



## Initial six-year expansion of an introduced piscivorous fish in a tropical Central American lake

Anne Tate Bedarf<sup>1,5,\*</sup>, Kenneth R. McKaye<sup>2,3</sup>, Eric P. Van Den Berghe<sup>2</sup>, Lorenzo J.L. Perez<sup>3</sup> & David H. Secor<sup>4</sup>

<sup>1</sup>Department of Natural Sciences, University of Maryland Eastern Shore, Princess Anne, MD 21853, USA;

<sup>2</sup>Appalachian Laboratory, University of Maryland Center for Environmental Science, 301 Braddock Road,

Frostburg, MD 21532, USA; <sup>3</sup>University of Central America, Managua, Nicaragua; <sup>4</sup>Chesapeake Biological

Laboratory, University of Maryland, P.O. Box 38, Solomons, MD 20688, USA; <sup>5</sup>Current address:

The Environmental Company, Inc., 2496 Old Ivy Road, Suite 300, Charlottesville, VA 22903, USA;

\*Author for correspondence (e-mail: Annebedarf@aol.com; fax: +1-434-295-5535)

Received 21 December 1998; accepted in revised form 29 November 2001

**Key words:** aquatic invasion, cannibalism, *Cichlasoma*, eleotridae, *Gobiomorus dormitor*, introduced species, Lake Apoyo, Nicaragua, piscivore, population growth, translocation

### Abstract

Two populations of the piscivorous fish *Gobiomorus dormitor* (the 'guabina') were examined in two separate crater lakes in Nicaragua, Central America. At Lake Apoyo, *G. dormitor* were introduced in May 1991 by local fishermen and have invaded successfully; at Lake Xiloá, the population is naturally occurring. To provide baseline life history data for *G. dormitor* in both lakes and to test hypotheses related to population growth and invasion success, this study aimed to (1) document and define the population growth and depth distribution of the fish through video transects in Lake Apoyo; (2) compare diet composition between lakes; and (3) compare life history parameters between lakes, including relative growth rates and reproduction. Videotaped transect studies, designed originally to examine cichlid breeding, began in both lakes in 1990 and have documented the subsequent increase of *G. dormitor*. Yearly means generally fit the exponential growth model. *G. dormitor* foraged mainly in shallow waters in Lake Apoyo and preyed mostly upon the atherinid *Melaniris cf. sardina* throughout seasons. In Lake Xiloá, cichlid fry constituted the majority of the diet overall and cannibalism was more common, although this trend varied with the cichlid breeding season. Relative growth rates were significantly different, based on otolith mass regressions on standard length. Lake Apoyo *G. dormitor* generally behaved as a successful invading species, displaying exponential growth, year-round reproduction, and higher foraging success than the natural population of Lake Xiloá. Further research is planned to explore the *G. dormitor* invasion when the population becomes integrated into the community.

### Introduction

Introduced species invasions commonly play a role in the alteration of terrestrial and aquatic ecosystems, and detrimental effects often result, the most serious of which is the extinction of native fauna (Elton 1958; Zaret and Paine 1973; Groves and Burdon 1986; Bruton 1990; Kaufman 1992; McKaye et al. 1995). Throughout the world, virtually every type

of organism has been successfully introduced, from algae and plants, to invertebrates, amphibians, reptiles, fishes, birds, and mammals (Hedgpeth 1993; Lodge 1993). Study of introductions at the population level usually occurs after ecosystems have changed, although initial colonization events and their eventual effect upon native communities are of increasing interest to ecologists (Courtenay and Stauffer 1984; Miller 1989; US EPA 1991).

In Nicaragua, the piscivorous fish *Gobiomorus dormitor*, known locally as the guabina, was translocated by local fishermen into Lake Apoyo from the population in Lake Masaya, 6 km northwest of Lake Apoyo, in May 1991 (McKaye, personal communication). Translocation of species is a more localized movement, an introduction from the same region. This type of movement is fairly common in the aquatic environment, but the problem receives far less attention than species introductions from more distant locations, although it can cause impacts as well (Barlow et al. 1987; Arthington 1991; Holčik 1991).

*Gobiomorus dormitor* is an ambush-type predator occurring naturally in New World tropical and subtropical riverine, lacustrine, and estuarine systems, with a range from southern Texas and Florida southward to Suriname (Miller 1966; Villa 1982).

This study aimed to define the population growth, depth distribution, diet composition, relative growth rate, morphometrics, and reproductive traits of the invading *G. dormitor* population in Lake Apoyo, Nicaragua. The population in Lake Xiloá offered a useful baseline for comparison, as this lake is in the same region and has a similar fish community and substrate structure as Lake Apoyo. Objectives included the gathering of baseline life history data for *G. dormitor* in both lakes as well as hypothesis testing related to population growth. Hypotheses included: (1) the exponential growth model will fit in Lake Apoyo, (2) prey composition will differ between lakes, both from varying relative prey densities and intraspecific competition, (3) cannibalism will be more prevalent in Lake Xiloá than in Lake Apoyo, although in time it will become more common in Lake Apoyo, (4) *G. dormitor* breed year-round, although a breeding peak may be present, and (5) Lake Apoyo fish will grow faster and reproduce at a younger age than Lake Xiloá fish.

## Methods

### Study sites

Lake Apoyo, the site of *G. dormitor* translocation, is the largest and deepest Nicaraguan crater lake with an area of 21 km<sup>2</sup> and maximum depth of 200 m. Located at 11°56' N and 86°3' W, Lake Apoyo is surrounded by high-rimmed crater walls that rise up to 400 m above its surface (Waid 1991). The heterogeneous substrate consists mostly of silt and sand with scattered rocky

areas close to shore, a typical feature of Nicaraguan crater lakes. Cliff walls and submerged aquatic vegetation (*Chara* spp.) also are present in Lake Apoyo. Lake Apoyo is an oligotrophic lake, with visibility ranging from 5 to 15 m (Barlow 1976). Lake Xiloá (= Jilóa, McKaye 1977), a crater lake on the Pacific side of Nicaragua at 12°13' N, 86°19' W, provides the baseline site for this research. Lake Xiloá, located 40 km northwest of Lake Apoyo, is smaller than Lake Apoyo at 360 ha, and has a maximum depth of 92 m (Reidel 1965). Lake Xiloá is a mesotrophic lake, with visibility ranging from 2 to 7 m (Barlow 1976). Its other features are very similar to Lake Apoyo, with a substrate also consisting of sand, rocky areas, cliff walls, and *Chara* spp.

### Transect studies

Videotaping in Lake Apoyo was done by a diver who videotaped three sites once every month, each consisting of transects distributed by 3 m intervals from 1.5 to 28.5 m. Taping in Lake Xiloá was done by a diver who swam biweekly over three similar depth-distributed study sites. These video transects, begun in 1990, were over rocky sites that were originally chosen to monitor breeding of the cichlid fish *Amphilophus* species. A Sony videocamera in an Amphibico housing was used for the taping. The diver swam approximately 1 m above the substrate at a speed of approximately 15 m/min and filmed 2 m on each side of the transect. Visual surveys along the same transect lines were used to acquire data from February to June 1997, as the videocamera was not functional during this time period. During visual transects, data were recorded on a slate during the dive and immediately transcribed afterward. Transect data have been collected and analyzed from January 1991 through August 1997 for Lake Apoyo, and from September 1990 to November 1995 for Lake Xiloá.

### Sampling

Life history data were obtained from September 1995 through March 1996, during both wet (June through November) and dry (November through June) seasons. Throughout both lakes, *G. dormitor* were captured mostly by spear (99% in Lake Apoyo and 83% in Lake Xiloá), although a few times block nets, gill nets, and hand nets were used. No fish were observed to have

lost stomach contents upon capture. Individuals were captured from different substrates, including rocky reefs, sandy areas, cliff walls and rock ledges, and vegetation beds (*Chara* spp.). Fish were collected between 0 and 36 m (120 ft) depths. Sampling took place randomly, covering the entire day as well as the crepuscular periods. Recorded were: general area within lake, date, capture method, depth, time of day, substrate type. The fish studied from the various areas, substrates and collection times are assumed to be a representative sample of fish throughout the entire lake, as all parameters were covered and randomly selected. Fish were either kept cool and examined the same day (no more than 4 h elapsed between collection and examination), or frozen and processed at a later date.

Fish were weighed to the nearest gram and the standard length (SL) measured to the nearest millimeter. Gonads were also examined macroscopically for level of sexual maturity following methods similar to other large-scale studies of fish reproduction (Heins and Baker 1989; Demestre et al. 1993). If fish were not sexually mature, and consequently the sex not identifiable, the gonads were given a rank of 1. Otherwise, the specimens were sexed and ranked on a scale of 2–5. A rank of 2 indicated sexually mature but non-ripe gonads; however, it is likely that some individuals given a ranking of 2 had already spawned (were ‘spawned out’). For females, ripeness was indicated by the presence of yellow eggs inside the ovary, and for males, wide, flat gonads filled with white semen constituted ripeness. A subset of gonads was weighed with a 5 g Pesola® scale to quantify these rankings (Table 1).

Subsequent to gonad classification, stomach contents were identified to species (if possible) and counted. An ‘other’ was recorded if the contents were unidentifiable.

Otoliths (sagittae) were collected from a representative sample of individuals covering all sexes, size ranges, and gonadal rankings. They were washed with distilled water, then kept in plastic vials. Subsequently,

the otoliths were weighed to the nearest tenth of a milligram. If two otoliths were obtained from the same individual, they were both weighed. A paired *t*-test was performed for those specimens with two otoliths, and it showed that the mass of the two were not significantly different from each other ( $P > 0.01$ ). Therefore, for those specimens where only one undamaged otolith was obtained, the mass of that otolith was doubled. Otoliths of 95 fish from Lake Apoyo and 118 fish from Lake Xiloá were collected and weighed.

### Analyses

Population growth data derived from both Lake Apoyo and Lake Xiloá video transects were fitted to an exponential growth model using Microsoft Excel, which calculated an intrinsic rate of increase and coefficient of determination using the equation  $N_t = N_0 e^{rt}$ . Although transect data appeared consistent among transect sites within each lake, water clarity, cryptic coloration, and group movements of *G. dormitor* in and out of the transect area during the short time span of videotaping can result in fluctuating distribution data when analyzed on a monthly basis. Therefore, all three transect sites within each lake were pooled for data analysis. Both monthly and yearly data were used, because the fluctuations in monthly data obscured growth trends. Monthly data values, rather than yearly, were used to calculate an annual intrinsic rate of increase ( $r$ ). The finite rate of increase ( $\lambda$ ) was estimated as  $e^r$  (per individual per year).

Diet composition data were analyzed both by percent occurrence and percent by number using the following equations. Bioenergetic analysis was not within the scope of this study.

% occurrence

$$= \# \text{ of guts with prey } i / \sum \# \text{ guts examined} \\ \text{(where stomach contents were present)}$$

$$\% \text{ by number} = \# \text{ of prey } i \text{ in gut} / \sum \# \text{ in gut} \\ \text{(where stomach contents were present)}$$

Table 1. Average gonado-somatic index (gonad weight/body weight) for gonad rankings for *G. dormitor* for both lakes.

Rank	Females	<i>N</i>	Standard error	Males	<i>N</i>	Standard error
2	0.64%	14	0.06	0.21%	3	0.03
3	1.55%	4	0.16	0.50%	6	0.09
4	2.89%	15	0.19	0.65%	8	0.04
5	5.39%	12	0.41	1.01%	12	0.09

These two parameters were calculated for both lakes for overall prey composition and for prey composition between cichlid breeding and non-breeding seasons to determine if feeding seasonality occurred. Because prey item distributions were not able to be directly measured, electivity indices were not appropriate, although relative prey densities were ascertained from long-term researcher observations.

Five fish, originally tagged to obtain spatial movement data, were recaptured and remeasured to obtain a gross estimate of growth rates in Lake Xiloá. Using the largest fish (29.4 SL), the most conservative growth rate of 6.3 cm/year, and a resultant maximum age of 4.9 years, an estimate of natural mortality ( $M$ ) was calculated using Hoenig's (1983) equation:

$$\ln M = 1.46 - 1.01 \ln(\text{maximum age})$$

This gives a mortality rate ( $M$ ) of 0.847. Pauly's (1980) equation was used to get an estimate of  $K$  (growth coefficient) in order to plot a growth curve:

$$M = 10^{\frac{[-0.0066 - 0.279 \log_{10}(L_{\infty}) + 0.6543 \log_{10}(K)]}{+0.463 \log_{10}(T)}}$$

where  $T = 36.4^{\circ}\text{C}$  ( $83^{\circ}\text{F}$ ), and  $L_{\infty} =$  maximum SL = 29.4 cm.  $K$  was found to = 0.266.

Both mass (g) and otolith mass (g) were regressed on SL (cm) from each lake to obtain length/weight curves and power regression lines. Using the method suggested by Reznick et al. (1989), an analysis of covariance test (ANCOVA) was performed on the otolith mass regressions to determine if the slopes differed between lakes.

## Results

### Population growth

Transects in Lake Apoyo show that large *G. dormitor* (greater than 10 cm) appeared for the first time in October 1991, five months after the introduction in May (Figure 1a). Small individuals (<10 cm) appeared for the first time in February 1992, nine months after the introduction. This size class was represented mostly by fry schools (approximately <4 cm) that continually moved through the water column in and out of the transects. Because of this movement, small fish (<10 cm) were not included in transect analyses for either lake.

On a monthly basis (Figure 1a), the densities of *G. dormitor* fit the exponential growth model more closely than linear or power models. The yearly intrinsic rate of increase ( $r$ ) was estimated as 0.44 from the exponential regression using monthly data and the coefficient of determination ( $R^2$ ) was 0.44. The finite rate of increase ( $\lambda$ ), calculated using  $r = 0.44$ , was 1.55. On a yearly basis (Figure 1b), the  $R^2$  value was higher at 0.71, and the analysis yielded a larger

yearly intrinsic rate of increase of 0.65 with the power regression line providing the best fit. Either way the data were analyzed, it appears that the population of *G. dormitor* in Lake Apoyo has displayed exponential growth.

The population density of *G. dormitor* in Lake Xiloá (Figure 2) was viewed over the five years for which data were available (1991–1995). As with Lake Apoyo, all three transect sites were found to have similar patterns and therefore were pooled. The population density mean was 2.52 fish per 100 m<sup>2</sup> when viewed over all five years over all transect sites.

### Depth distributions

From 1991 to 1997 in Lake Apoyo, large *G. dormitor* spread from a mean depth of 6.0–11.8 m. Differences between dry and wet seasons were small. In Lake Xiloá, data from 1990 to 1995 show a more uniform depth distribution, although there is a slightly deeper average depth for 1995 (Figure 3). Because of the difficulty in diving at depths greater than 29 m, no transects are set up any deeper, although *G. dormitor* were occasionally observed at deeper depths. Regression analyses indicate that for Lake Apoyo, the year is significant in predicting the average depth ( $P = 0.009$ ), with an  $R^2$  of 77.9% and a regression equation of  $Y = 17.0 + 2.64 X$ . For Lake Xiloá, the yearly average depth differences were not significant.

### Growth and morphometrics

Length/weight regressions for Lakes Apoyo and Xiloá are not significantly different. However, the otolith masses do show a significant difference. The significant difference in otolith masses (Figure 4) suggest a faster growth rate in Lake Apoyo and further suggest that fish of a given length were younger in Lake Apoyo than in Lake Xiloá.

Five fish (one marked 11/4/95 and recaptured 2/13/96, four others marked 1/26/96 and recaptured 3/19/96), with original SL of 11.4–19.0 cm, showed growth rates of 6.3–18.6 cm/year. Although the sample size for this section was low, the sample is believed to represent the population and the variances attributed to non-linear growth associated with fish age and maturity. Using the maximum sized fish of 29.4 cm, these growth rates translated into longevities ranging from 1.6 to 4.9 years, with a longevity of 4.9 years resulting from the most conservative growth rate value.

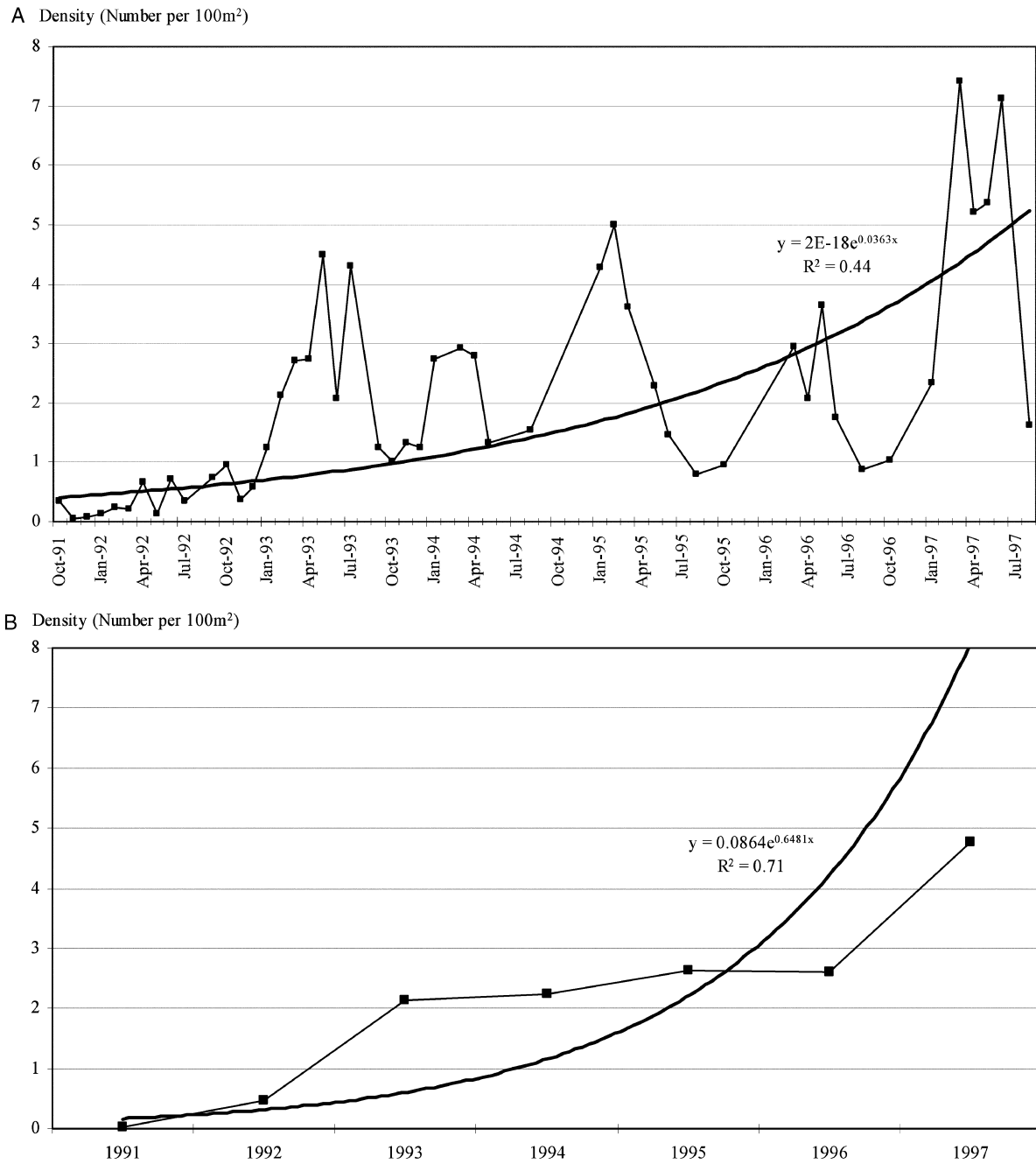


Figure 1. Densities of large ( $\geq 10$  cm) *G. dormitor* on rocky transect sites in Lake Apoyo, Nicaragua (a) by month (cichlid breeding season is September through December) and (b) by year.

#### Diet composition

Across all size classes, seasons, and depths, 31% (285 of 911) of *G. dormitor* in Lake Apoyo had food items in

their stomachs; 27% (247 of 911) had identifiable items (4% unidentifiable because of digestion). Of those identifiable stomach contents, the sardine *Melaniris cf. sardina* was the most prevalent food item, followed by

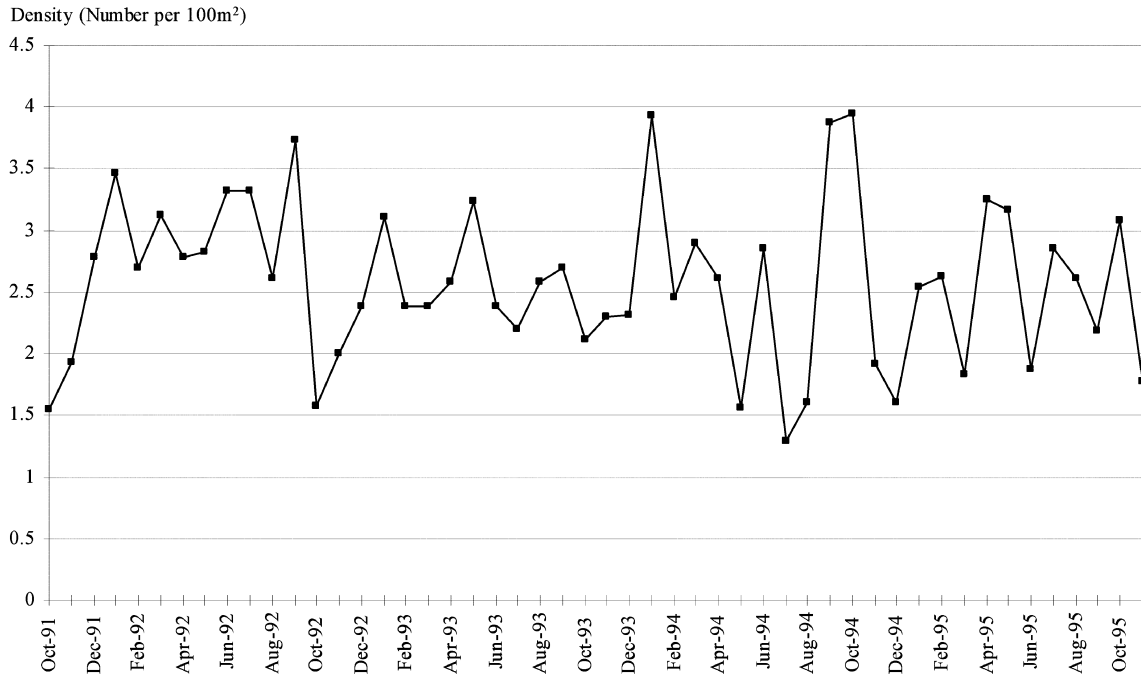


Figure 2. Densities of large ( $\geq 10$  cm) *G. dormitor* on rocky transect sites in Lake Xiloá, Nicaragua.

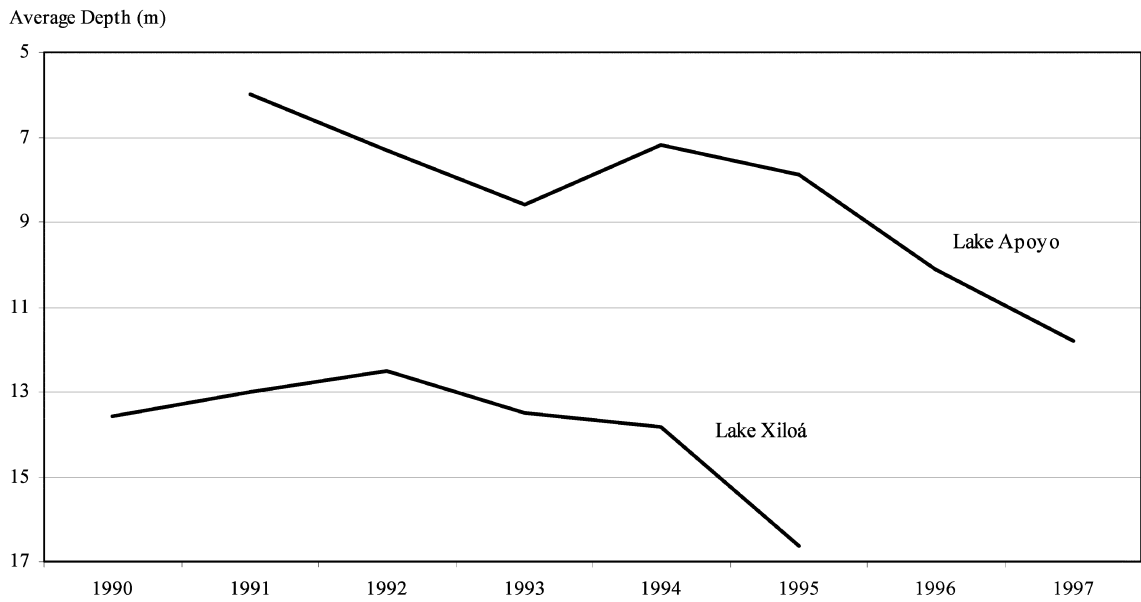


Figure 3. Average depth of large ( $\geq 10$  cm) *G. dormitor* on rocky transect sites in Lakes Apoyo and Xiloá, Nicaragua.

cichlid fry, and conspecifics. Other prey items included insects, the only identifiable group being odonates, adult cichlids, the crab *Potamocarcinus nicaraguensis*, and the molly *Poecilia cf. sphenops*.

Of the fish from Lake Xiloá across sizes, seasons, and depths 23% (319 of 1362) had food items in the stomach; 19% (260 of 1362) had an identifiable item (4% unidentifiable). Overall, cichlid fry were found

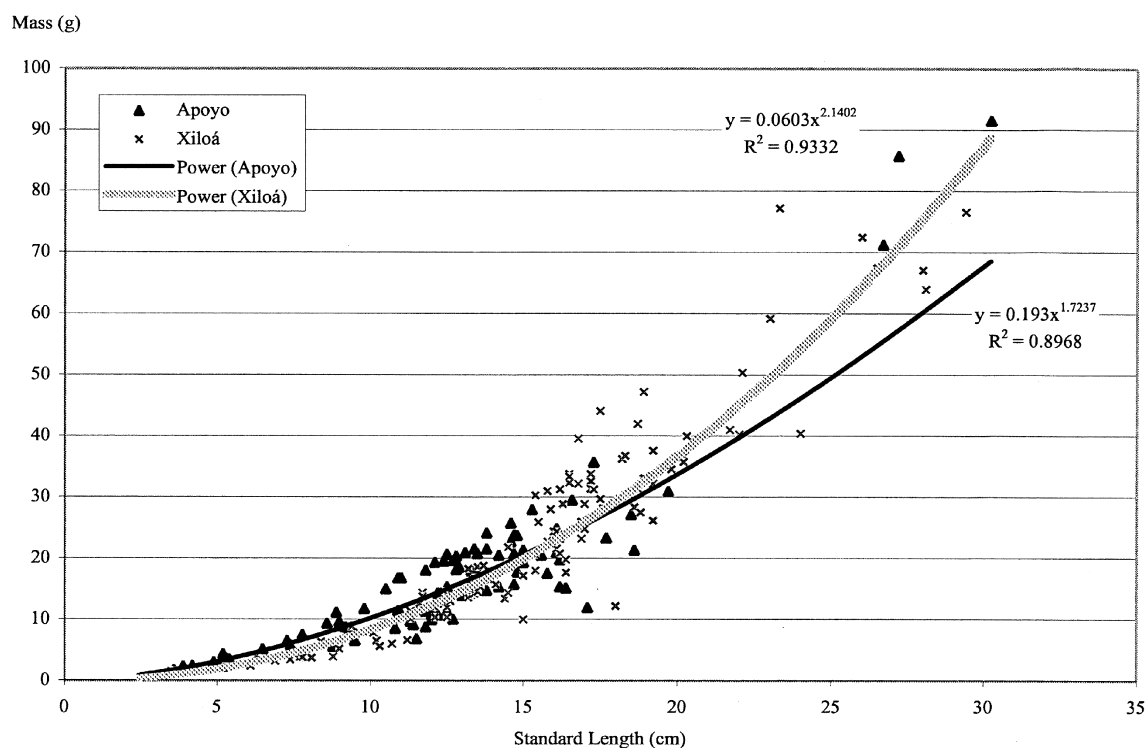


Figure 4. Otolith power regressions of *G. dormitor* in Lakes Apoyo and Xiloá, Nicaragua.

Table 2. Overall diet composition.

Prey item	Lake Apoyo percent by occurrence	Lake Apoyo percent by number	Lake Xiloá percent by occurrence	Lake Xiloá percent by number
Sardines	77.1	78.0	23.9	16.1
Cichlid fry	12.2	14.2	44.0	63.8
Conspecifics	5.6	4.1	20.2	11.8
Insects	2.8	2.0	5.6	4.1
Adult cichlids	1.2	0.9	1.9	1.0
Crab	0.8	0.6	0.0	0.0
Poeciliid	0.4	0.3	0.4	0.2
Catfish	0.0	0.0	1.1	0.6
Shad	0.0	0.0	3.7	2.4

most often, followed by sardines and conspecifics (Table 2). Other prey items included insects, shad (*Dorosoma chavesi*), adult cichlids, catfish (*Rhamdia nicaraguensis*), and the molly. More fish with more than one prey item in the stomach were found here (8%) than in Lake Apoyo (<1%).

The data were also examined to take the cichlid breeding season (September through December) into account, since cichlid fry constituted a majority of

the diet during this time-frame. Data were analyzed using a one-sided test for proportions ( $\alpha = 0.05$ ). No significant difference existed in diet composition of *G. dormitor* between cichlid breeding seasons in Lake Apoyo ( $P = 0.5438$ ) using percent by occurrence (Figure 5a). The October data point includes September data because of the low sample size ( $n = 5$ ) for September in Lake Apoyo.

A significant seasonal pattern of diet composition ( $P = 0.003$ ) did occur in Lake Xiloá (Figure 5b), also using percent by occurrence. During the breeding season (September through December), cichlid fry were the most important prey item, followed by sardines and conspecifics. During the cichlid non-breeding season (January through March), there was a dietary shift from cichlid fry to sardines and conspecifics. This correlated with the relative prey availability at these times.

Additionally, we compared seasonal conspecific predation data between lakes using a two-sided test for proportions ( $\alpha = 0.05$ ). We ran these analyses for both the cichlid breeding and non-breeding seasons, and found that the two lakes had significantly different levels of cannibalism in both seasons ( $P = 0.006$ ,  $P = 0$ ) respectively.

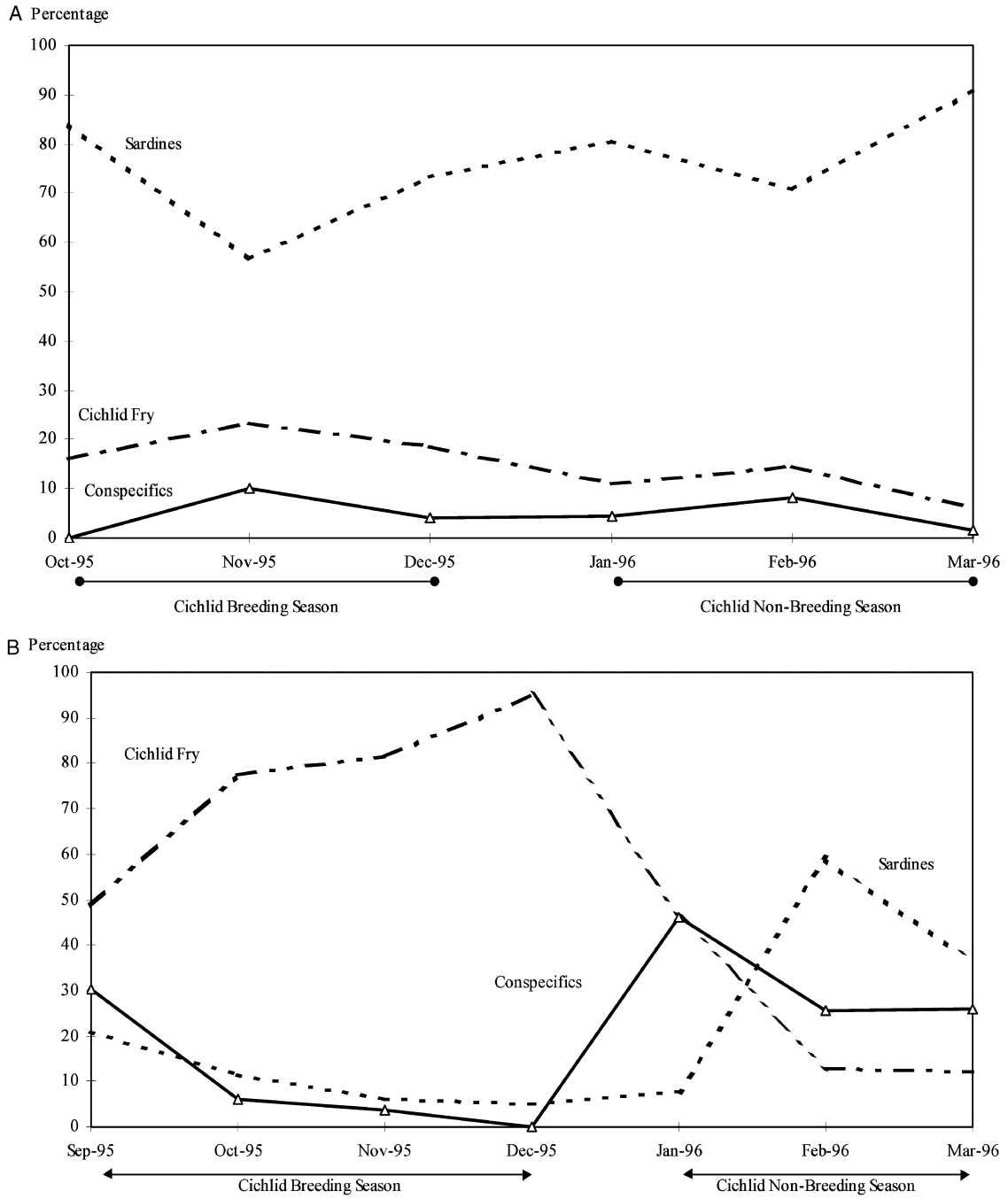


Figure 5. Top prey numbers of introduced *G. dormitor* in (a) Lake Apoyo, Nicaragua, and (b) Lake Xiloá, Nicaragua, over time.

**Reproduction**

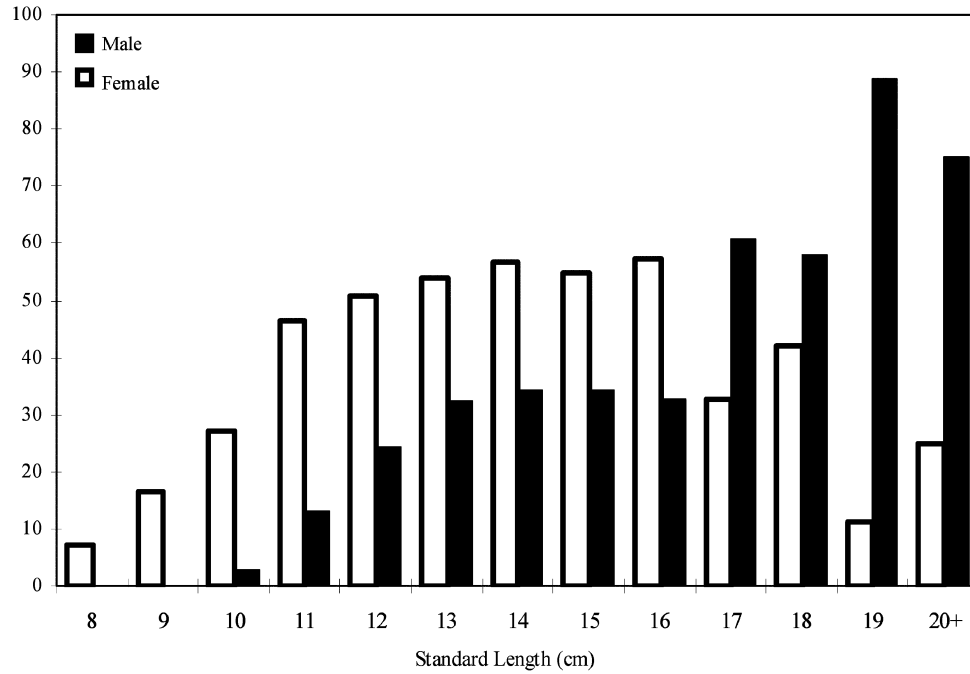
*Gobiomorus dormitor* fry were observed year-round by divers and in the videotaped transects in both lakes. In addition, ripe fish were found in varying percentages throughout the year. Even with year-round spawning,

however, there did appear to be a breeding peak, indicated by the high percentage of ripe *G. dormitor* specimens in March and June for both lakes.

The percent frequency of individuals of identifiable gender (Figure 6a) indicated that in Lake Apoyo, females matured at a minimum SL of 8 cm while males



A Percent of Individuals per Size Class



B Percent of Individuals per Size Class

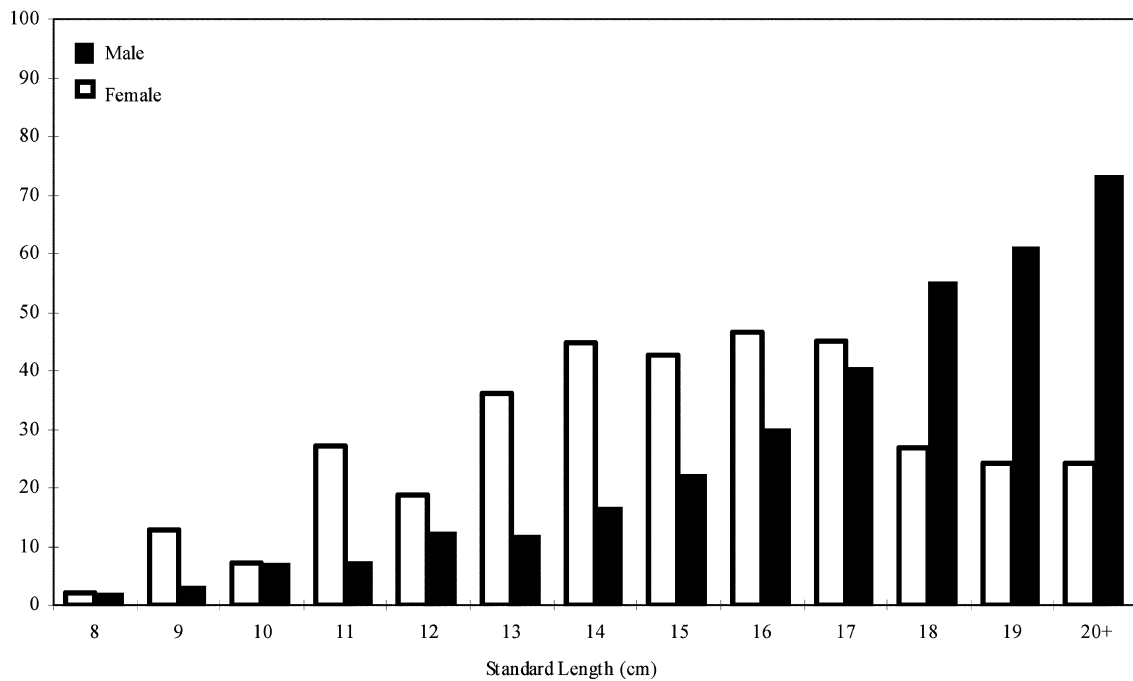


Figure 6. Length-frequency distribution of introduced mature *G. dormitor* in (a) Lake Apoyo and (b) Lake Xiloá.

matured at a minimum of 10 cm. Lake Xiloá fish (Figure 6b) matured at a minimum of 8 cm.

Size at maturity could not be determined using cumulative frequency analysis, because of reproductive

senescence of larger fish, possibly resulting in a classification of immature. Instead, length frequency distribution was used to approximate the size at which 50% of the population sampled was mature

(Beverton and Holt 1957). Overall, 50% of fish were mature in Lake Apoyo at 11 cm and in Lake Xiloá at 14 cm; 25% of females were mature in Lake Apoyo at 10 cm and in Lake Xiloá at 11 cm; and 25% of males were mature in Lake Apoyo at 13 cm and in Lake Xiloá at 16 cm.

Fisher's Exact Test was used to examine the association between gender and SL at maturation for each lake. For Lake Apoyo, a significant association was evident between SL at maturation and gender ( $P = 0$ ). For Lake Xiloá, the program did not converge; however, an initial chi-squared test of association yielded a test statistic value of 139.89, resulting in a  $P$  value approximating zero. We cannot rely on these results since we had expected cell counts less than 5, however we are confident that the Fisher's Exact Test would have resulted in the same conclusion as that of the chi-squared test and, hence, a significant association exists between SL at maturation and gender for Lake Xiloá as well.

Using the maximum sized fish (29.4 cm), the most conservative growth rate of 6.3 cm/year, and a maximum age of five years, a rough estimate of age at maturity was determined to be 1.1 years for Lake Xiloá. No fish were tagged in Lake Apoyo.

We compared sex ratio data between lakes using a two-sided test for proportions ( $\alpha = 0.05$ ). We found a significant difference between the proportion of male and female fish in both Lake Apoyo ( $P < 0.01$ ) and Lake Xiloá ( $P < 0.01$ ); in addition, we found a significant difference in the sex ratios between lakes ( $P < 0.01$ ). For Lake Apoyo, the overall female to male sex ratio was 1.7; the corresponding value for Lake Xiloá was 1.1.

## Discussion

### *Population growth*

The transect survey data of *G. dormitor* in Lake Apoyo showed an expanding population with exponential growth. This type of increase is common for invading species, and has been shown for other lakes where successful predators have been introduced. African tilapia in Lake Nicaragua have shown increased catches corresponding with an inverse catch rate of the native cichlids (McKaye et al. 1995). The Nile perch in Lake Victoria exhibited this type of growth, increasing slowly for 20 years before showing rapid population growth in 1984 (Kaufman 1992).

The growth of the *G. dormitor* population in Lake Apoyo should eventually reach an asymptote which will represent the carrying capacity (logistic growth). We believe the relatively low coefficient of determination of 0.497 for the monthly data is due to fluctuations resulting from immigration and emigration of *G. dormitor* to and from the transect sites. These transects are over rocks because they were originally chosen to monitor breeding of cichlid species, and therefore the survey data for the population growth estimates does not include populations over sand or vegetation beds where *G. dormitor* also occurs. Therefore, they are not necessarily representative of the entire lake's population; however, the attributes of transect sites are consistent between lakes and offer useful comparisons.

A cyclic pattern similar to the Lake Xiloá density curve could eventually occur in Lake Apoyo, when the carrying capacity is attained. The spread to deeper water by large individuals in Lake Apoyo is most likely driven by prey availability and intraspecific competition. Because sardine schools often contain thousands of individuals and have no physical refuge from predation, they are heavily preyed upon. Therefore, as sardine numbers become reduced through heavy predation, reduced availability of the main prey item may force *G. dormitor* to move deeper to find alternative prey. In addition, as the population expands, more intraspecific competition occurs at each depth, causing the population to spatially spread. Finally, the presence of two other piscivorous fish make interspecific competition a third factor in the *G. dormitor* depth expansion.

Although parameters such as temperature, oxygen content, habitat type, and predation pressure also can influence depth distributions of species, food availability is often the main mechanism behind distributions (Miltner et al. 1995). Piscivorous birds such as the cormorant (*Phalacrocorax olivaceus*) and herons (Family Ardeidae) prey upon young *G. dormitor*; however, transect and depth distribution analysis used only large (>10 cm) individuals; in addition, research team observations indicate that piscivorous birds do not heavily prey upon *G. dormitor*. Ontogenetic shifts in *G. dormitor* distribution can not be examined, because smaller fish usually occur in schools and moved rapidly in and out of the video transects, and because video does not allow detailed SL calculations; therefore, transect data could only be analyzed using only large (>10 cm SL) individuals. The depth distribution of *G. dormitor* is likely to continue to expand its range

gradually as a result of increased intraspecific competition, interspecific competition, and decreased prey availability.

#### *Growth and morphometrics*

Although there were large sample sizes for calculation of length/weight regressions, the slopes of the two lines for Lakes Apoyo and Xiloá are not significantly different. However, the otolith mass regressions on SL data do show a significant difference. This suggests that growth rates are different between lakes, with a faster growth rate possibly in Lake Apoyo. Although this method has not often been used to compare relative growth rates (Pawson 1990), studies have shown that unlike somatic growth, otolith growth is continuous throughout the life of a fish, making otolith mass a better indicator of fish age (Templeman and Squires 1956; Mosegaard et al. 1988; Francis et al. 1993). Thus, slower somatic growth can result in relatively larger otoliths, providing an index of relative growth rates between populations as we see between these two lakes (Spratt 1972; Marshall and Parker 1982; McGurk 1984; Wilson 1984; Neilson et al. 1985; Penny and Evans 1985; Reznick et al. 1989; Secor and Dean 1989). It should be noted, however, that this relationship between otolith mass and growth rate has not always been found to hold true (Geen et al. 1985; Rice et al. 1985), and that the relationship in this case remains to be verified.

Lake Apoyo fish of a certain length, therefore, may be younger than those of the same length in Lake Xiloá. Since the population in Lake Apoyo has been expanding, interspecific and intraspecific competition are relatively lower and overall food availability is higher per individual, possibly resulting in faster somatic growth rates and the achievement of maturity at a younger age.

#### *Diet composition*

A higher percentage of *G. dormitor* had food items in their stomachs in Lake Apoyo than in Lake Xiloá. Again, lower intraspecific competition and greater relative availability of selected food contribute to foraging success. Since effort was made to avoid sample bias, all times of day and depths were sampled randomly and sample sizes are high; therefore this trend is not believed to be a result of sampling inconsistency. *G. dormitor* appears to be inactive at night and

therefore no samples were taken then, although sampling did take place during the crepuscular periods. Although prey electivity indices could not be calculated because of the patchy prey distributions, in Lake Apoyo sardine schools containing hundreds to thousands of individuals were common and were seen on almost every dive. The invading population here exploited this widely available food resource. Cichlid broods were also available in Lake Apoyo as prey for *G. dormitor*, but at a lower density than either comparable cichlid broods or sardines in Lake Xiloá (McKaye, in preparation). Accordingly, this food source appears at a much reduced frequency in stomach analyses in Lake Apoyo, and no seasonality according to cichlid breeding season appeared. The third largest prey item, conspecifics, were present in reduced numbers throughout the year. The two prevalent cichlids in Lake Apoyo, adult *Parachromis managuense* and *Amphilophus zaliosum*, are piscivores and likely prey upon sardines as well, so interspecific competition plays a role in diet composition. Eventually, as the sardine population decreases from this new predation pressure, *G. dormitor* may actively seek other prey and therefore predation upon cichlid fry and conspecifics will increase.

#### *Cannibalism*

Cannibalism was present in both lakes, relatively low in Lake Apoyo year-round and in Lake Xiloá during the non-breeding season. As the population expands in Lake Apoyo, sardine schools may become reduced, necessitating *G. dormitor* to seek other sources of food with increasing frequency. Therefore, cannibalism will probably increase as a function of increased *G. dormitor* density and a lowered availability of alternate prey, resulting in a seasonal feeding pattern based on cichlid breeding in accordance with increasing cannibalism as sardine densities are reduced.

Systems with lower densities of alternative prey have been shown to favor higher rates of cannibalism (Leonardsson 1991). This is consistent with optimal foraging theory, which predicts that cannibalism will increase with decreasing quality and/or quantity of alternative prey (Polis 1981). Although alternative prey items are present, including catfish and shad, they are either in low abundance or have developed time refuges and therefore are not readily available. Therefore, cannibalism becomes most important in Lake Xiloá in the cichlid non-breeding seasons, a function both of an ecosystem at its carrying capacity and the seasonal

availability of prey items. Conspecifics can provide high nutritive value, especially with increasing size, and larger *G. dormitor* have a wider size range of conspecifics to forage upon.

McKaye et al. (1979b) found 45% cannibalism by *G. dormitor* in Lake Xiloá. Although they do not discuss the seasonality of feeding, a rate this high is consistent with the values of 46% and 50% found during the months immediately preceding and following the peak of the cichlid breeding seasons. This is also consistent with Gabriel's (1985) findings that cannibalism can help to stabilize a population during and after periods of food shortage. McKaye et al. (1979b) found that even when abundances of conspecific juveniles were low, adult *G. dormitor* attacked these juveniles more frequently than would be predicted by their numbers. This would indicate that *G. dormitor* may obtain relatively high nutritional value from cannibalism. The schooling behavior of *G. dormitor* fry supports this hypothesis, as it may have developed in response to intraspecific predation. In fact, in Lake Xiloá, McKaye et al. (1979a) showed that *G. dormitor* fry had a higher chance of being eaten if they were individually swimming rather than swimming in a school. Again, cannibalism is expected to become more important in Lake Apoyo as sardines are depleted and both intraspecific and interspecific competition resulting from increased population density occurs.

### Reproduction

The timing of breeding agrees with McKaye (1977), who found that a breeding peak occurred in May in Lake Xiloá for *G. dormitor*. He attributed this timing to the fact that competition for breeding sites between *G. dormitor* and larger cichlid species was low during this time, since the cichlids had completed their breeding cycle. Otherwise, during cichlid breeding, *G. dormitor* were found to be selectively mobbed out of breeding sites. Although the breeding seasonality for cichlids appears to have changed since the early 1970s (McKaye, in preparation), there still is little cichlid breeding occurring in the April–June time period.

Males appear to be the larger of the two sexes in both lakes, but females mature at a smaller size and age. Females in an expanding population often exhibit reproduction at an earlier age, a likely result of rapid growth and the attainment of maturity at a smaller size. In addition, the guarding of a nest would favor larger males than females. McKaye (1977) found that pair-

ing occurs prior to breeding in Lake Xiloá and that both parents defend an area from the point of territory acquisition through egg hatching. No care is provided after eggs hatch and fry become free swimming. We observed what appeared to be territory acquisition and courtship by a male in Lake Apoyo. Males obtain and defend a territory in order to attract gravid females. Thus, it is advantageous for a male to be large in that a larger nest area can be obtained and a greater number of eggs can be fertilized and cared for (Gross and Sargent 1985).

The size at which 50% of the population is mature differs (14 cm in Lake Xiloá vs 11 cm in Lake Apoyo), and since growth rates appear to be relatively faster in Lake Apoyo as shown by otolith mass vs SL regressions, fish are maturing not only at a smaller size but also younger age in Lake Apoyo. Relative to Lake Xiloá, higher prey resources, less intraspecific competition, and less interspecific competition all have contributed to the success of *G. dormitor* in its initial invasion of Lake Apoyo, Nicaragua.

### Conclusion

The population of *G. dormitor* in Lake Apoyo, Nicaragua displayed traits of a successfully invading, *r*-selected species – exponential growth achieved through high resource exploitation, rapid growth, early maturity, and year-round reproduction. Eventually, the population in Lake Apoyo will likely reach a carrying capacity and the population will be regulated by more density-dependent factors, including cannibalism from intraspecific competition, interspecific competition, and reduced prey availability.

The impact on the Lake Apoyo ecosystem during the integration phase of this invasion is uncertain. Oligotrophic lakes have shown sensitivity to disturbance, as with Lakes Tahoe and Gatun, Panama (Li and Moyle 1981). In Lake Gatun, the introduced peacock bass preyed heavily on *Melaniris chagresi*, also fed upon by *G. dormitor* in that lake; increased competition for a limited prey rendered this trophic web unstable and resulted in native fish extirpation (Zaret and Paine 1973). Piscivorous fish have been shown to have dramatic effects in lakes and streams where they have been introduced, especially where the system lacks a top-level piscivore, and invasions are more likely to be successful in systems geographically near native habitats (Moyle and Light 1996; Townsend 1996). Thus, the characteristics of both *G. dormitor* biology and the

Lake Apoyo ecosystem have contributed to invasion success.

If Moyle and Light's empirical rules for biological invasions of fresh water hold true for this invasion, the low diversity in this oligotrophic lake, the disturbance of this lake as a result of overfishing and poaching with explosives (Kenneth R. McKaye, personal communication), and the piscivorous habits of *G. dormitor* will likely result in trophic changes throughout Lake Apoyo (Strong 1992). However, since *G. dormitor* coexists with *Melaniris* spp. and cichlids in other tropical lakes, native species extinctions are not likely. Further studies are planned, especially in light of attempts to introduce additional species such as the Nile tilapia *Oreochromis niloticus* into Lake Apoyo.

### Acknowledgements

We thank the Universidad CentroAmericana in Managua and Nicaraguan Ministry of Natural Resources (MARENA) for their help and cooperation in making this study possible. We especially wish to thank Jamie Alonzo, Ramon Garcia, Jeremy Hale, Aldolfo Lopez, Mario Majia, Brent Murry, and Mona Schweighofer for their field assistance, and Stephanie Dunbar for statistics assistance. This study was supported by grants from the National Science Foundation, United States Agency for International Development and Fulbright Fellowships to McKaye and van den Berghe.

### References

- Arthington AH (1991) Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. *Canadian Journal of Fisheries and Aquatic Sciences* 48(Suppl 1): 33–43
- Barlow GW (1976) The Midas cichlid in Nicaragua. In: Thorson TB (ed) *Investigations of the Ichthyofauna of Nicaraguan Lakes*, pp 333–358. University of Nebraska, Lincoln
- Barlow CG, Hogan AE and Rodgers LJ (1987) Implication of translocated fishes in the apparent extinction in the wild of the Lake Eacham rainbowfish, *Melanotaenia eachamensis*. *Australian Journal of Marine and Freshwater Resources* 38: 897–902
- Beverton RJH and Holt SJ (1957) *On the dynamics of exploited fish populations*. Ministry of Agriculture, Fisheries and Food. *Fishery Investigations Series II, Vol XIX*. Her Majesty's Stationary Office, London, 533 pp
- Bruton MN (1990) The conservation of the fishes of Lake Victoria, Africa: an ecological perspective. *Environmental Biology of Fishes* 27: 161–175
- Courtenay WR, Jr and Stauffer JR, Jr (eds) (1984) *Distribution, Biology, and Management of Exotic Fishes*, Johns Hopkins University Press, Baltimore, Maryland, 430 pp
- Demestre M, Moli B, Recasens L and Sánchez P (1993) Life history and fishery of *Lepidopus caudatus* (Pisces: Trichiuridae) in the Catalan Sea (Northwestern Mediterranean). *Marine Biology* 115: 23–32
- Elton CS (1958) *The Ecology of Invasion by Plants and Animals*, Methuen, London, 181 pp
- Francis MP, William MW, Pryce AC, Pollard S and Scott SG (1993) Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). *Fisheries Bulletin* 91: 159–164
- Gabriel W (1985) Overcoming food limitation by cannibalism: a model study on cyclopoids. *Archiv für Hydrobiologie* 21: 373–381
- Geen GH, Neilson JD and Bradford M (1985) Effects of pH on the early development and growth and otolith microstructure of chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Zoology* 63: 22–27
- Gross MR and Sargent RC (1985) The evolution of male and female parental care in fishes. *American Zoology* 25: 807–822
- Groves RH and Burdon JJ (1986) *Ecology of Biological Invasions*. Cambridge University Press, Cambridge
- Hedgpeth JW (1993) Foreign invaders. *Science* 261: 34–35
- Heins DC and Baker JA (1989) Growth, population structure, and reproduction of the percid fish *Percina vigil*. *Copeia* 3: 727–736
- Hoenig JM (1983) Empirical use of longevity data to estimate mortality rates. *Fisheries Bulletin* 82: 898–903
- Holčik J (1991) Fish introduction in Europe with particular reference to its Central and Eastern part. *Canadian Journal of Fisheries and Aquatic Sciences* 48(Suppl 1): 13–23
- Kaufman L (1992) Catastrophic change in species-rich freshwater ecosystems: The lessons of Lake Victoria. *BioScience* 42(11): 846–858
- Leonardsson K (1991) Effects of cannibalism and alternative prey on population dynamics of *Saduria entomon* (Isopoda). *Ecology* 72(4): 1273–1285
- Li HW and Moyle PB (1981) Ecological analysis of species introductions into aquatic systems. *Transactions of the American Fisheries Society* 110: 772–782
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8(4): 133–137
- Marshall SL and Parker SS (1982) Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 542–547
- McGurk MD (1984) Ring deposition in the otoliths of larval pacific herring, *Clupea harengus pallasii*. *Fisheries Bulletin* 82: 113–120
- McKaye KR (1977) Competition for breeding sites between the cichlid fishes of Lake Xiloá, Nicaragua. *Ecology* 58: 291–302
- McKaye KR, Weiland DJ and Lim TM (1979a) Comments on the breeding biology of *Gobiomorus dormitor* (Osteichthyes: Eleotridae) and the advantage of schooling behavior to its fry. *Copeia* 1979(3): 542–544
- McKaye KR, Weiland DJ and Lim TM (1979b) The effect of luminance upon the distribution and behavior of the eleotrid fish, *Gobiomorus dormitor* and its prey. *Review Canadian Biology* 38: 27–36
- McKaye KR, Ryan JD, Stauffer JR, Jr, Lopez Perez LJ, Gabriel I Vega and van den Berghe EP (1995) African tilapia in Nicaragua: ecosystem in transition. *BioScience* 45(6): 406–411

- Miller DJ (1989) Introductions and extinction of fish in the African Great Lakes. *Trends in Ecology and Evolution* 4(2): 56–59
- Miller RR (1966) Geographical distribution of Central American freshwater fishes. *Copeia* 4: 773–802
- Miltner RJ, Ross SW and Posey MH (1995) Influence of food and predation on the depth distribution of juvenile spot (*Leiostomus xanthurus*) in tidal nurseries. *Canadian Journal of Fisheries and Aquatic Sciences* 52(5): 971–982
- Mosegaard H, Svedäng H and Taberman K (1988) Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1514–1524
- Moyle PB and Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78: 149–161
- Neilson JS, Geen GH and Bottom D (1985) Estuarine growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 899–908
- Ogutu-Ohwayo R (1990) The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fish* 27: 81–96
- Pawson MG (1990) Using otolith weight to age fish. *Journal of Fish Biology* 36: 521–531
- Penny RW and Evans GT (1985) Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1452–1464
- Polis GA (1981) The evolution and dynamics of intraspecific predation. *Annual Review of Ecological Systems* 12: 225–251
- Reidel D (1965) Some remarks on the fecundity of Tilapia (*T. mossambica* Peters) and its introduction into middle Central America (Nicaragua) together with a first contribution towards the limnology of Nicaragua. *Hydrobiologica* 25: 357–388
- Reznick DN, Lindbeck E and Bryga H (1989) Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 46: 108–112
- Rice JA, Crowder LB and Binkowski FP (1985) Evaluating otolith analysis for bloater *Coregonus hoyi*: do otoliths ring true? *Transactions of the American Fisheries Society* 114: 532–539
- Secor DH and Dean JM (1989) Somatic growth effects on the otolith–fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 113–121
- Spratt JD (1972) The use of otoliths to separate groups of northern anchovies. California Department of Fish and Game Marine Technical Report 1: 25 pp
- Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747–754
- Templeman W and Squires HJ (1956) Relationship of otolith lengths and weights in the haddock *Melanogrammus aeglefinus* (L.) to the rate of growth of the fish. *Journal of the Fisheries Research Board of Canada* 13(4): 467–487
- Townsend CR (1996) Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation* 78: 13–22
- United States Environmental Protection Agency (February 1991) Ecology and management of the zebra mussel and other introduced aquatic nuisance species. EPA/600/3-91/003, Washington, DC
- Villa J (1982) Peces nicaraguenses de agua dulce. Colección Cultural, Banco de America, Managua, Nicaragua, 253 pp
- Waid R (1991) The distribution of the fishes of the crater lakes of Nicaragua. MS thesis, Frostburg State University, Frostburg, Maryland, Department of Biology, Wildlife/Fisheries Biology Program
- Wilson CA (1984) Age and growth aspects of the life history of billfishes. PhD thesis, University of South Carolina, Columbia, South Carolina
- Zaret TM and Paine RT (1973) Species introduction in a tropical lake: a newly introduced piscivore can produce population changes in a wide range of trophic levels. *Science* 182: 449–455