

## Habitat Use, Social Behavior, and Female and Male Size Distributions of Juvenile Midas Cichlids, *Amphilophus* cf. *citrinellus*, in Lake Apoyo, Nicaragua

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**ABSTRACT.**—The Midas cichlid complex contains many closely related species throughout Nicaragua. One of the species from Lake Masaya, *Amphilophus* cf. *citrinellus*, has been previously described to undergo socially controlled sex determination. A field study of the Midas cichlid was conducted in Lake Apoyo, a clear crater lake near Lake Masaya. We used visual observations to quantify habitat use of Midas cichlids and other fishes at three shallow water sites. Behavior was recorded and aggression rates and time budgets were calculated for juvenile Midas cichlids. Three predictions were tested that would be consistent with socially controlled sex determination. Aggressive interactions potentially capable of influencing direction of sex differentiation would be common, social groups of juveniles would be expected to be assorted by age/body size, and males would be larger than females in individual social groups. Small juvenile Midas cichlids were present at one of the shallow water sites, which was characterized by large boulders and complex three-dimensional structure. They were solitary, but temporarily formed small groups in which aggressive interactions occurred. Midas cichlids were socially assorted by body size. Two shoals of larger juveniles were captured in deeper water and their gonads analyzed histologically. In one group, some of the fish were sexually undifferentiated. Sex was not associated with body size in either group. The results were not consistent with a hypothesis of socially controlled sex determination. Greater post-maturation growth in males is an alternative process that could result in the sexual size dimorphism found in adults of this species.

**KEYWORDS.**—Fish, cichlid, behavior, sexual lability, environmental sex determination, sex change

### INTRODUCTION

Cichlid nomenclature in Central America is in a state of controversy. Stauffer and McKaye (2002) discussed the nomenclatural problems surrounding the Midas cichlid, *Amphilophus citrinellus*, complex in Nicaragua. Stauffer et al. (1995) have been cautious in assigning specific status to the many newly discovered forms and instead have referred to various taxa as Evolutionary Significant Units. Nevertheless, the Midas cichlid taxa in the various crater lakes are most likely different species (McKaye et al. 2002). There is a rich literature by George Barlow and his students concerning the behavior of the Midas cichlid (Barlow 2000). The majority of Barlow's work fo-

cused on Midas cichlids from Lake Masaya, Nicaragua.

Francis and Barlow (1993) reported evidence for social control of sex determination at the juvenile stage in the Midas cichlid, and their study posed interesting questions concerning the evolution of sequential hermaphroditism in fishes. They proposed that the social control of sex determination observed in this species is a heterochronic variant of the behaviorally controlled sex change observed in sequentially hermaphroditic marine fishes. Variation in timing of the sexually labile period has suggested that changes in developmental timing may be involved in the evolution of sequential hermaphroditism (Shapiro 1987; Francis 1992). Cichlids are the only group of fishes that exhibit sexual lability at three distinct life stages (Oldfield 2005).

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Growth can be controlled socially in fishes (Brown, 1957), especially in cichlids (Koebele 1985; Fernandes and Volpato 1993; Hofmann and Fernald 2000). In the Midas cichlid, differences in body size occur randomly soon after hatching. Larger fish are not intrinsically more aggressive than smaller ones, but once they have attained a size advantage their aggressive dominance may suppress growth in smaller members of their social group (Francis 1988). Francis (1990) found a stable size hierarchy in a captive group of 12 individuals from the early juvenile (10 weeks) to adult stage (18 months). He proposed that the social interactions that control growth also control direction of sex differentiation.

Because Midas cichlid males are generally larger than females in adult groups, it was hypothesized that juveniles that are small relative to other group members differentiate as females, and those that are relatively large as males. Under laboratory conditions, Francis and Barlow (1993) divided a brood of juveniles into two groups based on body size. If sex were determined only by genetic factors, then all of the fish in the 'large' group would mature as males, and all of the fish in the 'small' group as females. Those in the 'small' group experienced growth compensation (see Ali et al. 2003), and became as large as the fish in the 'large' group at maturity, and both groups had similar male/female proportions and gendered size rankings, with males larger than females. The authors concluded that the fish assessed their size via aggressive interactions and differentiated as the sex that would grant them the best reproductive success, because large body size is more important to males than to females. Although Francis and Barlow (1993) have often been cited (Helfman et al. 1997; Baroiller et al. 1999; Baroiller and D'Cotta 2001; Devlin and Nagahama 2002; Godwin et al. 2003; Oldfield 2005; Oliveira, 2006; Liu and Sadovy, 2004), their findings remain untested.

Although *in situ* behavior of adult Midas cichlids from several crater lakes has been well described (Barlow 1976; McKaye and Barlow 1976; McKaye and van den Berghe

1996; Murry et al. 2001; Vivas and McKaye 2001), juveniles have received little attention. Francis and Barlow (1993) predicted that juveniles would assort by size during the period of sex differentiation. We therefore hypothesized that (1) there would be aggressive intraspecific interactions in social groups of juvenile Midas cichlids, (2) fish would assort into social groups according to body size, and (3) males in given social groups would be larger in size than the females.

We studied habitat use and social behavior in juvenile Midas cichlids under natural conditions in order to better understand how communicatory interactions might function in controlling sex differentiation. In order to obtain a complete understanding of behavior in Midas cichlids, co-occurring fish species were also noted and interactions with these species recorded. Gonad development was compared among Midas cichlids within social groups and compared to the patterns observed by Francis and Barlow (1993).

## MATERIALS AND METHODS

### *Lake Apoyo*

Field work took place in February 2004, and was based at Proyecto Ecológico, a field station situated near the western shore of Lake Apoyo, Nicaragua (Fig. 1). The Lake formed from a volcanic explosion approximately 20,000 years ago and measures 6 km across and 200 m deep (Waid et al. 1999). The terrestrial ecosystem in the crater has been classified as a tropical dry forest with a wet season occurring between May and November (Incer 1975). At least five fish species are native: *Atherinella sardina*, *Parachromis managuensis*, *Poecilia sphenops*, and *Amphilophus* cf. *citrinellus*, which may be a complex of four Midas cichlid species (McKaye et al. 2002), including *Amphilophus zaliosus* (Barlow and Munsey 1976). Introductions to the lake include the blue tilapia, *Oreochromis aureus*, introduced in 1983, the eleotrid goby *Gobiomorus dormitor* in 1991 (Bedarf et al. 2002), and the Nile tilapia, *Oreochromis niloticus*, in 1992 (McCrary et al. 2001).

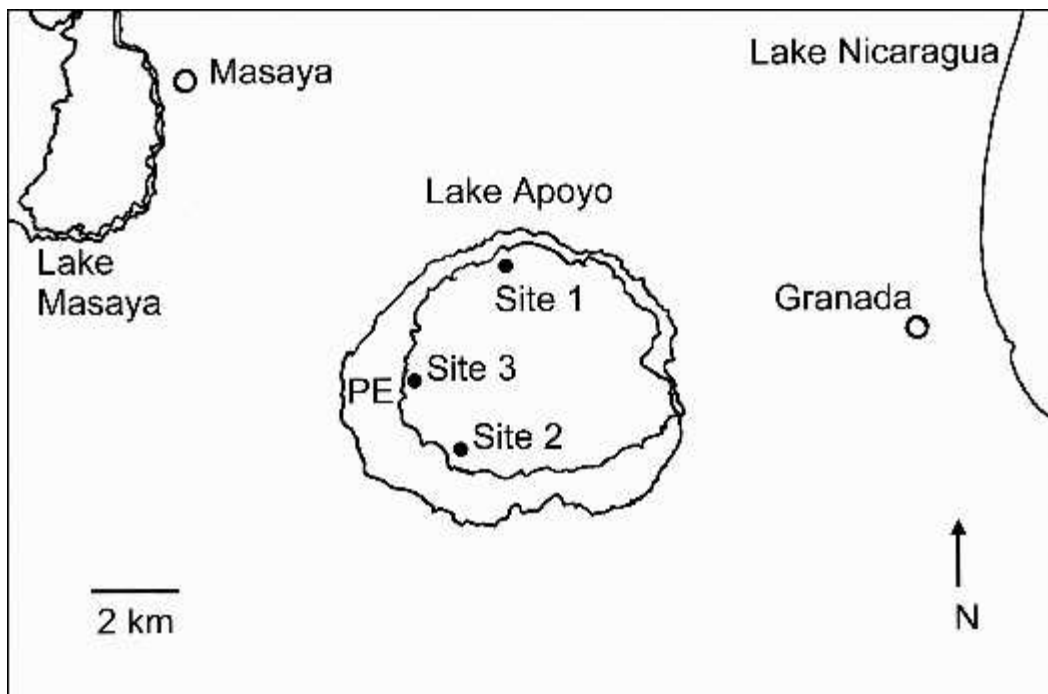


FIG. 1. Map of Lake Apoyo, Nicaragua ( $11^{\circ} 56' N$ ,  $83^{\circ} 3' W$ ). The field station Proyecto Ecológico (PE) and the three field sites are indicated.

Lake Apoyo was an ideal setting in which to observe social behavior in juvenile Midas cichlids. Its low species richness allowed observation with few interspecific interactions, which would complicate interpretation in a more species-rich environment such as Lake Xiloa. Excellent visibility was afforded by the clear water of Lake Apoyo, unlike the muddy or green waters found in some of the other Nicaraguan lakes. Lake Masaya, the source of the fish used by Francis and Barlow (1993), had become too polluted and is therefore an unsafe environment in which to work.

#### *Habitat use*

Three sites with differing substrate characteristics and anthropogenic influences were selected in different areas of Lake Apoyo. At each site, one transect of approximately 25 continuous  $1 \text{ m}^2$  quadrats was laid out parallel to the shore so that the deepest edge was 1 m deep (Fig. 2). Each transect was traversed between two and

four times, never more than once in the same day. No effort was made to traverse the quadrats at the same time each day. At each observation session, percent cover of different types of substrate was estimated in each quadrat. Substrate was classified as one of three types: 'boulder', which was a large ( $>0.5 \text{ m}$ ) flat rock surface, 'rubble', which represented smaller rocks, and grain sized 'sand'.

The number of fish of each species observed was recorded according to body size (fry, juvenile, adult). The mobile nature of the fish indicated that each observation should be considered independent in data analysis. When multiple Midas cichlids were observed, we noted whether at least two of them were in close proximity ( $<20 \text{ cm}$ ) to one another.

#### *Site 1*

Site 1 was located on the northern shore of the lake, at the first rocky outcropping east of the row of houses that lined the lake

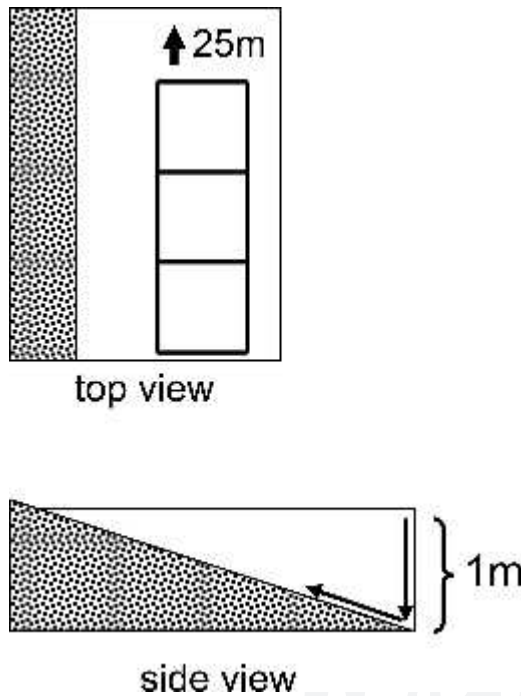


FIG. 2. At each site a transect of approximately 25 m was laid parallel to the shore at the distance where water depth reached 1 m. The transect was composed of adjacent 1 m<sup>2</sup> quadrats.

shore (Fig. 1). Part of the site included a rock wall that rose 5 m vertically out of the water and continued down below its surface. A variety of rocks, ranging from large boulders to small stones, were scattered in the vicinity. Access to the site would have been difficult from land. There were cattle paths directly above the site along the crater wall, but the site was reached by kayak. The shallow (<1 m deep) area of the site was between 0 and 3 m from the shore. After this distance the bottom sharply dropped off.

The transect at this site consisted of 26 quadrats, and was traversed four times. Due to the rocky, uneven nature of this site, water depth on the shallow edge of the transect was variable, but was generally around 0.75 m. After the final observation at Site 1, rocks were overturned in order to determine how many fish were hiding and therefore overlooked during the data collecting periods. Fish were absent except for one occasion when a small Midas cichlid

swam away, indicating that the previous observations represented nearly all of the fish in the transect.

### Site 2

Located on the southern shore of Lake Apoyo, Site 2 was reached by following the low road south from Proyecto Ecológico. Past the old walkways and many sets of stone stairs that descended to the shore, the water line turned to the right. At this point the stairs no longer reached the water. The transect was located about halfway between this turn and an isolated hut (Fig. 1). The substrate here was clay, intermittently covered by a thin layer of sand. The water was shallow (<1 m) until it dropped off at about 20 m off shore. From the shore, about  $\frac{3}{4}$  of this distance was covered in rubble (20-30 cm diameter). The lakeside border of the transect followed the lakeside border of this stone field and was approximately 0.95 to 1 m deep. The transect consisted of 26 quadrats and was traversed twice.

### Site 3

Site 3 was located just off the heavily populated western shore of Lake Apoyo, directly in front of Proyecto Ecológico. It was used as a boat launch by the field station and was commonly used by swimmers, people washing clothes, etc. Garbage was scattered on the shore. Approximately 95% of all the houses on the lake were located on the western shore. One couple was in the water at the time of sampling on Day 1, and two groups of people were in the water on Day 2. The substrate was thick sand. The slope descended very slowly until about 20 m from shore, to a depth of about 1.5 m, and then dropped off to about 10 m deep. Rubble (20 cm diameter) overlaid the sand for about the first 3 m off shore. The transect was about 10 m off shore, over sand mixed with a few small pebbles. It consisted of 22 quadrats and was traversed twice.

*Amphilophus* cf. *citrinellus*, *P. managuensis*, and *G. dormitor* were tested for associations between density and substrate characteristics within each site with linear regressions.

Also, substrate characteristics were compared between observations in which a species was present and those in which it was absent within a site with Mann-Whitney tests. Fish densities among sites were compared using Kruskal-Wallis tests. Statistical analyses were performed using SPSS 11.0 computer software with alpha set at 0.05.

### *Social behavior*

Each of 33 juvenile Midas cichlids were individually chosen and followed for the duration of a preset period, either 2.5 or 5 minutes, or until it was lost, whichever occurred first. Numbers of aggressive and submissive interactions were recorded for each focal fish. A bout of aggressive behavior was defined as any deviation from an individual's previous action or trajectory with redirection toward another individual in an apparent effort to displace it, followed by cessation of aggression for more than 1 s. Displays and attacks (Baerends and Baerends van Roon 1950) were not differentiated, as an approach seemed to be the most important component of an aggressive action. Submission was defined as a change in position or posture, apparently to avoid physical contact with an antagonistic fish. Behavior was also recorded at predetermined time points (either every 15 s or every 30 s) and used to calculate time budgets. Behavior recorded was previously interpreted from lab observations (Table 1). In the current *in situ* observations, a fish 'hiding' may also have been performing other acts that went unrecorded. It was usually under a rock and temporarily out of view. All data were taken from Site 1,

although observations were not restricted to the transect.

### *Sex Distributions*

Gonad differentiation was investigated in two social groups of Midas cichlids. Two professional divers employed an underwater seining technique with a nylon gillnet to capture all of the members of each of two shoals of juveniles offshore near Site 3 at depths between 12 to 15 m. The first shoal, Group 1, contained 14 specimens. The second, Group 2, contained 15 specimens. All specimens from both groups were fixed in modified Davison's fluid and were later transferred to 70% ethanol. They were measured for Standard Length and dissected. Their gonads were removed, embedded in paraffin, sectioned at 4  $\mu\text{m}$ , stained with hematoxylin and eosin, and examined under a light microscope. Specimens were deposited at the University of Michigan Museum of Zoology (Group 1: UMMZ #246209, Group 2: UMMZ #246213).

To determine if males and females were assorted by size within each group, a chi-square test was used to compare number of males and number of females above and below the median SL. Standard Length was compared between males and females with a Mann-Whitney test.

## RESULTS

### *Habitat Use*

During data collecting observations, no Midas cichlids were seen in the transects at Sites 2 and 3, and only juveniles were observed at Site 1. This indicated an affinity for rocks. Association of juvenile Midas

TABLE 1. Behavior observed in juvenile *Amphilophus cf. citrinellus* used to describe the fish's time budget.

Behavior	Description
Hovering	Hanging motionless in the water column.
Swimming	Moving through water, but not doing anything else.
Hiding	Avoiding a line of site between itself and other animals, usually under a rock or in a crevice.
Foraging	Trying to find food. Looking at the substrate, sifting particles in the gravel, or approaching and chewing a particle in the water column or at the surface.
Aggression	Any kind of chase, bite, or display.
Submission	Evading an attack, display, or perceived attack.

cichlids with both rubble and boulders at Site 1 was tested by performing a regression to determine if the number of Midas cichlids decreased with increasing proportions of sand. No association was found ( $R^2 = 0.057$ ). However, quadrats that contained Midas cichlids had significantly greater percent cover (combined 'rubble' and 'boulder') than those that did not (Mann-Whitney test, one tailed:  $Z = -2.303$ ,  $p = 0.011$ , Fig. 3). Similar results were found for *P. managuensis* ( $R^2 = 0.048$  and Mann-Whitney test, one tailed:  $Z = -2.418$ ,  $p = 0.008$ , Fig. 3). Whereas no adult Midas cichlids were observed, adult *P. managuensis* were occasionally observed and included in the analysis. The occurrences of these two species were also tested for associations with 'rubble' alone and found to be insignificant ( $R^2 = 0.039$ ,  $R^2 = 7.47 \times 10^{-5}$  respectively).

Out of 104 total quadrat observations at Site 1, Midas cichlids were observed in 68. Of these 68 observations, two or more individuals were in close proximity (<20 cm)

to each other in 22 cases. *Parachromis managuensis* were observed in 10 of 104 observations. These were always solitary.

*Gobiomorus dormitor* was common at all three sites. Like the cichlids, there was no linear association between the occurrence of *G. dormitor* and percent sand at Site 1 ( $R^2 = 0.001$ ). A similar lack of association was found at Sites 2 ( $R^2 = 0.029$ ) and 3 ( $R^2 = 0.018$ ). In contrast to the cichlids, there was no difference in percent cover between the quadrats that contained *G. dormitor* and those that did not at Site 1 (Mann-Whitney test, two tailed:  $Z = -1.414$ ,  $p = 0.157$ , Fig. 3), or at Site 2 (Mann-Whitney test, two tailed:  $Z = 0.954$ ,  $p = 0.34$ ) or Site 3 (Mann-Whitney test, two tailed:  $Z = 0.183$ ,  $p = 0.855$ ). In addition, differences in *G. dormitor* density among sites were tested by the Kruskal-Wallis test and found to be insignificant ( $\chi^2 = 0.349$ ,  $p = 0.840$ ). Individuals of *G. dormitor* in the shallow waters were mostly juveniles [approximately 5 cm TL (Total Length) or less], but adults were recorded occasionally. No adults were ob-

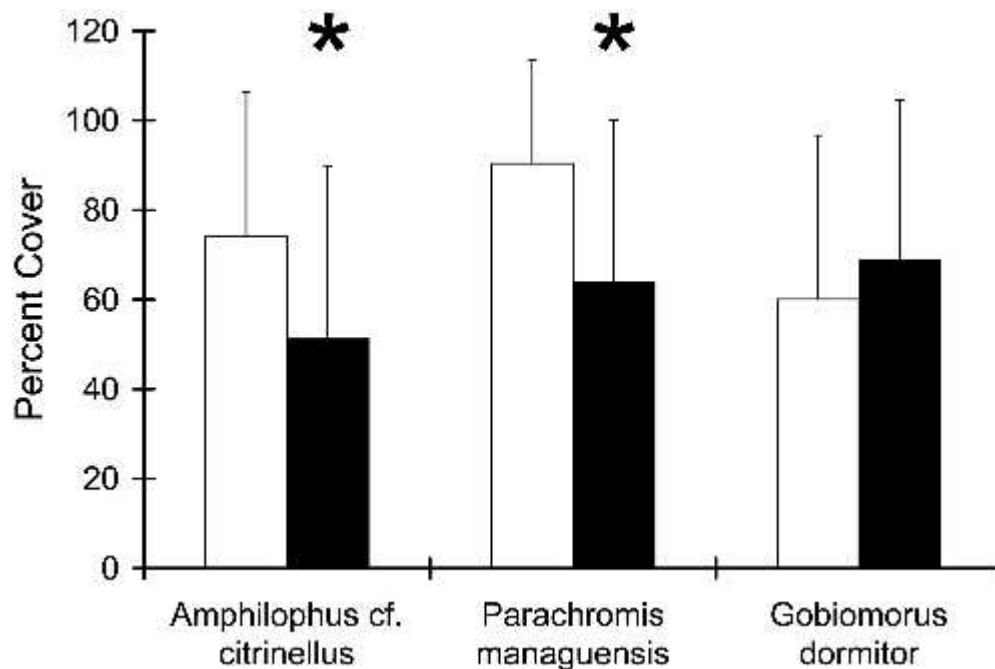


FIG. 3. Mean percent cover for quadrats at Site 1 in which fishes were present (white bars) or absent (black bars). Significantly (\*) greater percent cover observed in quadrats where individuals were present indicates a preference for rubble and boulders in *Amphilophus cf. citrinellus* and *Parachromis managuensis*, but not in *Gobiomorus dormitor*. Error bars represent Std. Dev.

served at Sites 2 or 3, but 10 of the total 140 *G. dormitor* observed at Site 1 were adults.

Occurrence of *A. sardina* and *P. sphenops* would not be expected to be associated with substrate type as these species are not demersal. Indeed, they were only observed at Site 1. Out of the 104 quadrat observations at Site 1, *A. sardina* was observed 27 times, with 15 of these being only 1 or 2 fish. However, groups of up to approximately 40 fish were observed. The mean of approximated group sizes was 8.3 fish per group. The large groups caused *A. sardina* to be the most abundant fish at Site 1 (Fig. 4).

4. *Poecilia sphenops* was observed on two occasions. The first was an observation of a school of seven fish, each approximately 5 cm TL, moving very quickly through the area. The second was a sighting of one large (15 cm TL) individual which was seen hiding in a cave deep in the rock face. It was positioned vertically in the cave, had two wounds on its body, and appeared to be stressed (rapid breathing and pectoral fin movement). No *Oreochromis* species were observed.

### Social behavior

One Midas cichlid was omitted when calculating mean rate of aggression because it was observed for less than 30 s, leaving

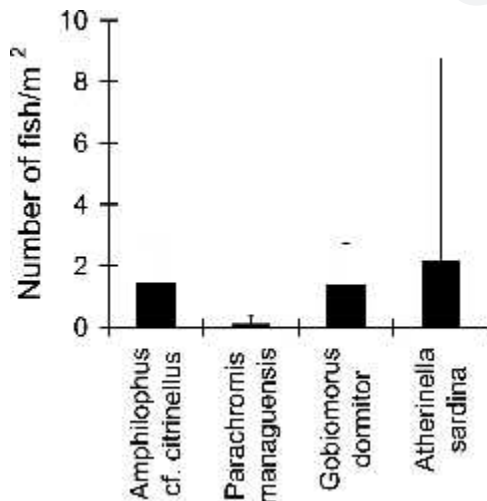


FIG. 4. Density (# fish per m<sup>2</sup>) of fishes regularly observed at Site 1 in Lake Apoyo. Error bars represent Std. Dev.

data from 32 fish in the analysis. Fish performed 0.76 mean aggressive bouts per minute. Submission was observed 0.37 times per minute. The difference between aggression and submission was attributed mostly to aggressive displays which did not result in obvious submissive reactions. Aggressive interactions also occurred between Midas cichlids and *P. managuensis* and *G. dormitor*, but much less frequently (only six with *P. managuensis*, and one with *G. dormitor*).

Four fish were excluded from the time budget analysis because only three behavior samples were recorded for each. This sample was not considered to be sufficient for representing their time budgets. The remaining 29 fish were used to calculate a mean time budget (Fig. 5). *Amphilophus cf. citrinellus* spent most of their time swimming (33.7%) or just hovering in the water (21.9%). They also spent considerable proportions of time foraging (20.0%) and hiding under rocks (17.6%). Communicatory interactions made up considerably smaller proportions of time. Fish engaged in attacks or displays accounted for 4.6% of the time while fishes submissively responding to the aggression of other individuals accounted for 2.2% of the time.

### Sex distributions

Gonad structure was consistent with the descriptions provided for *Cichlasoma di-*

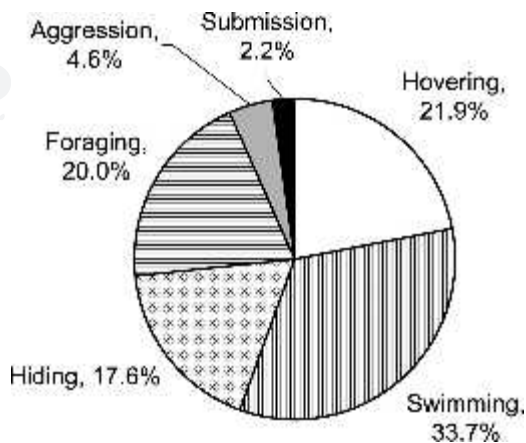


FIG. 5. Time budget of solitary young juvenile *Amphilophus cf. citrinellus* in shallow water.

merus by Meijide et al. (2005). Females were identified by the presence of oocytes at various stages of development and an early **F** ovarian lumen (Fig 6a). Males were identified by testicular lobules consisting of spermatocysts and sperm ducts that contained sperm in various stages of development (Fig. 6b). No bisexual gonads were observed: all contained exclusively either female or male tissue.

A two-tailed t-test revealed that the Midas cichlids in Group 1 were significantly larger than those in Group 2 ( $t = 2.428$ , d.f. = 27,  $p = 0.022$ ). In addition, they were more developed (Table 2). Sex was identified in all of the fish in Group 1, whereas three fish in Group 2 were undifferentiated and not identifiable to sex even through histological analysis (Fig. 6c). Within the smallest seven individuals of Group 1, four were females and three were males. There were also four females and three males among the largest seven fish. Therefore, sexes were not assorted by size ( $\chi^2 = 0.000$ ,  $p = 1.000$ ). Males were not generally larger than females in Group 1 (Mann Whitney  $U = 23.500$ ,  $Z = -0.065$ , two tailed  $p = 0.948$ ). In Group 2, three of the four fish identifiable as females were above the median body size and there were no identifiable females below the median.

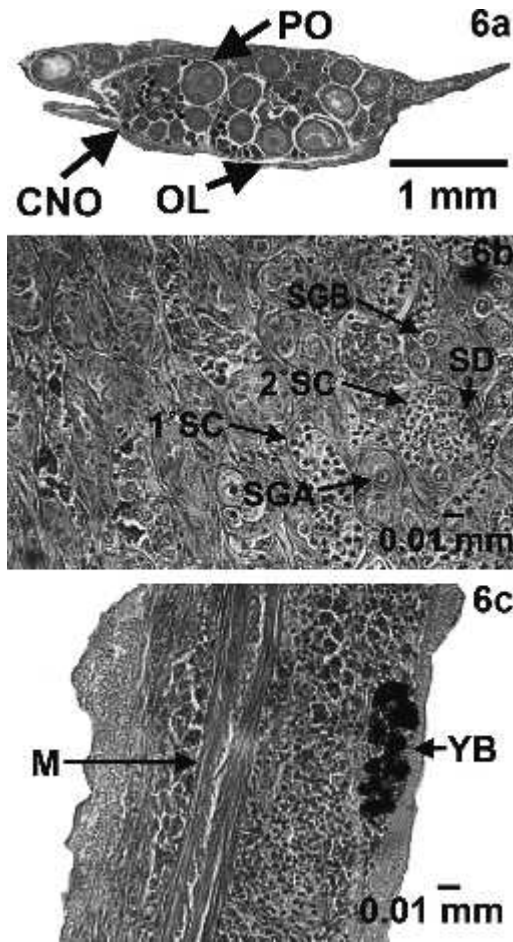


FIG. 6. Histological sections of typical (6a) female, (6b) male, and (6c) undifferentiated gonads observed in two shoals of late juvenile *Ampilophus cf. citrinellus* from deep water. 6a and 6b are transverse sections, 6c is a longitudinal section. CNO = chromatin nucleolus phase oocyte, M = mesorchium, OL = ovarian lumen, PO = perinucleolar phase oocyte, 1°SC = primary spermatocyte, 2°SC = secondary spermatocyte, SD = sperm duct containing spermatids and spermatozoa, SGA = spermatogonia A, SGB = spermatogonia B, YB = yellow body.

## DISCUSSION

### Habitat use

Juvenile cichlids occupied only a portion of the shallow water habitats of Lake

TABLE 2. Size distributions of two shoals of *Ampilophus cf. citrinellus*. Three individuals in Group 2 were undifferentiated. The 72.5 mm specimen in Group 2 was not sexed due to problems in preservation. Bold font indicates median sizes.

Group 1		Group 2	
SL (mm)	Sex	SL (mm)	Sex
63	F	60	M
64	F	61	?
65	F	61	M
<b>65.5</b>	M	61	M
67	M	64	?
67	M	65	?
70	F	66	F
<b>70</b>	M	66	M
71	F	66	M
72	F	66.5	M
72.5	M	69	F
73	M	69	M
77	F	70	F
77	F	70	F
		72.5	?
Mean SL: 69.6		Mean SL: 65.8	
Std. Dev.: 4.5		Std. Dev.: 3.9	

Apoyo. They were absent from habitats without rock structure. The presence of three-dimensional structure seemed to provide juvenile cichlids with shelter from predation by larger cichlids, *G. dormitor*, and presumably predatory birds.

Midas cichlids were more common than *P. managuensis* at Site 1. Although *P. managuensis* had been previously observed infrequently in Lake Apoyo (Barlow 1976), they were fairly common at Site 1. While no adult Midas cichlids were present during data collecting periods, adult *P. managuensis* were. Neither adults nor juveniles were observed feeding, and they were always solitary. Perhaps their more predatory nature brought them into the shallow water to prey upon young cichlids. Juvenile *G. dormitor* did not require extensive structure and were found in more diverse habitats than the cichlids. Their cryptic coloration and benthic behavior probably enabled them to avoid predation in the more barren habitats of the lake. Both large and small *G. dormitor* at Site 1 were observed preying on *A. sardina*. Although *A. sardina* was observed considerably less often than most other species, its large schools compensated to make it the most abundant fish at Site 1. Schools of many hundreds were observed outside of the data collecting periods. *Poecilia sphenops* was very rare. These exotic fishes may have detrimentally affected the *P. sphenops* population as they have native fishes in other Nicaraguan Lakes (McKaye et al. 1995). This species seemed to be under predation pressure from the introduced *Gobiomorus* and from habitat (*Chara* sp.) loss induced by introduced tilapia (McCrary et al. 2001). No *Oreochromis* species were observed at any time, even outside of the data collecting periods. However, presence of *Oreochromis* cannot be ruled out as tilapia have recently been caught in deep water.

Outside of data collecting periods, larger and smaller fish were present at the sites. Large Midas cichlids and *P. managuensis* were present at low densities at Site 1, but were easily scared off and were generally gone by the beginning of each sampling period. Many large Midas cichlids were seen by free diving. On Day 1, a free-diving har-

poon fisherman had two adult *P. managuensis* that he reported to have captured at about 10 m depth. On Day 1 one school (approximately 30 fish) of Midas cichlid fry and one school (approximately 20 fish) of *G. dormitor* fry were observed at Site 1. Near Site 2, two anglers were observed with one large Midas cichlid and one large *P. managuensis* on Day 2. Near Site 3, a shoal of nine adult Midas cichlids was observed in shallow (1 m) water on Day 1.

Most of the Midas cichlids observed in shallow water were very small (2.5 cm TL). Unquantified SCUBA observations and free dives found larger fish and fewer small fish at depths greater than 1 m. Individuals smaller than 2.5 cm TL occurred in tight schools that appeared to be natal broods. These occupied a variety of depths. After the fish leave these broods they apparently move into shallow water and are solitary until they reach between 2.5 and 5 cm TL, when they move into deeper water and form small shoals that contain similarly sized individuals. Considering the seasonality of cichlid reproduction in Lake Xilola (McKaye 1977), this size segregation may represent age segregation. If so, then intra-cohort social interactions may be much more common than inter-cohort interactions, and social interactions at the late juvenile stage would be particularly informative of an individual's size relative to other members of its cohort.

#### Social Behavior

Juvenile Midas cichlids in the shallow water were very active. The purpose of their activity seemed to be to eat periphytic algae and associated fauna as well as free vegetable material that appeared to be allochthonous—probably fruit and pollen from shoreline trees. They were generally solitary, although they did engage in frequent social interactions that could possibly influence sex differentiation. Some interactions occurred with only an approach followed by a submissive acknowledgment. Apparently in these cases the antagonistic fish's intent was aggression, but it was not cost-effective to expend a large amount of energy when only an aggressive

approach was necessary to elicit a response 50% of the time. Analyses by numbers of aggressive and submissive bouts and by proportions of time spent performing aggressive and submissive behavior both indicated that submissive behavior occurred at levels of about half of those of aggressive behavior.

#### Sex Distributions

All of the individuals from Group 1 were differentiated sexually, but three of the fish in Group 2 had undifferentiated gonads. This finding is consistent with the predictions of Francis and Barlow (1993). If juveniles were sexually undifferentiated at the time they formed small shoals in deeper waters, then behaviors within each shoal could provide a good indicator of relative size and possibly influence direction of gonad differentiation.

Distribution of males and females among the size ranks within each shoal did not support the Francis and Barlow (1993) hypothesis. According to their hypothesis, size hierarchies within social groups are stable over time. Because adult males are larger than adult females, at any point past the onset of sex differentiation individuals larger than the median size should be predominantly males and those smaller should be females. Instead, there was no association between large size and maleness in either group. Sex is determined genetically in the closely related *Archocentrus nigrofasciatus* (George and Pandian 1996). We cannot rule out genetic factors in sex determination in Midas cichlids, with size differences between adult males and females resulting from intrinsically greater post-maturational growth rates in males. This type of growth pattern seems to be responsible for sexual size dimorphism in the closely related Mayan cichlid, '*Cichlasoma urophthalmus*' (Faunce et al. 2002).

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