, fish mortalities, and captures rates between adult *G. cypha* and potential prey. If adult *G. cypha* are in fact highly piscivorous, then they may structure the life history traits of potential prey throughout the system.

METHODS

Study areas.-The ~573 km long LCR drains a 69,870 km² river basin encompassing much of northern Arizona and part of northwestern New Mexico (Johnson 1975). This system often floods following Spring thaws (March and April) and after Summer rains (August and September). During periods of no runoff, baseflow between 6.14 to 6.57 m³/sec is maintained in the terminal 21 km by perennial springs (Johnson and Sanderson 1968). At baseflow, travertine deposition occurs within this highly bicarbonated system which produces an assortment of features including sluices, terraces, cascades, and dams. The bulk of the travertine deposition occurs between 12 and 16 km upriver of the confluence (Cooley 1976). Also during baseflow, heavy precipitation of unconsolidated CaCO₃ (marl) in much of the lower portion of the river is common. The travertine dam "Chute Fall" restricts the natives *G. cypha*, *C. discobolus* and *C.*

latipinnis to the lower ~14.2 km of the LCR (Kaeding and Zimmerman 1983; Mattes 1993; Minckley 1996).

Two separate study reaches, each of which were divided into two 500 m. study sites, were established in the LCR below Chute Falls (Figure 1). The Powell Canyon reach was located approximately 2.3-3.8 km upstream of the confluence with the Colorado River (36°11'45"N, 111°46'0"W) and the Salt Canyon reach was located further upriver at approximately 10.5-11.9 km (36°10'42"N, 111°42'16"W). These combined sampling reaches constituted 14% of the LCR corridor occupied by *G. cypha*. Because of greater travertine deposition in upriver locations (Cooley 1976), the Salt reach contained a greater abundance of large travertine dams, deeper pools, and a broader array of habitat types than the Powell reach. These study reaches were sampled concurrently in 11 of 14 field trips between 1992-1995, in 3 field trips only the Salt reach was sampled (See table 1).

Fish sampling.-Cross-channel transects were established at 20 m intervals throughout the study reaches. In each study reach, the 500 m sites were sampled alternately between field trips. Transects were systematically staggered (eg., fish two, skip one etc.) to cover each site in 10 days; transects that were not selected initially were sampled in subsequent field trips. Ropes were tied to opposite stream banks at the transect locations to be sampled. Miniature

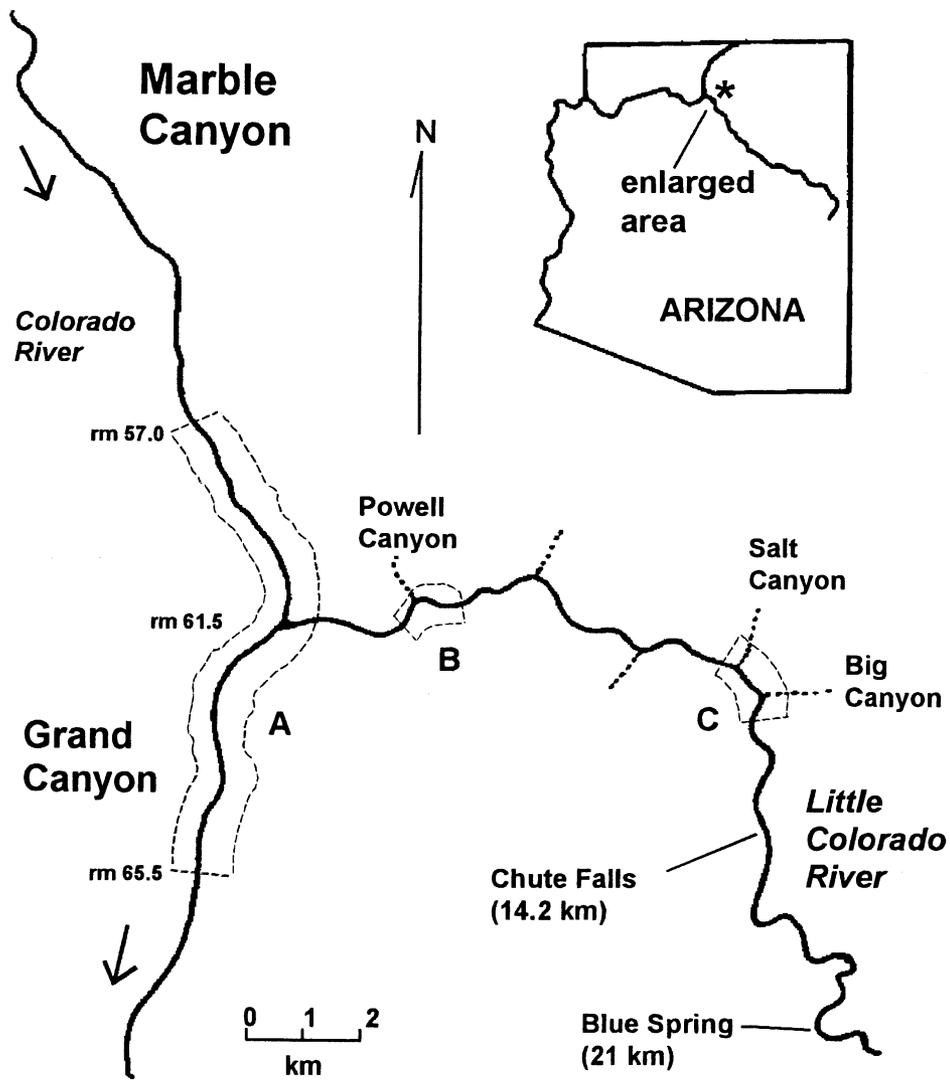


Figure 1. Map of the lower Little Colorado River (LCR) from Blue Spring to the confluence with the Colorado River (CR), Coconino County, Arizona. The perennial flows in this lower portion of the LCR are maintained by Blue Spring. Powell Canyon study reach (A) was located ~2.3-3.8 km upstream of the confluence with the CR and Salt Canyon study reach (B) was located further upriver at ~10.5-11.9 km. In the majority of ~10 day duration research trips, both study reaches were worked simultaneously. *Gila cypha*, *Catostomus discobolus* and *C. latipinnis* were restricted to below the travertine dam, Chute Falls. The CR reach between 57-65.5 river miles (rm) downstream from Lees Ferry contains many adult *G. cypha* that migrate up the LCR during the spring to spawn (see Valdez and Ryel 1995).

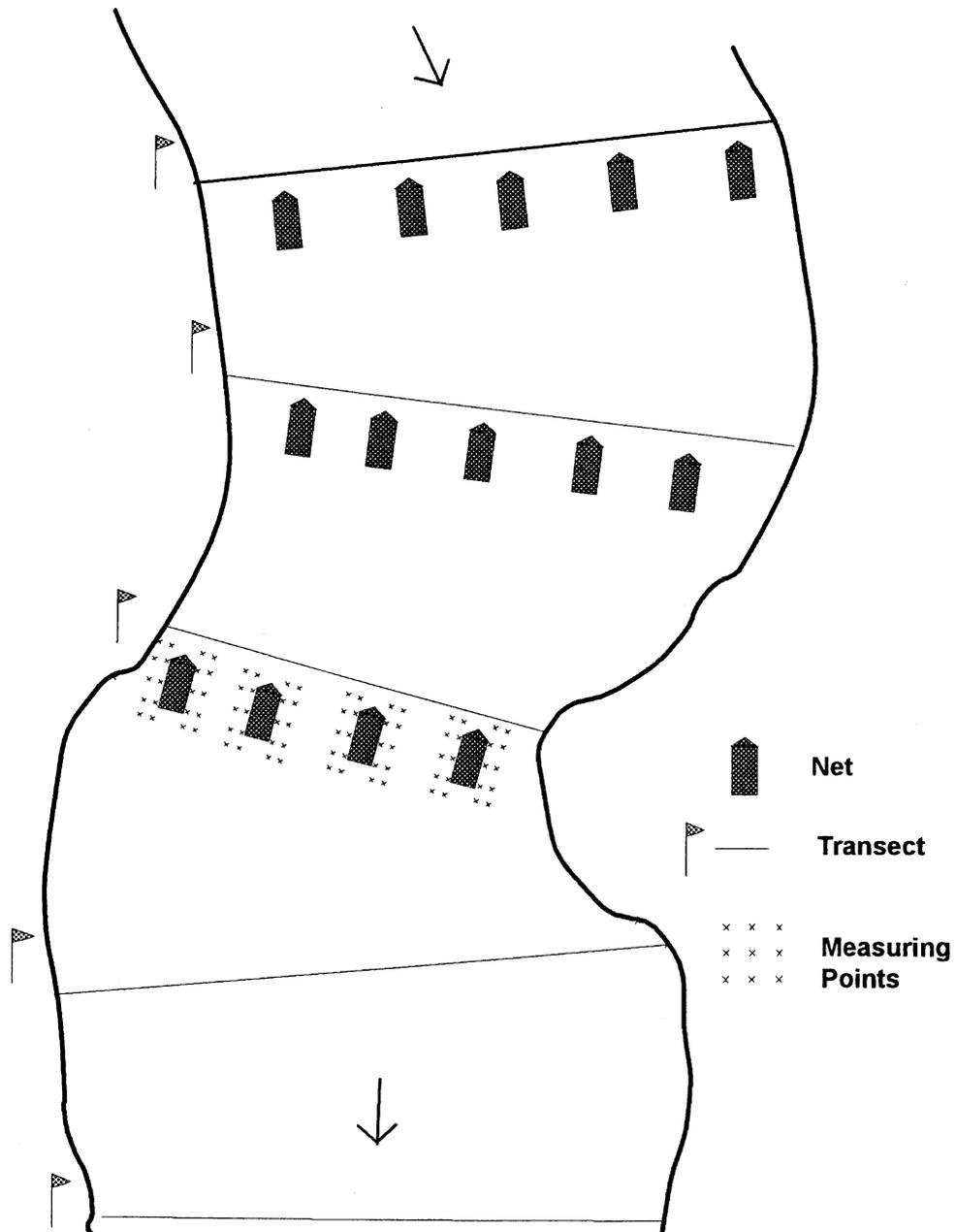


Figure 2. Fish sampling grid used in the Little Colorado River, Arizona from 1991-1995. Cross-channel transects were spaced 20 m apart. Transects selected for fish sampling were staggered to cover each 500 m study site in 10 days. Miniature hoopnets (Net) were fastened at 3-4 m intervals along ropes located at the selected transects. Habitat measurements were made at 20 points located over a 1.5 X 2.0 meter grid around each net.

hoopnets (net; 50 cm diameter X 100 cm length, 10 cm throat, 6 mm nylon mesh) were fastened to transect ropes at 3-4 m lateral intervals (Figure 2). These nets were set to sample day and night over a 24h period and then relocated to the next upstream transect.

To assess differences of fish habitat use within the diel cycle, nets were checked during daylight within two hours of sunset and sunrise. All fish captured were identified to species, measured to total length (TL; mm), weighed to nearest gram, and when possible, sexed. The physical condition of each fish was noted including scars, parasites, abrasions, and reproductive condition.

Gila cypha were separated into three different size classes for analyses. Kaeding and Zimmerman (1983) found that *G. cypha* in the LCR grew to ~100 mm TL in the first year, an approximation that was consistent with our findings. Therefore, fish ≤ 90 mm were classified as young-of-the-year (YOY), although some may have been yearlings. *Gila cypha* ≥ 180 mm were unlikely to be cannibalized (see L'Abée-Lund et al. 1992) and exhibited nocturnal activity patterns similar to larger adults (Chapter 2). In addition, males of ~180 mm in length occasionally mature sexually (USFWS unpub. data.). Therefore, *G. cypha* ≥ 180 mm were classified as adults. To avoid overlap in size related behavior, the intermediate size class was separated from YOY and adults by 20 mm (110-160 mm); these were classified as

juveniles. Because *R. osculus* are short lived (~1-2 years) and must quickly develop, we included all dace into a single size class for analyses.

Habitat measurements.-Habitat measurements were conducted at 20 points, each spaced 50 cm from their adjacent points, located over a 1.5 X 2.0 m grid (50 cm spacing) around each net (Figure 2; Gorman and Stone 1999). Depth, current velocity, and substrate were measured at these points using the method of Gorman and Karr (1978). The measuring pole consisted of 1.9 cm diameter PVC pipe of various lengths and marked at 5 cm increments. The pole was placed at each point and habitat variables were measured. Later, net statistics were calculated for each habitat variable using data collected from the 20 sampling point grid.

Point measurements for depths were analyzed as mean depth (cm) per net set (MDPH). Standard deviation of depths (cm; SDDPH) per net provided a measure of bottom profile heterogeneity for each net set, sensu Gore (1978). The angle from each point to the next highest point, located adjacent to it on the grid or to an emergent edge located <100 cm away, were calculated and summarized as mean positive vertical angles (MPVA; Gorman and Stone 1999). In this manner MPVA could use information from points not confined to the net grid and provided a measure of the angular variation associated with bottom contours underlying each net set.

Current meters were only indirectly used because they were time consuming, difficult to use in deep habitats, and were subject to malfunction. Instead, current velocity was categorized by observing how the water flowed around the pole. There were six major current velocity categories (0-5), each of which, except zero, could be further subdivided with a plus or minus, yielding 16 separate categories. These current velocity categories were later translated to numeric values (m/s) by comparison with readings taken from a Marsh-McBirney (Model 201) portable water flow meter. Mean current velocity (MCURV) and standard deviation of current velocities (SDCURV;) were calculated from the 20 sample points surrounding each net; SDCURV measures the variability of current flows, MCURV is self explanatory. Points where the direction of flow was upstream were recorded as eddy currents. Eddy frequency (FEDDY) was expressed as the number of eddy points per net.

Substrate was categorized for each of the 20 net sample points as fines (≤ 0.10 mm) which contained predominately silt but also fine precipitate of CaCO_3 (marl); sand (0.11-2.0 mm); gravel and small rocks (2.1-100mm); cobble (101-256mm); and boulders (>256 mm). Substrate frequencies (FFINES, FGRAVL, FCOBBL, FBOULD) for each net represented the number of times each substrate category occurred over the 20 sample point grid.

Mean lateral position (MLATP) for each net was calculated as the mean distance (cm) of the 20 sample points to the nearest emergent edge (boulder, shoreline, travertine dam, sand bar). Lateral distance (LATDS) was the distance (cm) from the center of the net sample grid to the nearest shoreline. MLATP and LATDS were viewed as separate variables because the LCR contained many large boulders and travertine dams in the midsection of the river.

The 12 habitat variables described above were calculated for 2,723 net sets. Habitat associations of 4,994 *R. osculus* and 10,299 *G. cypha* were generated by linking each individual fish to the corresponding net from which it was captured (Table 1).

Data analyses.-Turbidities above and below 30 nephelometric turbidity units (NTUs) have been found to alter *G. cypha* diel activity patterns (Valdez and Ryel 1995; Chapter 2) and nearshore occupancy by *R. osculus* and *G. cypha* (Valdez and Ryle 1995; Chapter 3). Therefore, data collected in different sampling trips were divided between those where median water turbidities were <30 NTUs (clear water) and ≥30 NTUs (turbid water; Table 1). During each sampling trip, except during June 1992, turbidity was measured with a Hach Model 16800 or Model 2100P turbidimeter. The June 1992 trip was grouped with clear water conditions based on observations in trip reports and photographs. Because we were unable to set a full complement of nets during floods,

data from trips with discharges $>19 \text{ m}^3/\text{s}$ were omitted from the analyses. Total fishing effort was 1,534 clear water net sets over 61 days and 1,189 turbid water net sets over 50 days (Table 1).

Table 1. Sampling trips used in the Wilcoxon-Mann-Whitney tests (WMW) and Tests of Association. Included for each sampling trip are dates of fish sampling (FDATES), study reaches sampled (RCH; B=both, S=Salt only), median turbidity in nephelometric turbidity units (NTU), # nets deployed, and numbers of *Gila cypha* young-of-the-year (YOY; $\leq 90 \text{ mm}$), juvenile (JUV; 110-160 mm) and adults ($\geq 180 \text{ mm}$), and *Rhinichthys osculus* (DACE) captured. Totals of nets and fish used in clear and turbid water condition analyses are given.

FDATES	RCH	NTU	# nets	DACE	<i>Gila cypha</i>		
					YOY	JUV	ADULT
6/15-23/92	B	-	172	354	87	127	75
5/10-18/93	B	17	178	202	0	79	98
6/8-14/93	B	3	222	483	84	58	54
7/12-19/93	B	4	230	759	2048	16	74
8/9-16/93	B	5	256	1248	3818	21	62
11/4-7/93	S	7	46	98	189	1	14
6/6-13/94	B	3	203	430	385	147	73
8/9-16/94	B	13	227	507	945	109	35
CLEAR WATER TOTAL			1534	4081	7556	558	485
4/12-20/93	B	1888	183	62	0	9	47
9/10-15/93	B	967	157	50	343	4	35
4/12-20/94	B	180	219	276	243	50	85
5/10-18/94	B	379	254	101	114	86	136
4/11-19/95	S	37	191	304	111	107	107
5/8-15/95	S	129	185	120	30	107	86
TURBID WATER TOTAL			1189	913	841	363	496

Diel movements. -Diel shifts in habitat use by adult, juvenile and YOY *G. cypha*, and *R. osculus* were detected by comparing habitat use between day and night sampling periods. Analyses were conducted separately for clear and turbid water conditions. Data from sampling trips and study sites that occurred in similar water clarities were grouped to increase sample size. Grouping data was justified because previous analyses showed concordant habitat use patterns by different *G. cypha* size classes from data collected during different sampling trips and river reaches when water clarity and sampling periods were similar (Chapter 3). Nighttime shifts in habitat use were described relative to daytime use. Because of nonnormal data distributions the nonparametric Wilcoxon-Mann-Whitney test (WMW) was used to detect significant shifts in habitat use. Tests were conducted using SPSS version 6.1.2 (1995) and only those comparisons with $P < 0.1$ were considered significantly different.

Fish-habitat associations. -Tests of association were conducted to provide additional insight of fish-habitat relationships. Because nets were deployed ~10 h during the day and ~14 h during the night, associations were effectively testing the use of similar habitats by different fish categories. Although these tests may reflect inter- and intraspecific associations to a degree, this was considered too speculative for consideration.

We followed the methods of Ludwig and Reynolds (1988) in conducting tests of association. Associations were tested separately between adult *G. cypha* and each of the two smaller *G. cypha* size classes (YOY, juvenile) and *R. osculus* for day and night periods in both clear and turbid water conditions. Nets were treated as independent sampling units. Occupancy of nets by each *G. cypha* size class (YOY, juveniles, adults) and *R. osculus* was binary coded as a one for presence and zero for absence. There are four possible outcomes for each paired comparison of net captures. For example, in a paired comparison of adult *G. cypha* and *R. osculus*, each net may contain: a) adult(s) but no *R. osculus*, b) no adult(s) but *R. osculus*, c) both adult(s) and *R. osculus*, or d) neither fish. The resulting paired comparisons for adult *G. cypha* and *R. osculus* from all nets were summed in a 2X2 contingency table and significant associations were identified with a Chi square test of independence, using one degree of freedom and significance levels from Rohlf and Sokal (1981). Associations were also tested for juvenile *G. cypha* against YOY chubs and *R. osculus*. In addition, Ochiai, Dice and Jaccard indices were calculated for each separate test of association to provide a measure of association between fish groups (Ludwig and Reynolds 1988); these indices range from zero (no association) to one (maximum association). All three

indices were presented because the preferred index differs among researchers.

Associations with small fish mortalities.-Small fish were occasionally found dead in nets; many of which appeared to be partially digested. Elevated mortalities of small fish during a particular sampling period may be associated with periods of elevated predator activities. The numbers and percent of small fish mortalities were tabulated for the day and night sampling periods in both clear and turbid water conditions. To examine possible associations between small fish mortalities and adult *G. cypha*, the percentage of small fish mortalities found with an adult *G. cypha* also present were determined for each sampling period in each water clarity condition. For comparison, the percentage of small live fish (YOY *G. cypha* or *R. osculus*) captured with an adult *G. cypha* present were calculated as above.

If the ratios of small fish mortalities from different species do not correspond to the ratio of live fish (≤ 90 mm TL) from different species captured during this study, this may suggest higher predation on a particular species.

Mortalities for each fish species were summed separately in both clear and turbid water conditions and the percentage of each species found dead during the nighttime was calculated.

Captures during the Spring *G. cypha* spawning periods.-We examined the capture data from Spring sampling trips over three years (1993-1995) to investigate if a noticeable

reduction in smaller fish (YOY and juvenile *G. cypha*, and *R. osculus*) was apparent when adult chubs were most plentiful in the LCR. Sampling trips in 1993 included two short trips in March and one longer trip in April; data from May were not used because of the appearance of new YOY fish. The months of April and May were used for both 1994 and 1995. These Spring sampling trips occurred after flooding had receded so consecutive sampling trips all contained stable flows in turbid water conditions. Catch-per-unit-effort (CPUE) was calculated for each sampling trip by dividing the numbers of fish captured for each of YOY, juvenile, and adult *G. cypha*, and *R. osculus* by the numbers of nets deployed.

RESULTS

Diel habitat shifts in clear water.-During nighttime in clear water, adults and YOY *G. cypha* were often captured in close proximity to each other within nearshore habitats (Table 2). Adult *G. cypha* shifted inshore from deeper, midchannel habitats at night, while YOY *G. cypha* remained near shorelines throughout the diel cycle. Also during the night, both adults and YOY shifted closer to emergent edges, to areas of more heterogeneous bottoms with high angular

structure containing less sand and more boulder substrates. Because adults were shifting from midchannel habitats toward shore, while YOY were moving within nearshore habitats, the contrasting habitat shifts between these two size classes with respect to depth, current velocity and cobble substrates may have resulted in both size classes occupying the same general vicinity. YOY also showed a significant shift to areas containing more eddies during the night.

In contrast to adult and YOY *G. cypha*, both juvenile *G. cypha* and *R. osculus* shifted significantly further away from shorelines and emergent edges at night (Table 2). The juveniles shifted to areas of more homogeneous bottom types containing less cobble, less variable current velocities, but more eddies. At night, *R. osculus* were associated with greater depths and channel bottoms that were more heterogeneous, but less angular than during the day. These areas contained significantly less gravel and boulder substrates.

Table 2. Wilcoxon-Mann-Whitney test results for diel shifts in habitat use by *Rhinichthys osculus* and three different size classes of *Gila cypha* within selected habitat variables in clear water conditions (<30 NTUs) in the Little Colorado River. Habitat variables are defined in the Methods. All results are from daytime to nighttime perspective and significant shifts (P<0.1) are highlighted.

	ADULT <i>G. cypha</i> ≥180 mm	JUV <i>G. cypha</i> 110-160 mm	YOY <i>G. cypha</i> ≤90 mm	<i>R. osculus</i>
SAMPLE SIZE	485	558	7556	4081
LATDS	CLOSER 0.00145	FARTHER 0.0195	CLOSER-NS 0.15075	FARTHER 0.00065
MLATP	CLOSER 0.00245	FARTHER 0.0272	CLOSER 0.0034	FARTHER <0.0000
MDPH	SHALLOWER 0.0206	DEEPER-NS 0.3825	DEEPER <0.0000	DEEPER <0.0000
SDDPH	GREATER 0.0483	LESS 0.0234	GREATER 0.00015	GREATER 0.0637
MPVA	GREATER 0.06305	LESS 0.0083	GREATER 0.00625	LESS 0.00505
MCURV	SLOWER 0.00185	FASTER-NS 0.49675	FASTER 0.0257	FASTER-NS 0.23815
SDCURV	LESS 0.01655	LESS 0.00605	LESS-NS 0.23155	LESS-NS 0.22745
FEDDY	MORE-NS 0.4737	MORE 0.0127	MORE <0.0000	LESS-NS 0.1302
FFINES	MORE 0.00005	MORE-NS 0.1705	LESS-NS 0.43165	LESS-NS 0.3234
FSAND	LESS 0.0198	LESS-NS 0.14855	LESS 0.00535	MORE-NS 0.1490
FGRAVL	MORE-NS 0.4757	LESS-NS 0.4688	MORE-NS 0.38525	LESS 0.02935
FCOBBL	LESS 0.01815	LESS 0.05325	MORE <0.0000	MORE-NS 0.3003
FBOULD	MORE 0.0469	MORE-NS 0.4989	MORE 0.00765	LESS 0.04215

Diel habitat shifts in turbid water.-Diel habitat shifts by adult *G. cypha* were similar between clear (Table 2) and turbid water conditions (Table 3). At night in both water clarities, adults shifted closer to shorelines and emergent edges, into areas of shallower depths and slower current velocities, with channel bottoms containing higher mean positive vertical angles. The overall diel shifts in habitat use were more distinctive in clear than turbid water conditions. For example, the diel shifts expressed by eight habitat parameters resulted in higher significance in clear than turbid water conditions, whereas only two habitat parameters resulted in higher significance in turbid water. The main contrast of nighttime habitat shifts by adults between the two water clarities was that adults were associated with less cobble in clear water (Table 2), but more cobble in turbid water (Table 3).

The nighttime habitat shifts by YOY *G. cypha* differed between turbid (Table 3) and clear water conditions (Table 2). During nighttime in turbid water, YOY shifted further away from structure, into areas of slower, less variable current velocities. These habitats contained highly homogeneous channel bottoms, as shown by the reductions of mean positive vertical angle and standard deviation of depth, decreased frequency of cobble and increase of sandy bottoms.

In contrast to nighttime shifts in clear water (Table 2), juvenile *G. cypha* did not move further midchannel at night in turbid water (Table 3). During the night in turbid water, juvenile *G. cypha* moved into areas of shallower depth, with slower, less variable current velocities. These areas contained homogeneous bottoms with significantly less gravel and boulder substrates, and more sand. Reductions in mean positive vertical angle and standard deviation of current velocity were the only significant nighttime habitat shifts that occurred in both turbid and clear water conditions. These nighttime shifts in turbid water more closely resembled those of YOY in respect to shifts to slower, less variable current velocities, and more homogeneous bottoms containing more sand and less gravel substrates.

Diel shifts in habitat by *R. osculus* in turbid water (Table 3) were very similar to those in clear water (Table 2). During nighttime of both water clarities, they were found significantly further from shorelines and emergent edges, and in areas of reduced mean positive vertical angles and less gravel. During nighttime in turbid water they shifted to areas containing less variable current velocities. Although many habitat parameters were nonsignificant in both clear and turbid water analyses, *R. osculus* habitat shifts followed the same directional pattern in 11 out of 13 habitat parameters (Tables 2&3).

Because the majority of the turbid water data were collected during the adult *G. cypha* Spring spawning period, we conducted additional Wilcoxon-Mann-Whitney (WMW) tests solely on habitat differences between reproductive (n=138; freely expressing gametes, high tuberculation etc.) and non-reproductive adults (n=358), irrespective of sampling period. Compared to non-reproductive adults, reproductive adults were captured significantly ($P < 0.100$) closer to shoreline and emergent edges, in areas of greater current velocities, and more heterogeneous and angular bottoms that contained less fines and sand, but more gravel, cobble and boulders. Although both reproductive and nonreproductive adults demonstrate nocturnal inshore movements, they often occupied different habitats. The nighttime shifts of YOY and juvenile *G. cypha*, and *R. osculus* to areas of less angular structure, lower current variability, and less gravel, contrasted those of reproductive adults.

To examine how reproductive fish effected our original turbid water WMW test results for adults (Table 3), we conducted WMW tests that excluded adult *G. cypha* in reproductive condition. These analyses resulted in similar diel habitat shifts of non-reproductive adults (n=358, statistics not shown) as shown in Table 3, with the exception that MPVA was nonsignificant.

Table 3. Wilcoxon-Mann-Whitney test results for diel shifts in habitat use by *Rhinichthys osculus* and three different size classes of *Gila cypha* within selected habitat variables in turbid water conditions (≥ 30 NTUs) in the Little Colorado River. Habitat variables are defined in the Methods. All results are from daytime to nighttime perspective and significant shifts ($P < 0.1$) are highlighted.

	ADULT <i>G. cypha</i> ≥ 180 mm	JUV <i>G. cypha</i> 110-160 mm	YOY <i>G. cypha</i> (≤ 90 mm)	<i>R. osculus</i>
SAMPLE SIZE	496	363	841	913
LATDS	CLOSER 0.01395	CLOSER-NS 0.31055	FARTHER-NS 0.10065	FARTHER 0.0009
MLATP	CLOSER 0.00345	FARTHER-NS 0.3484	FARTHER 0.03415	FARTHER 0.0001
MDPH	SHALLOWER 0.0115	SHALLOWER 0.08905	DEEPER-NS 0.2721	DEEPER-NS 0.13005
SDDPH	GREATER-NS 0.1401	LESS-NS 0.3868	LESS 0.06705	LESS-NS 0.1513
MPVA	GREATER 0.0428	LESS 0.06455	LESS 0.0935	LESS <0.0000
MCURV	SLOWER 0.00925	SLOWER 0.08925	SLOWER 0.0691	FASTER-NS 0.1660
SDCURV	LESS-NS 0.3130	LESS 0.06985	LESS <0.0000	LESS 0.0142
FEDDY	MORE-NS 0.17835	MORE-NS 0.38505	MORE-NS 0.31355	LESS-NS 0.16255
FFINES	LESS-NS 0.1389	MORE-NS 0.17425	MORE-NS 0.20545	LESS-NS 0.35095
FSAND	LESS-NS 0.1131	MORE 0.06135	MORE 0.03985	MORE-NS 0.4457
FGRAVL	MORE-NS 0.1495	LESS 0.0269	LESS 0.0021	LESS 0.0001
FCOBBL	MORE 0.01805	MORE-NS 0.21185	LESS 0.0178	LESS-NS 0.42245
FBOULD	MORE-NS 0.4168	LESS 0.0602	LESS-NS 0.12445	LESS-NS 0.3958

Fish-habitat associations with adult *G. cypha*.-In clear water, adult *G. cypha* were significantly associated with habitats occupied by YOY chubs and *R. osculus* during the nighttime. The Ochiai, Dice and Jaccard indices showed a slightly higher nighttime association of adult *G. cypha* to habitats containing *R. osculus*, than YOY *G. cypha* (Table 4). However, none of these indices were very high, showing that although significant associations were found, there were also much separations between these fish categories. The greater nighttime association of adults with small fish is likely the result of nocturnal inshore habitat shifts by adults.

During the daytime in turbid water, adult *G. cypha* were significantly associated with habitats occupied by YOY chubs. Although the nighttime Chi square only bordered on significant habitat associations between adults and YOY ($\chi^2=2.587$ compared to 2.706 necessary for $P<0.1$), all three YOY association indices were higher during the night than the day. During the night in turbid water, *Rhinichthys osculus* associations were nonsignificant.

Table 4.-Associations between habitats occupied by adult *Gila cypha* and three smaller fish categories (YOY *G. cypha*, *Rhinichthys osculus*, juvenile *G. cypha*) in the Little Colorado River, AZ during 1992-1995. Tests were conducted through Chi Square Test of Independence using nets as independent sampling units with 1 DF. Measures of association included Ochiai (OI), Dice (DI) and Jaccard (JI) indices. Separate tests were conducted for the daytime and nighttime sampling periods of the clear (n=1,534 nets) and turbid (n=1,189 nets) water conditions. Note: All significant associations ($P < 0.1$) were positive.

	YOY <i>G. cypha</i>		<i>R. osculus</i>		JUV <i>G. cypha</i>	
	NIGHT	DAY	NIGHT	DAY	NIGHT	DAY
CLEAR						
X ² TS	11.181	0.0007	45.718	0.536	69.137	63.374
Prob	<0.001	NS (>0.99)	<0.001	NS (>0.1)	<0.001	<0.001
OI	0.279	0.122	0.358	0.147	0.320	0.250
DI	0.255	0.077	0.315	0.087	0.320	0.238
JI	0.146	0.040	0.187	0.046	0.190	0.135
TURBID						
X ² TS	2.587	4.756	0.347	0.033	27.662	12.754
Prob	NS (>0.1)	<0.05	NS (>0.5)	NS (>0.5)	<0.001	<0.001
OI	0.204	0.191	0.167	0.150	0.267	0.193
DI	0.204	0.182	0.167	0.141	0.258	0.193
JI	0.113	0.100	0.091	0.076	0.148	0.107

Fish-habitat associations with juvenile *G. cypha*.-Juvenile *G. cypha* were significantly associated with habitats occupied by adult chubs during all sampling periods in both water clarity conditions (Tables 4&5). In clear water, juveniles were significantly associated with *R. osculus* habitats during the nighttime and those occupied by YOY chubs during the daytime (Table 5). This likely was the

result of nighttime shifts of juveniles and *R. osculus* away from edge habitats. In turbid water, all fish categories showed a diel habitat association with juveniles.

Table 5.-Associations between habitats occupied by juvenile *Gila cypha* and three fish categories (YOY *G. cypha*, *Rhinichthys osculus*, adult *G. cypha*) in the Little Colorado River, AZ during 1992-1995. Tests were conducted through Chi Square Test of Independence using nets as independent sampling units with 1 DF. Measures of association included Ochiai (OI), Dice (DI) and Jaccard (JI) indices. Separate tests were conducted for the daytime and nighttime sampling periods of the clear (n=1,534 nets) and turbid (n=1,189 nets) water conditions. Note: All significant associations ($P < 0.1$) were positive.

	YOY <i>G. cypha</i>		<i>R. osculus</i>		Adult <i>G. cypha</i>	
	NIGHT	DAY	NIGHT	DAY	NIGHT	DAY
CLEAR						
X^2 TS	1.117	11.786	10.810	1.755	69.137	63.374
Prob	NS(>0.1)	<0.001	<0.005	NS(>0.1)	<0.001	<0.001
OI	0.232	0.236	0.290	0.207	0.320	0.250
DI	0.210	0.186	0.253	0.155	0.320	0.238
JI	0.117	0.103	0.145	0.084	0.190	0.135
TURBID						
X^2 TS	7.575	30.657	9.249	27.897	27.662	12.754
Prob	<0.01	<0.001	<0.005	<0.001	<0.001	<0.001
OI	0.197	0.273	0.216	0.274	0.267	0.193
DI	0.194	0.260	0.207	0.255	0.258	0.193
JI	0.107	0.150	0.115	0.146	0.148	0.107

Associations with small fish mortalities.-More than 70% of all fish mortalities were found during the nighttime sampling periods in either water clarity condition (Table 6). Overall, adults co-occurred with ~26% of these mortalities. Except for the nighttime in clear water, the percentages of small dead fish with an adult present were all higher than live fish with an adult present. Although analyses of Gee's standard minnow trap were not included in this paper, there were no fish mortalities found in 1,588 minnow trap sets, which captured 9,031 fish but excluded larger fish.

Table 6.-Numbers of small fish found dead-in-the-net during the different diel sampling periods of both river conditions. Percent of mortalities are the percent of dead fish found from the night vs. day sampling periods. Also given are the percent of mortalities found with an adult *Gila cypha* also present in the net at the time that it was run. For comparison, the percent of live small fish (YOY *G. cypha* & *Rhinichthys osculus*) with an adult *G. cypha* present are given.

Sampling period	Clear Water		Turbid Water	
	night	day	night	day
# morts	47	16	7	3
% of morts	74.6%	25.4%	70.0%	30.0%
% of morts with an adult <i>G. cypha</i> present	25.5%	18.8%	28.7%	66.0%
% of live small fish with an adult <i>G. cypha</i> present.	27.8%	3.6%	21.1%	15.1%

From 67 to 100% of small fish mortalities from all species were found dead after nighttime sampling periods (Table 7). YOY *G. cypha* were the most common fish found dead, followed by *R. osculus*, and young *C. discobolus* and *C. latipinnis*. Our data showed that the ratio of fish mortalities from different species (54% *G. cypha* : 40% *R. osculus*: 5% *C. discobolus* : 2% *C. latipinnis*), was roughly comparable to the ratio of live fish (≤ 90 mm) from different species captured during this study (60% *G. cypha*: 34% *R. osculus*: 5% *C. discobolus*: 1% *C. latipinnis*).

Table 7.-Numbers of small fish from each species that were found dead in the nets in clear and turbid water conditions. Also included are the percent of fish species that were found dead from nighttime sampling periods (XX% Night).

	Clear Water	Turbid Water
<i>G. cypha</i>	33 (73% Night)	6 (67% Night)
<i>R. osculus</i>	24 (75% Night)	4 (75% Night)
<i>C. discobolus</i>	3 (67% Night)	0
<i>C. latipinnis</i>	1 (100% Night)	0
SPP UNKNOWN	2 (100% Night)	0
TOTAL	63 (75% Night)	10 (70% Night)

In addition to small fish mortalities found in the nets, there were six observations of *G. cypha* either regurgitating whole fish or defecating partially digested fish while being handled (Table 8). The bodies of many of these *G. cypha* seemed abnormally swollen as if their digestive tracts were gorged with food. Because all fish were lightly handled and defecated materials were not normally inspected, this phenomenon may have been overlooked in other *G. cypha*.

Table 8: Summary of known piscivorous activities by *Gila cypha* at Salt Canyon reach, LCR, AZ. Total length (TL), weight (WGHT) and sex (S) are given for the predaceous *G. cypha*.

Date	TL	WGHT	S	Predation Account
7/17/93	279mm	155g	F	Regurgitated 47 mm TL <i>G. cypha</i> and was defecating large quantities of incompletely digested fish parts.
7/17/93	237mm	77g	?	Regurgitated a <i>R. osculus</i> and parts of at least two other fish; seemed to be full of other fish.
7/18/93	176mm	34g	?	Regurgitated a 48 mm TL <i>G. cypha</i> .
8/15/93	280mm	157g	F	Defecated many fish bones and scales.
11/7/93	187mm	38g	?	Defecated many fish bones and scales.
05/1/99	166mm	35g	?	Regurgitated a 64 mm SL <i>R. osculus</i> .

Captures during Spring *G. cypha* spawning periods.-The relationship between CPUE of YOY, juvenile, adult *G. cypha* and *R. osculus* among sequential sampling trips during three separate years were very similar (Figure 3). A pattern of decline in CPUE for small fish (YOY *G. cypha* and *R. osculus*) between early and late Spring sampling periods for three consecutive years was apparent (Figure 3). The absence of YOY during 1993 was the result of the decimation of the 1992 cohort by continuous flooding. The CPUE for juveniles was also lower between adjacent trips in 1993 & 1994, but slightly higher during 1995. In contrast, CPUE of adults was higher between adjacent trips during 1993 & 1994. The CPUE was slightly lower during May than April of 1995, possibly resulting from post-spawn migrations back to the mainstem Colorado River.

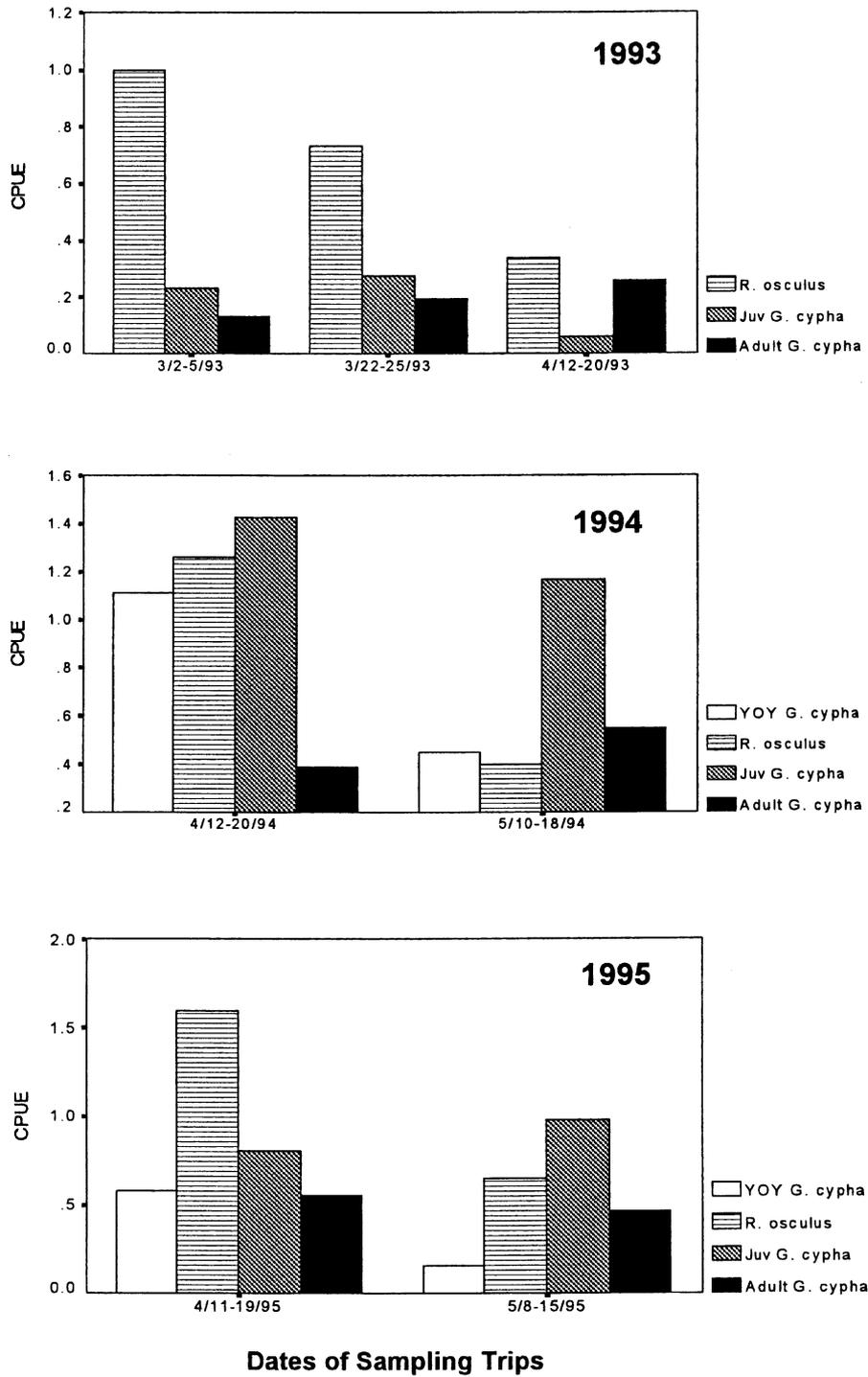


Figure 3. Catch per unit effort (CPUE) in miniature hoopnets of YOY, juvenile, and adult *Gila cypha* size classes and *Rhinichthys osculus* during spring *G. cypha* spawning periods in the Little Colorado River, Grand Canyon, AZ. Catch data were collected from both Powell and Salt study reaches during 1993 & 1994 and from Salt study reach during 1995.

DISCUSSION

Fish may constitute a substantial portion of the *G. cypha* diet, at least in the Little Colorado River. Because of the scarce documentation of piscivory by this species, two additional observations are given showing that adult *G. cypha* will instinctively prey on small fish. First, Roger Hamman (USFWS Dexter National Fish Hatchery and Technology Center pers. comm.) was responsible for 15 wild caught LCR *G. cypha* that were brought to Willow Beach National Fish Hatchery in 1978 for propagation purposes. Because the chubs refused to eat the hatchery's trout feed, feeding was attempted using 20-30 live rainbow trout (*Oncorhynchus mykiss*; <75 mm TL), these trout were consumed by the chubs in less than five minutes. Trout were subsequently given to the chubs as a daily dietary supplement for the next four years. Secondly, during the Summer of 1994 in the LCR, over a two day, Van Haverbeke (USFWS biologist, pers. comm.) witnessed adult *G. cypha* (300-400 mm) swim up from a 3-4 m deep pool and attempt to prey upon YOY chubs located near the surface. After each attack, whether successful or not, the adults returned to the shaded bottoms.

Adult *G. cypha* likely have a greater influence than nonnative piscine predators on the general life histories of small LCR fish. Marsh and Douglas (1997) listed *O. mykiss* and channel catfish (*Ictalurus punctatus*) as the most common

nonnative predatory fish species in the LCR. The high percentages of trout stomachs' containing algae (47%), primarily *Cladophora*, and *Gammarus lacustris* (12%), both of which are much more common in the mainstem Colorado River than LCR (Kubly 1990; Oberlin et al. 1999), suggest that the majority of these trout were collected near the mouth of the LCR. Apparently water chemistry and/or elevated temperatures must prohibit trout from establishing residency in the LCR because trout were seldom observed far above the mouth in either our or Kaeding and Zimmerman (1983) research projects. Although channel catfish are well established in the LCR, visual observations and catch records of these fish were infrequent in our study reaches, suggesting that their numbers must be substantially lower than the estimated *G. cypha* (>150 mm) population of 4,508-10,444 located within the terminal 14 km of the LCR (Douglas and Marsh 1996).

An analogous cyprinid to *G. cypha*, in respect to feeding ecology and life history traits, is the predaceous eastern creek chub (*Semotilus atromaculatus*). Both *G. cypha* and *S. atromaculatus* grow to relatively large sizes. The largest *G. cypha* captured in this study was 445 mm TL and *S. atromaculatus* is known to reach >302 mm TL (Trautman 1981). Sexual maturity occurs in the third and fourth year for both species (Kaeding and Zimmerman 1983; Gorman and Stone 1999; Etnier and Starnes 1993). Both species are tolerant to high turbidities (Gradall and Swenson 1982) and are relatively

long-lived; the life span of *G. cypha* is >20 years (Hendrickson 1977), while *S. atromaculatus* live ~6 years (Etnier and Starnes 1993). The abundance of published literature on the *S. atromaculatus* make it an excellent model for comparison of life history traits with *G. cypha*.

In the LCR, adult *G. cypha* are chiefly nocturnally active, while all small native fish including the young-of-the-year of *G. cypha*, *C. discobolus*, *C. latipinnis*, and all age classes of *R. osculus* are diurnally active (chapter 2). Similar activity patterns were found in assemblages containing piscivorous creek chubs; adult creek chubs were sedentary during the daytime, whereas blacknose dace (*Rhinichthys atratulus*) and young *S. atromaculatus* were diurnal (Fraser and Cerri 1982; Magnan and FitzGerald 1984).

In the LCR assemblage, the nighttime inshore movements and elevated nocturnal activity patterns of adult *G. cypha*, coupled with the greater percentage of small fish mortalities found at night, suggests that most piscivory by adult *G. cypha* also occurs at night. In an analogous study, Cerri (1983) found that predation by *S. atromaculatus* on *R. atratulus* was lowest during bright light and greatest in darkness. Because *R. osculus* are described as a nocturnally active species by Sigler and Sigler (1996, 1987), their diurnal activity in the LCR may show a behavioral response to nocturnal predators. Whether the diurnal activity of small LCR fish resulted from undeveloped sensory abilities,

predator avoidance, or for some other reason needs further investigation. Opposing activity patterns between predators and prey have been described in other freshwater systems by Helfman (1981), Schwassman (1971) and Bourke et al. (1996).

The nighttime shifts away from shorelines by *R. osculus* in both river clarities, and juvenile *G. cypha* in clear water may have been an avoidance response to adult chubs as they shifted inshore. Fraser and Cerri (1982) observed juvenile *S. atromaculatus* (41-66mm TL) and *R. atratulus* (37-51 mm TL) shifting out of areas containing predaceous adult creek chubs. Shifts away from normally utilized habitats because of the presence of predators has also been reported in other freshwater fish assemblages by L'Abée-Lund et al. (1992), Tonn et al. (1992), Tonn and Paskowski (1987), Imbrock et al. (1996), and Helfman (1981); see Sogard (1994) for detailed review.

Fraser and Emmons (1984) found the degree of avoidance of *S. atromaculatus* by *R. atratulus* was dependent on the amount of structure. At night in the LCR, *R. osculus* seemed to vacate the nearshore habitats, whether their nighttime shifts in clear water to areas containing a more convoluted bottom profile was synonymous with seeking shelter is uncertain. However, during the night in clear water, YOY *G. cypha* shifted closer to emergent edges, in areas containing high angular structure, and heterogeneous bottoms of containing boulder and cobble substrates. These habitats

definitely contained greater cover than the exposed sandy areas occupied by YOY chubs during the day.

In the LCR, daytime piscivory by adult *G. cypha* may increase in turbid water. Adult chubs showed less distinctive diel habitat shifts and increased diurnal activity levels (Chapter 2) in turbid water. In turbid water adult *G. cypha* showed similar associations with habitats occupied by YOY chubs between day and night, while only night associations were found in clear water. In the mainstem Colorado River, adults were also found to be more active and occupy nearshore habitats more during the daytime in turbid, than clear water conditions (Valdez and Ryel 1995).

Because adults were active both day and night in turbid water, spawning habitats were one of the most predictable areas where adult chubs would aggregate during crepuscular or nighttime periods (Gorman and Stone 1999). The nighttime shifts of YOY and juvenile *G. cypha*, and *R. osculus* away from these habitats suggest that they were avoiding reproductive adult chubs. The occupancy of smaller fish in these habitats during the day may have been to forage on food items stirred up or eggs deposited during nighttime spawning activities.

Although juveniles and adults *G. cypha* were associated in similar habitats during both sampling periods and in both river clarities, this does not necessarily imply an

intraspecific association. The association tests show that somewhere during ~14 h of night and ~10 h of day sampling the juveniles and adults swam into many of the same nets, while the order of entry is unknown. Other analyses have shown that juveniles usually occupy intermediate habitats between YOY and adult chubs (Chapter 3) and have different diel activity patterns than adults (Chapter 2). However if these spatial and temporal separations are indicative of active avoidance, it may be related more to competition rather than risk of piscivory. Juanes (1994) collectively analyzed the results from 32 separate studies and found a consistent pattern of selection for small-sized prey with only a few exceptions. Also, smaller fish are often easier predation targets because of their physiological and sensory limitations (Sogard 1994).

Juvenile *G. cypha* may actually benefit from the presence of piscivorous adult chubs. At night in clear water, juvenile chubs shifted toward midchannel as the adults moved inshore; these shifts resulted in juveniles occupying habitats further midchannel than adults (Chapter 3). Thus, the presence of adult *G. cypha* may have excluded YOY chubs from exploiting food reserves in offshore habitats, while an opportunity for offshore foraging by juvenile chubs occurred at night, as adults resided inshore with the YOY. A similar scenario was described by Tonn et al. (1992) who found that larger stages of crucian carp

(*Carassius carassius*) used the more optimal offshore habitats, while smaller conspecifics were restricted to nearshore habitats by piscivorous Eurasian perch (*Perca fluviatilis*).

In turbid water, the diel habitat shifts of juvenile *G. cypha* more closely paralleled those of YOY chubs; often juveniles were closer to shorelines at night than YOY (Chapter 3). Because most of our turbid water data were collected during Spring *G. cypha* spawning periods, the adult chub population was supplemented by mainstem Colorado River fish, while numbers of small fish had dwindled from the preceding year. As many juvenile *G. cypha* were within the edible range ($\leq 1/3$ body length of predator) of the largest adults (see L'Abée-Lund et al. 1992), the reduced numbers of small fish may have increased the likelihood of juvenile chubs being targeted for food, forcing them to occupy safer, and possibly suboptimal habitats. An alternate hypothesis is that juvenile chubs were also opportunistic piscivores on smaller fish. The size that *G. cypha* turns piscivorous in the LCR is unknown. We observed a 166 mm *G. cypha* regurgitating a 64 mm *R. osculus* (Table 8), but *G. cypha* smaller than this are probably piscivorous. In the upper Colorado River Basin, Grabowski and Hiebert (1988, 1989) found that 4 of 66 *Gila* digestive tracts (species unknown; 21-80 mm TL) contained fish, the smallest piscivorous *Gila* was 55 mm TL. High levels of piscivory were reported in

juvenile *S. atromaculatus* between 51-80 mm SL (Barber and Minckley 1971) and between 100-150 mm TL (Fraser and Cerri 1982), which were similar size ranges of the juvenile *G. cypha* in our study.

Summary.-The differences in diel activity patterns and habitat shifts between small native fish and adult *G. cypha*, the inferred displacement of small fish to different habitats during the night, and the observations of adults eating, regurgitating and defecating undigested fish parts suggest that piscivory by *G. cypha* may be relatively common in the LCR. Compared to other systems, the LCR supports a large fish biomass with relatively low food resources. Lower quantity and quality of foods have been found to increase both piscivory (Starrett 1950) and cannibalism (Smith and Reay 1991). During the Spring *G. cypha* spawning period, the consecutive monthly declines of CPUE for small fish, while adult CPUE were relatively stable may reflect large scale piscivory.

During the Spring *G. cypha* spawning period, piscivory may increase adult survivorship and enhance recruitment. Spawning migration, gametogenesis, and the spawning act itself consumes energy. Standard metabolism would also increase due to warmer water temperatures and higher salinities found in the LCR than the mainstem Colorado River (Wootton 1990). As a food item, fish have a higher caloric value (Stahl and Stein 1994; Cummins and Wuycheck 1971),

greater assimilation efficiency (Brett and Groves 1979), and larger food volume per capture compared to most invertebrates. Ultimately, piscivory may increase the longevity and fitness of adult *G. cypha*. In systems that have limited food reserves, such as the LCR, predator reduction of prey populations results in greater food resources for surviving fish which leads to increased growth and recruitment of survivors (Fox 1975).

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