

## ARTICLE

# Age, Growth, and Mortality Rates of the Giant Cichlid in Guatemala

Christian A. Barrientos\*<sup>1</sup> and Debra J. Murie

Program of Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, University of Florida,  
7922 Northwest 71st Street, Gainesville, Florida 32653, USA

Jeffrey E. Hill

Program of Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, University of Florida,  
7922 Northwest 71st Street, Gainesville, Florida 32653, USA; and Tropical Aquaculture Laboratory, Program of Fisheries  
and Aquatic Sciences, School of Forest Resources and Conservation, University of Florida, 1408 24th Street Southeast,  
Ruskin, Florida 33570, USA

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### Abstract

Age, growth, and mortality were assessed in Giant Cichlids *Petenia splendida* from lakes in northern Guatemala by using cross-sectioned sagittal otoliths. Marginal increment and edge analyses of Giant Cichlid otoliths indicated that one annulus formed per 12-month period in Lakes Yaxhá and Petén Itza. Opaque zone formation was associated with the peak of the rainy season from May to September. Ages ranged from 0 to 8 years for Giant Cichlids in Lake Yaxhá and from 0 to 5 years in Lake Petén Itza. Within both lakes, males were larger than females, although the difference was slight in Lake Petén Itza. Lake Yaxhá Giant Cichlids had faster growth rates than those from Lake Petén Itza, and fish over 2 years old from Lake Yaxhá were larger at age than fish from Lake Petén Itza. This is counter-intuitive because Lake Petén Itza is heavily exploited, whereas Lake Yaxhá is unfished. However, long-term exploitation in Lake Petén Itza may have resulted in selection for fish with reduced growth rates. Alternatively, the mesotrophic state of Lake Yaxhá may explain the differences in growth, although areas of Lake Petén Itza are changing from oligotrophic to meso-eutrophic due to rapid cultural eutrophication. Total mortality ( $Z$ ) estimates for Giant Cichlids were 0.81 for Lake Yaxhá, with most of the age structured on 2–4-year-old fish, and 1.05 for Lake Petén Itzá, where the age structure was dominated by 0–2-year-old fish; these results were consistent with expectations based on the low fishing pressure in Lake Yaxhá.

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Age estimation is critical in determination of growth, survival, and mortality of fishes and can be linked to different environmental factors that affect those life history variables. Today, growth models based on age are used routinely, and fish stocks are often managed with age-structured models (Walters and Martell 2004). Calcified structures in fish, such as otoliths, scales, and vertebrae, that display sub-annual (Bwanika et al. 2007) or annual

(Beckman and Wilson 1995) resolution are key in aging fishes.

Using otoliths to determine the age of fish is widely accepted and used mostly in temperate zones (Campana 2001) because of the strong intra-annual temperature differences, which in turn affect growth patterns in the otoliths, making them act as “natural data loggers” (Beckman and Wilson 1995). The physiological origin of the growth

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\*Corresponding author: cbarrientos@wcs.org

<sup>1</sup>Present address: Wildlife Conservation Society, Equatorial Guinea Coastal Resources Management Program, Edificio Candy Vistamar, Ciudad de Bata, Equatorial Guinea.

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zones in calcified structures is not clear (Ferreira and Russ 1994), but both abiotic and biotic factors probably play a role in creating “growth zones.” Aging of tropical fishes, however, is more difficult because of the less-extreme differences in temperature throughout the year and therefore more consistent year-round growth, which leads to difficulty in discerning “macro-zones” that correspond to fast- and slow-growth periods. Although seasonal fluctuations in temperature are not as extreme as in temperate latitudes, other seasonal cycles are important, such as wet and dry seasons (Bwanika et al. 2007). Although it is more difficult, otoliths can be used to age fish from tropical zones successfully (Beckman and Wilson 1995; Bwanika et al. 2007; Efitre et al. 2016).

Growth provides a general assessment of habitat suitability, prey availability, and the influence of management activities. Because fishing reduces intraspecific competition, populations at carrying capacity can be released from density-dependent processes, which results in faster growth (Law 2000). Faster growth provides larger fish for fishers. Individual growth rates can influence the size at which fish reach maturity, and vice versa. Thus, the assessment of growth is one of the most important steps in managing a fishery (Walters and Martell 2004).

Among the most conspicuous effects of fishing on populations is increased mortality. Fishing gear often selects for larger-sized individuals and indirectly selects for older or faster-growing individuals. Thus, high fishing mortality can result in overfished and depleted stocks largely consisting of smaller individuals that reach sexual maturity at younger ages (Meyers and Worm 2003; Orensanz et al. 2005). A consequence of this is that strong size-selective fishing mortality over time leads to a downward shift in the size at age (Olsen et al. 2004). Mortality can be estimated by a variety of methods (e.g., catch curve, telemetry, and mark-recapture), but the most well-known methods depend on reliable age estimates.

Only a few age and growth studies using otoliths of fish in tropical areas have been undertaken, mainly for African cichlids. Egger et al. (2004) found contrasting otolith growth zones in cichlids that were a consequence of seasonal rainfall differences in Lake Tanganyika. Bwanika et al. (2007) found definable “bi-annuli” (two opaque/translucent zones per year) in Nile Tilapia *Oreochromis niloticus*, which were related to wet and dry seasons in two lakes in Uganda. In tropical America, there are even fewer examples of comprehensive readings of macro-zone formation. Noiset and Micha (1996) compared aging with scales, otoliths, and length frequencies in Giant Cichlids *Petenia splendida* from the San Pedro River, Mexico, and reported that all of the hard structures formed a single annulus per year. A lack of older age-groups due to high fishing pressure made it impossible to determine all of the parameters in the growth model (i.e., asymptotic length

$L_{\infty}$ ). Because of these missing parameters, Noiset and Micha (1996) were unable to estimate mortality.

The Giant Cichlid is the target of the most important freshwater artisanal fishery in northern Guatemala and southern Mexico. Aquatic ecosystems like Lake Yaxhá, Guatemala, which have minimal habitat transformation and no artisanal fishery, are exceptionally difficult to find (Granados-Dieseldorff et al. 2012; Barrientos et al. 2016). Thus, Lake Yaxhá provides a rare unfished situation for comparison with Lake Petén Itzá, Guatemala, where an artisanal fishery has long been established. We examined the age, growth, and mortality of the Giant Cichlid in Lakes Petén Itzá and Yaxhá. The specific objectives were to (1) develop an aging method using otoliths, (2) create an age-length key to determine population age structure, (3) model sex-specific growth, and (4) estimate total mortality and survival rates by using age-based catch curves.

## METHODS

**Study area.**—Petén, Guatemala, is the southern extent of the Yucatan Peninsula, a large marine limestone platform in Central America. Petén encompasses a lake district comprising about 14 large water bodies, of which Lake Petén Itzá is the largest (~100 km<sup>2</sup>) and Lake Yaxhá is the second largest (~7.4 km<sup>2</sup>; Figure 1). Most of Petén lies within the greater Usumacinta River basin, which includes all of the major rivers and the border zone with Mexico. Annual rainfall can vary from about 1,200 to 2,000 mm, and such interannual precipitation fluctuations drive shifts in regional lake levels (Deevey et al. 1980).

Lake Petén Itzá owes its origin to a combination of limestone dissolution and tectonism. It is about 32 km long and 3 km wide, with a maximum water depth of approximately 165 m. It is thought to be the deepest lake in lowland Central America. The lake has two elongated basins that run east-west. The larger northern basin supports at least four towns along its shoreline, but the smaller southern basin supports the largest population (~160,000; National Statistics Institute 2016). The lake is a closed hydrologic basin with no visible outlet, and the water level fluctuates, with a slight lag, in response to the amount of precipitation. The lake is primarily oligotrophic, but the southern basin is changing to meso-eutrophic due to rapid cultural eutrophication. The littoral zone, with a variety of plant species, is most extensive in the shallow western part of the southern basin. Although fishing is not legal, there is an artisanal fishery with gill nets based on Giant Cichlids as well as other cichlids in the lake (Barrientos and Quintana 2012). The fish species are similar between Lake Petén Itzá and Lake Yaxhá except for two introduced taxa (Nile Tilapia and sailfin catfish *Pterygoplichthys* sp.) that are occasionally found in the former (Barrientos et al. 2016).

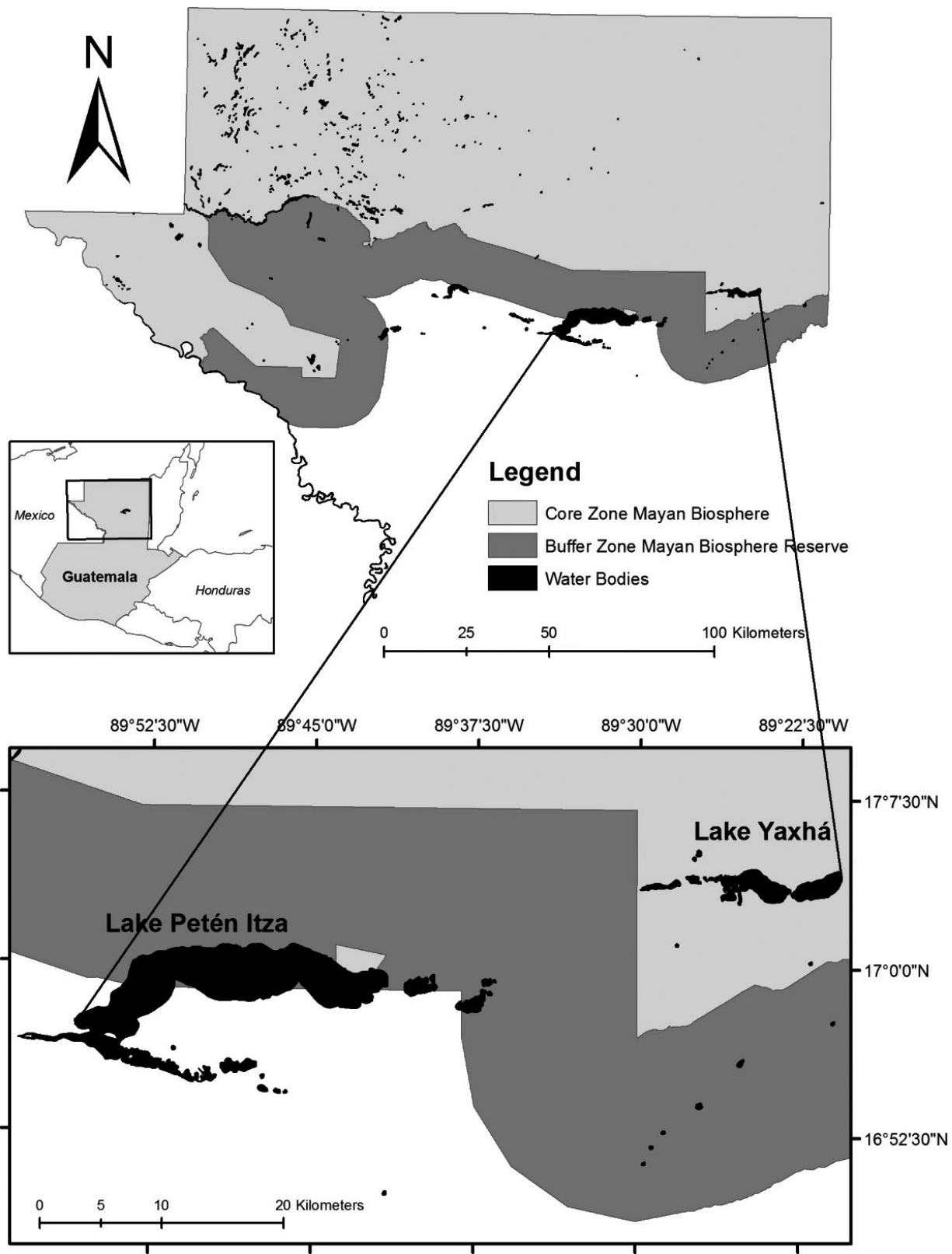


FIGURE 1. Map of the Mayan Biosphere Reserve, showing the locations of Lake Petén Itza and Lake Yaxhá in northern Guatemala.

Lake Yaxhá is part of the Mopan River basin, which is oriented in an east–west direction in the southern part of the Yaxhá-Nakum-Naranjo National Park. The lake's origin is attributed to tectonic/solution processes, similar to Lake Petén Itzá. It is about 4 km long and 1 km wide, with a maximum depth of about 26 m. Access to the lake is limited to approximately 15 km of nonpaved road, which restricts vehicle visits during the rainy season. Within the lake, there are only a few small boats that are used for transport to the archaeological site of Topoxte. Fishing in the lake is prohibited. The National Council of Protected Areas (Consejo Nacional de Areas Protegidas [CONAP]) and the Institute of Anthropology and History (Instituto de Antropología e Historia) share park administration. Lake Yaxhá is mesotrophic and differs from Lake Petén Itzá because cultural eutrophication does not play a large role due to (1) the location of Lake Yaxhá within the Mayan Biosphere Reserve (MBR) and (2) the lack of communities along Lake Yaxhá's shores. Only a few farms are located along the southern basin of Lake Yaxhá.

**Sampling.**—Fish were collected using a boat-mounted electrofisher (Model 1.5 kVA; Smith-Root, Vancouver, Washington) with an electrical output of 5–8 A of pulsed DC in shoreline areas where water depth usually ranged from 1.0 to 2.5 m. Sampling of the lakes was completed monthly from March to October 2011 in both lakes on the same dates. Sampling usually lasted 2 d, and an attempt was made to capture 30 fish per sampling day. All fish were stored on ice for transport to the laboratory. Fish were measured for TL to the nearest 1 mm, blotted dry, and weighed whole to the nearest 0.1 g. Both sagittal otoliths were extracted, cleaned, dried, and stored dry in plastic vials with a collection number until processed for aging. Gonads were removed and weighed, and the sex of individual fish was determined using visual examination of the gonads. Small fish (<100 mm TL) that could not be sexed were designated as immature.

The sex-specific and lake-specific condition of each fish was analyzed using a power function fitted to length and weight,

$$W = a(TL^b), \quad (1)$$

where  $W$  is the whole wet weight (g) without gonads,  $a$  is the coefficient, TL is the total length (mm) of the fish, and  $b$  is the power exponent. The length–weight relationship was fitted separately for males and females in each lake. We transformed the data ( $\log_e$ ) and used ANCOVA to determine whether the parameters of the length–weight relationship were different between lakes, between sexes, or among months sampled. Length frequencies for Giant Cichlid males and females were compared using Kolmogorov–Smirnov (K–S) tests to detect potential differences between

sexes and between lakes. For all statistical tests, the significance level  $\alpha$  was set at 0.05.

**Age estimates and validation.**—The left otolith was used to estimate Giant Cichlid age, whereas the right otolith was used in the case of loss or damage to the left otolith. Whole otoliths were used initially and were immersed in water and examined under a stereoscope (Figure 2). However, because of the difficulty in seeing more than one annulus in whole otoliths, which might result in an underestimate of age, any otolith with at least one annulus was cross-sectioned (Ferreira and Russ 1994; Newman et al. 2000). For this method, each otolith was secured to a frosted glass slide with mounting adhesive (Crystalbond 509; Arenco Products, Valley College, New York) and was cross-sectioned into two different thicknesses (0.2 and 0.4 mm) through the core region using a low-speed saw (350 rpm). The Crystalbond was then reheated to remove the otolith sections, with the sections then permanently mounted on a clear, labeled slide using Histomount (National Diagnostics, Atlanta; Figure 3).

Cross-sections of otoliths were used to identify the opaque and translucent growth zones. The opaque zones were counted close to the sulcus, but sections were still difficult to read because of problems such as split or indistinct opaque zones. Each otolith section was aged two times by the same reader using a Leica stereoscope (10–40 $\times$ ) with transmitted light to count opaque growth zones. There was a 6-week interval between the first and second readings. If there was a discrepancy between the first and second readings, then a third reading was performed 6 weeks later. All age estimations were made without knowledge of sampling date, TL, or any other information.

The periodicity of annulus formation was validated using edge analysis and marginal increment analysis. For edge analysis, the percentage of fish having otoliths with an

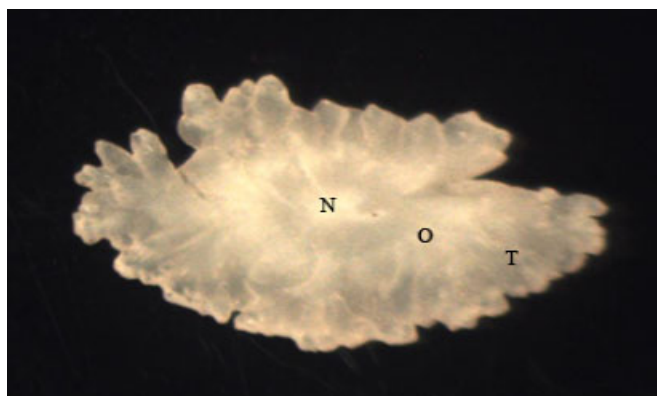


FIGURE 2. A whole sagittal otolith from a Giant Cichlid captured at Lake Petén Itzá, Guatemala, showing the nucleus (N), an opaque zone (O), and a translucent zone (T). [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]



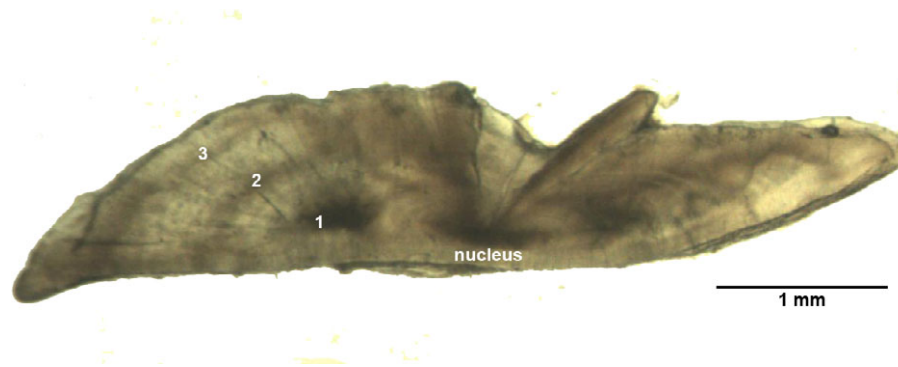


FIGURE 3. Otolith section from a 3-year-old Giant Cichlid sampled from Lake Petén Itzá, Guatemala, showing the annuli (alternating opaque and translucent zones) counted for age estimation. [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]

opaque zone versus a translucent zone on the edge was plotted monthly. One minimum and one maximum in a 12-month plot indicated annual deposition of the growth zones, whereas two minima and two maxima would indicate bi-annuli (two complete annuli per 12-month period). In marginal increment analysis, the relative amount of the translucent zone at the edge was measured. The periodicity in the marginal increment deposition was then determined using the index of completion ( $C$ ; Tanaka et al. 1981) as:

$$C = 100(W_n/W_{n-1}),$$

where  $W_n$  is the width of the marginal increment and  $W_{n-1}$  is the width of the previously completed annulus.

Fish were assigned to age-classes based on the number of annuli and the growth at the edge of the otolith, which was recorded as (a) opaque zone on the edge (edge code = 0); (b) narrow translucent zone at the edge (width less than about 30% of the previous increment; edge code = 1); (c) medium translucent zone at the edge (width about 30–60% of the previous increment; edge code = 2); and (d) wide translucent zone at the edge (width more than 60% of the previous increment, edge code = 3; Harris et al. 2007). Depending on the edge type and collection date, ages were assigned to individual fish through advancing or not advancing counts of annuli (i.e., fish with two annuli and an edge code = 3 in March were advanced to age-class 3). To assess the precision of age readings, we used Hoenig's test of symmetry (Hoenig et al. 1995), the coefficient of variation (CV; Chang 1982), and the average percent error (APE; Beamish and Fournier 1981).

**Growth of Giant Cichlids.**—To assign ages to Giant Cichlids that were only measured and not aged directly, age-length keys were constructed for each lake separately. Age-length keys were based on pooling of the sexes, however, because in the fishery the sexes are not distinguished. Age data were grouped into 20-mm length-classes.

To model age and growth of Giant Cichlids, von Bertalanffy growth curves were fitted to observed TL at observed age data for males and females from each of the

two lakes separately (Ricker 1975). The form of the von Bertalanffy growth curve for modeling fish length as a function of age was:

$$L_t = L_\infty \{1 - e^{[-k(t-t_0)]}\}, \quad (2)$$

where  $L_t$  is the TL (mm) at age  $t$  (years);  $L_\infty$  is the asymptotic TL (mm);  $k$  is the Brody growth coefficient, which measures the rate at which the average maximum size is reached; and  $t_0$  is the theoretical age (years) at zero length. We tested for homoscedasticity and normally distributed errors by using a plot with residuals versus fitted values and a histogram of the residuals. We used Akaike's information criterion (AIC) to test for differences among reduced or complete models. An AIC difference ( $\Delta AIC$ ) larger than 2 was considered significant (Taper 2004). For complete models, we used different  $L_\infty$ ,  $k$ , and  $t_0$  values for males and females in the same lake. Because we found differences between males and females ( $AIC > 2$ ), we compared sex-specific data between lakes. We also used a two-way ANOVA with main effects of lake and sex, using length as the response variable to test for differences in lengths for each age-class.

**Estimates of total mortality.**—Total mortality ( $Z$ ) was determined using catch curve analysis (Ricker 1975) with the Chapman and Robson (1960) mortality estimator. We used only fish that were fully recruited to the gear in the initial years (i.e., only the descending right limb of the catch curve). For Lake Petén Itzá, this was age 1; for Lake Yaxhá, it was age 2. Fish aged using a lake-specific age-length key (i.e., not directly aged using otoliths) were included in the catch curve analysis. Chapman and Robson (1960) suggested that age-classes older than the age when the catch falls below five individuals should be excluded. We followed the recommendation of Dunn et al. (2002), who suggested one individual as the cutoff and showed that the regression performed better when using all available age-classes based on error estimation and relative accuracy.

Survival ( $S$ ) was then estimated from  $S = e^{-Z}$ , where  $Z$  is the instantaneous total annual mortality (Ricker 1975).

We estimated the total annual survival using the following relationship:  $S = 1 - A$ , where  $A$  is annual mortality. We estimated natural mortality ( $M$ ) using the equation proposed by Hewitt and Hoenig (2005):  $M = 4.22/t_{max}$ , where  $t_{max}$  is the maximum age (years) observed. Considering that Lake Petén Itzá probably has a truncated size and age distribution, lacking in older fish due to fishing, we also used Lake Yaxhá's nonfishing situation to estimate  $M$  for both lakes since it is assumed that  $Z = M$  in that instance, and we used the Hewitt and Hoenig (2005) equation only as a comparative reference point.

## RESULTS

In total, 667 Giant Cichlids were collected in 2011: 339 from Lake Petén Itzá, the fished lake, and 327 from Lake Yaxhá, the nonfished lake. Fish ranged from 40 to 393 mm TL in Lake Petén Itzá and from 44 to 436 mm TL in Lake Yaxhá. The size distribution of males was skewed toward larger fish than the size distribution of females in both Lake Petén Itzá (K-S test:  $P < 0.0005$ ) and Lake Yaxhá (K-S test:  $P < 0.0001$ ); males and females were therefore separated in all analyses. In addition, the size distributions in Lake Petén Itzá showed a higher frequency of smaller fish, regardless of sex, compared to Lake Yaxhá (K-S test:  $P < 0.0001$ ; Figure 4).

There was a difference in the length–weight relationship between sexes in Lake Petén Itzá (ANCOVA slopes:  $P = 0.0146$ ; intercepts:  $P = 0.0143$ ), so we used different models for males ( $W = [2 \times 10^{-6}]TL^{3.2787}$ ;  $r^2 = 0.948$ ) and females ( $W = [3 \times 10^{-7}]TL^{3.6384}$ ;  $r^2 = 0.906$ ). However, we know that it is usually difficult for fishermen or enforcement agency personnel to distinguish the sex of the fish, and so we also calculated an equation using pooled data for Lake Petén Itzá ( $W = [5 \times 10^{-6}]TL^{3.1489}$ ;  $r^2 = 0.972$ ). Conversely, no difference between sexes was found for Lake Yaxhá (ANCOVA slopes:  $P = 0.64$ ; intercepts:  $P = 0.67$ ); thus, we pooled all data from the lake ( $W = [6 \times 10^{-6}]TL^{3.1245}$ ;  $r^2 = 0.984$ ). The common equation for both lakes combined (size range = 40–436 mm) was  $W = (5 \times 10^{-6})TL^{3.1311}$  ( $r^2 = 0.982$ ). Weight at length in March was lower than the values observed for all other months; thus, it was excluded from the common equation for both lakes (ANCOVA slopes:  $P = 0.0007$ ; Figure 5).

Edge analysis validated the aging criteria used to assign ages to Giant Cichlids. All Giant Cichlid ages ( $>0$ ) were used in the edge analysis. The majority of Giant Cichlids deposited an opaque zone between May and September, represented by the unimodal plot (Figure 6). The period of the opaque zone deposition coincided with the major peaks of the rainy season. Conversely, the translucent zones were widest at the beginning and end of the rainy season, as indicated by the higher  $C$ -values. Based on validation of the aging method for Giant Cichlids, fish age

was estimated as the number of opaque annuli in the otolith sections, which was reasonable despite the fact that we did not obtain samples during the dry season (i.e., November–February). Because of the unimodal plot, we assumed that fish sampled in March, April, and May with an edge code of 3 were going to form an opaque zone imminently, and these fish were therefore advanced 1 year (e.g., annulus count + 1) to assign them into the correct age cohort.

Giant Cichlids collected in Lake Petén Itzá were 0–5 years old ( $N = 225$ ), and those collected in Lake Yaxhá were 0–8 years old ( $N = 254$ ). Lake Petén Itzá was dominated by age-1 (35%) and age-0 (33%) fish, whereas Giant Cichlids sampled from Lake Yaxhá showed a unimodal age distribution dominated by age-3 individuals (30%; Figure 7). Despite difficulties in reading and interpreting otolith growth zones, the precision between age readings was relatively high, with 85% agreement between the first and second age estimates, a CV of 4.41%, and an APE of 3.12%. There was also no deviation from the 1:1 relationship in ages assigned between the first and second reads (Hoenig's test of symmetry:  $\chi^2 = 6.61$ ,  $df = 5$ ,  $P = 0.25$ ). An age bias plot with 95% confidence intervals did not reveal nonlinear biases in precision caused by underestimation or overestimation of age (Figure 8). All aging precision tests indicated that sagittal otolith sections were precise for use in aging Giant Cichlids.

The age–length keys for Giant Cichlids from each lake showed a range of ages for any given size, indicating variability in growth. For Lake Petén Itzá, a 290-mm TL fish could be 1–4 years old, with approximately 58% estimated to be age 2 (Table 1). In Lake Yaxhá, a 290-mm TL fish could be 1–5 years of age, with the majority estimated to be age 2 or 3 (Table 2). In addition, the largest (i.e.,  $>350$ -mm) fish in Lake Petén Itzá were all older fish (ages 4 and 5; Table 1). The largest fish from Lake Yaxhá, however, were not always the oldest (Table 2).

Based on a low AIC score (Tables 3, 4), the best model for the growth of Giant Cichlids in both lakes was observed when separate growth curves containing  $L_{\infty}$  and  $k$  were retained for each sex, but with an equal  $t_0$  set to an estimate for all pooled fish regardless of sex, despite a nonsignificant difference in the AIC score for Lake Petén Itzá (Table 5). Total length at age was larger for males than for females in Lake Petén Itzá ( $F_{3,1} = 31$ ,  $P < 0.0001$ ) and in Lake Yaxhá ( $F_{3,1} = 107$ ,  $P < 0.0001$ ; Figure 9; Table 6). On average, males from Lake Petén Itzá had lower TL at age than males in Lake Yaxhá ( $F_{3,1} = 15.32$ ,  $P < 0.0001$ ). On average, females from Lake Yaxhá were not significantly different in TL at ages greater than 2 ( $P > 0.05$ ), whereas males had no difference in TL at ages greater than 3 ( $P > 0.05$ ), indicating a reduced growth rate beyond age 2 in females and age 3 in males (Table 6).

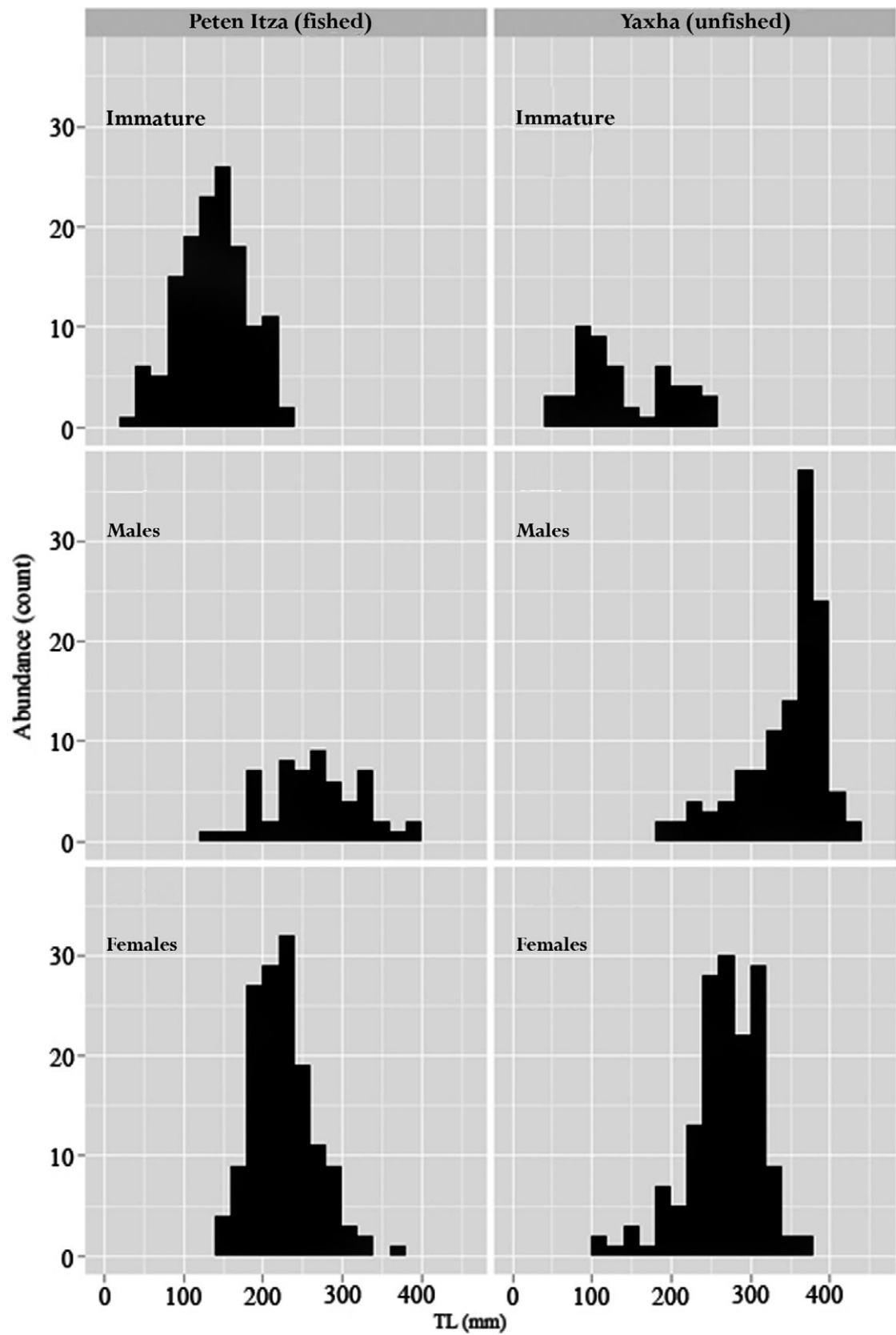


FIGURE 4. Length–frequency distribution by sex of Giant Cichlids from Lake Petén Itzá and Lake Yaxhá, Guatemala.

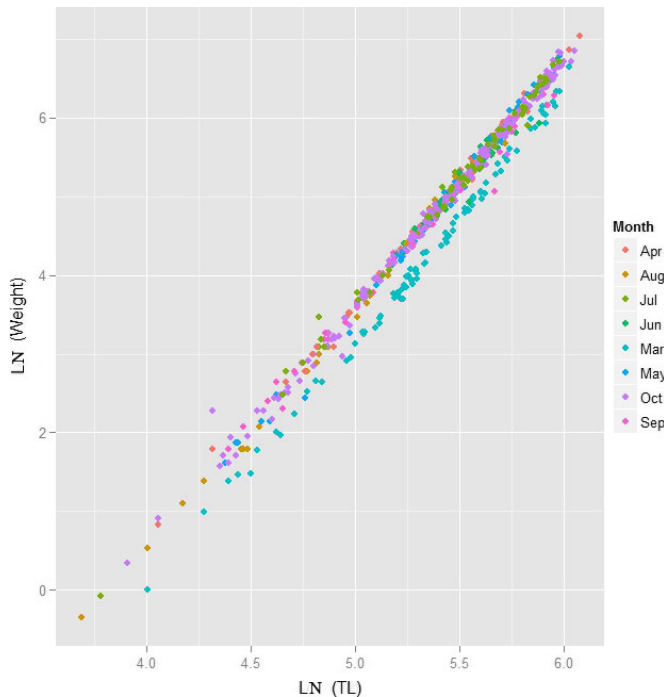


FIGURE 5.  $\text{Log}_e(\text{total body weight, g})$  as a function of  $\text{Log}_e(\text{TL, mm})$  by month for Giant Cichlids from Lake Petén Itzá and Lake Yaxhá, Guatemala. [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]

Instantaneous total mortality ( $Z$ ) did not differ among fully recruited females (ages 2–5) and males (ages 2–5) in Lake Petén Itzá (ANCOVA homogeneity of slopes:

$P = 0.51$ ); likewise, there was no difference in  $Z$  between females (ages 3–5) and males (ages 3–5) in Lake Yaxhá (ANCOVA homogeneity of slopes:  $P = 0.15$ ). Therefore, we pooled  $\text{log}_e(\text{catch})$  as a function of age for both sexes from Lake Yaxhá ( $r^2 = 0.76$ ) and Lake Petén Itzá ( $r^2 = 0.70$ ; Figure 10). The  $Z$ -value estimated for Lake Petén Itzá (ages 2–5) was not significantly different from that estimated for Lake Yaxhá (ages 2–5; ANCOVA homogeneity of slopes:  $P = 0.06$ ). Natural mortality for Lake Petén Itzá ( $M = 0.81$ ) was therefore set equal to  $Z$  from Lake Yaxhá ( $M = Z$ ) based on the unfished state of Lake Yaxhá (Table 7). The Hewitt and Hoenig (2005) estimator of  $M$  produced values of 0.84 for Lake Petén Itzá and 0.52 for Lake Yaxhá (Table 7).

## DISCUSSION

Contrasting Giant Cichlid age, growth, and size/age distribution in lakes that are subject to different fishing pressure scenarios adds to the understanding of fish population responses to induced high mortality of large individuals. Sex-specific differences in growth, size structure, and age structure were evident between Giant Cichlids from Lake Petén Itzá, which is a fished lake, and those from Lake Yaxhá, which is subject to no fishing. It was counterintuitive, however, that Giant Cichlids from Lake Petén Itzá grew slower than those from Lake Yaxhá. Growth can be influenced by a variety of factors, including environment, fishing, and genetics. Fishing pressure in Lake

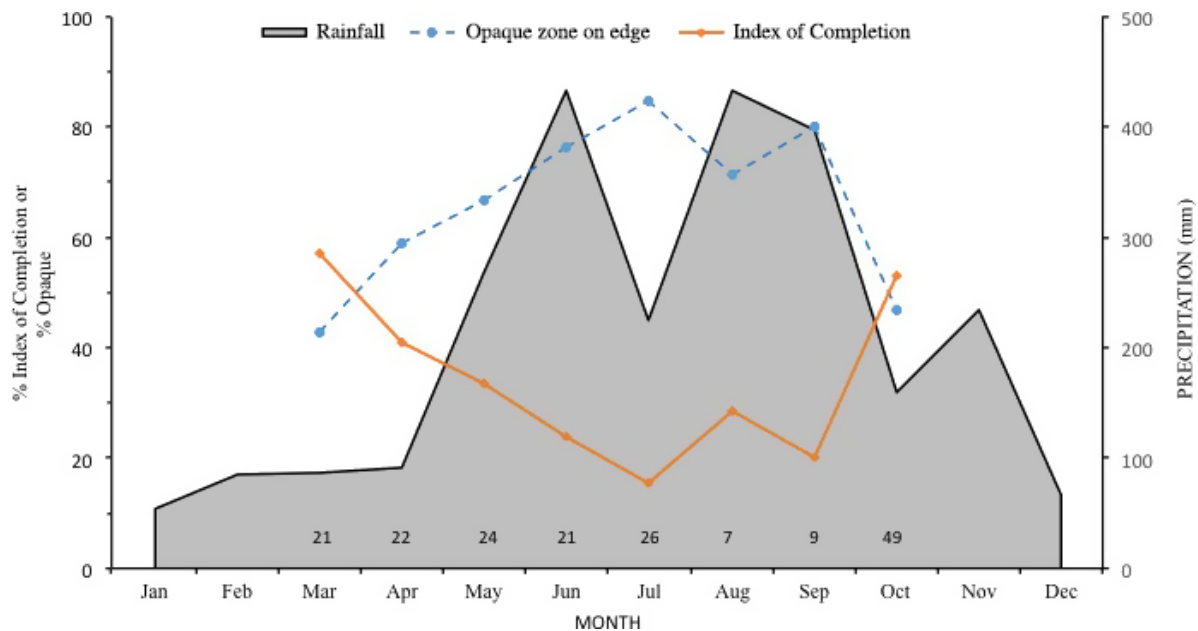


FIGURE 6. Monthly percent occurrence of the opaque zone at the edge and the percent index of completion of the translucent zone in otoliths of Giant Cichlids sampled from Lake Yaxhá and Lake Petén Itzá, Guatemala, relative to monthly precipitation at Lake Petén Itzá. Numbers above the x-axis represent sample sizes. [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]



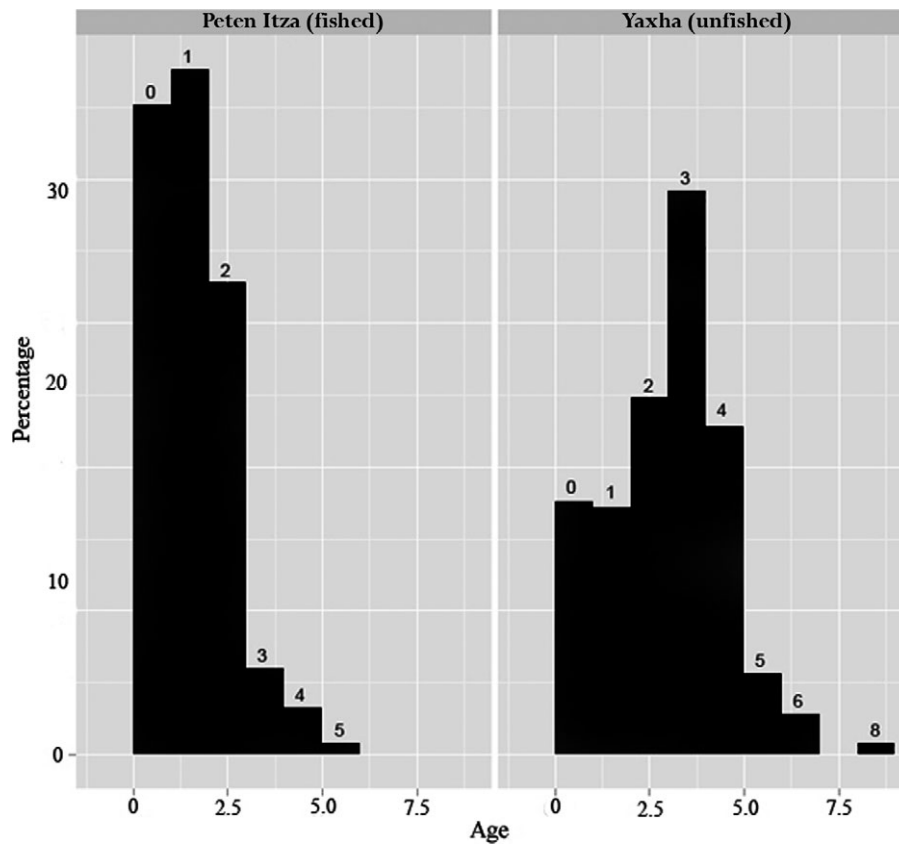


FIGURE 7. Age frequency distributions for Giant Cichlids collected by electrofishing in Lake Petén Itzá ( $n = 339$ ) and Lake Yaxhá ( $n = 327$ ), Guatemala.

Petén Itzá should reduce intraspecific competition, which in turn should result in higher growth rates (Walsh et al. 2006), but we found exactly the opposite with growth differences between Lakes Petén Itzá and Yaxhá. Conversely, low fishing pressure may result in high population density, which increases competition for resources, leading to density-dependent growth (i.e., slower growth), but we found the opposite in Lake Yaxhá. One plausible explanation could be that productivity differs between the two lakes. Based on Secchi disk measurements (Canfield et al. 1983; Perez et al. 2011), Lake Yaxhá is mesotrophic and Lake Petén Itzá is oligotrophic. The latter trophic state would naturally be associated with reduced food availability for fish and therefore reduced growth. However, Lake Petén Itzá's trophic state has recently changed to include areas localized with mesotrophy/eutrophy caused by cultural eutrophication (Rosenmeier et al. 2004), mainly in the southern basin. Although we sampled fish from the entire littoral zone in Lake Petén Itzá, most of the fish (~70%) were captured in the southern basin, which has received the largest impact from cultural eutrophication. Secchi disk readings in that area of Lake Petén Itzá are comparable to those obtained in Lake Yaxhá (C. A.

Barrientos, unpublished data), and we would therefore still expect the growth of Giant Cichlids in Lake Petén Itzá to be equal to or faster than their growth in Lake Yaxhá.

Another explanation for Giant Cichlid growth differences between the two lakes is that fishing is typically size-selective, targeting large individuals, which are presumably the faster-growing and older individuals in a population (Law 2000). This may favor the survival of slower-growing fish and hence over time may lead to a smaller size at age of females surviving to reproduce (Olsen et al. 2004; Walsh et al. 2006). In laboratory experiments with Atlantic Silversides *Menidia menidia*, Conover and Munch (2002) found selection for slower somatic growth after selective removal of the larger individuals in the population. Our data suggest a genetic response to robust directional selection for smaller, slower-growing individuals in Lake Petén Itzá. On the other hand, natural selection probably favors fast-growing individuals in Lake Yaxhá because slower-growing individuals are highly vulnerable to predation for a longer time and are less likely to reach a size for reproduction (Carlson et al. 2007; Edeline et al. 2007; Allendorf and Hard 2009).

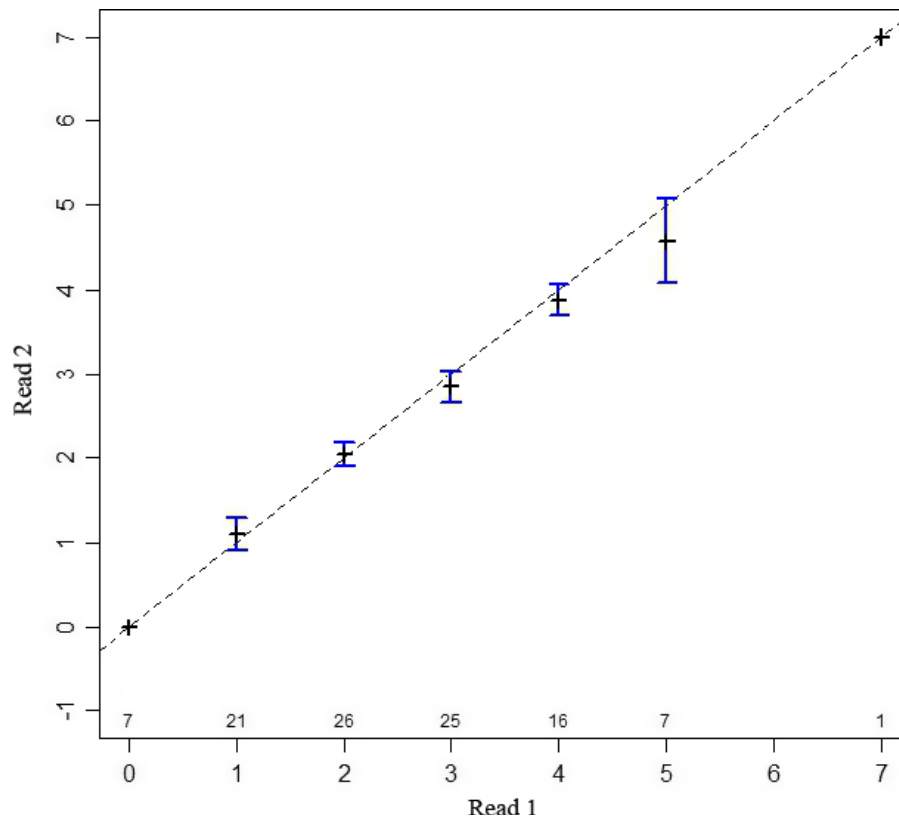


FIGURE 8. Bias plot for otolith age estimates from Giant Cichlids ( $n = 103$ ) sampled in Lakes Yaxhá and Petén Itzá, Guatemala. Numbers above the x-axis represent sample sizes. The dashed line depicts the 1:1 relationship. Bars represent the 95% confidence intervals. [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]

Factors other than fishing pressure should be considered in explaining the differences in size and age of Giant Cichlids between the two lakes, such as habitat differences and fish behavior. Larger fish (>150 mm) move in and out of the littoral zone, depending on their feeding behavior, moving considerably more than small fish that mainly reside in this zone (Barrientos and Allen 2008). Because we sampled similar habitats in both lakes, it is unlikely that large fish from only Lake Petén Itzá moved out of the littoral zone during our sampling. Moreover, fish were obtained on the same dates and with the same gear, which probably led to the sampling of fish with comparable nesting patterns in the littoral zone. It is also important to highlight that our results are attributable to a combination of factors that cannot be separated based on our present data.

The present study on Giant Cichlids advances the use of calcified structures to estimate age and growth parameters for tropical fish species. We used sagittal otoliths, which have been previously used for a small number of tropical species (e.g., Giant Cichlid: Noiset and Micha 1996; Nile Tilapia: Egger et al. 2004; Bwanika et al. 2007; and Efitre et al. 2016). Agreement between readers for fish sampled from temperate zones is usually over 90%, but

agreement can be lower for tropical species (Campana 2001). Tilapias and reef fishes are the tropical taxa described by the greatest number of age studies, probably because of their importance in fisheries and aquaculture. Bwanika et al. (2007), estimating the age of Nile Tilapia in tropical Africa, found an APE of 5.6% and a CV of 7.9%, which were within the range of most APE and CV values in a review by Campana (2001). Our results are within the same range, probably because of better-than-expected readability of the cross-sections of otoliths embedded in Histomount, which improves light penetration (Figure 3). The opaque zones become less distinct with increasing size of the otoliths, however, thereby increasing the variability between reads.

The timing of opaque zone deposition in Giant Cichlids was validated with edge analysis and coincided with the rainy season common for these tropical latitudes. Similar to other tropical species, increased rainfall potentially could increase Giant Cichlid growth with more food availability (Egger et al. 2004; Bwanika et al. 2007; Efitre et al. 2016). Conversely, Noiset and Micha (1996) hypothesized that annulus formation took place at the end of the dry season for Giant Cichlids; however, they did not validate the periodicity of annulus deposition. Moreover, Noiset

TABLE 1. Age-length key for Giant Cichlids from Lake Petén Itzá, Guatemala. Percentages of fish in 20-mm length categories are presented as a function of age.

TL (mm)	N	Age (years)					
		0	1	2	3	4	5
50–69	6	100					
70–89	5	100					
90–109	15	100					
110–129	18	100					
130–149	19	100					
150–169	12	92	8				
170–189	4	50	25	25			
190–209	9		67	22	11		
210–229	30		90	10			
230–249	34	3	59	35	3		
250–269	21		38	48	9	5	
270–289	17		29	65	6		
290–309	14		14	58	21	7	
310–329	7			43	43		14
330–349	8			50	25	25	
350–369	2				50	50	
370–389	2				50	50	
>390	2					50	50

TABLE 2. Age-length key for Giant Cichlids from Lake Yaxhá, Guatemala. Percentages of fish in 20-mm length categories are presented as a function of age.

TL (mm)	N	Age (years)								
		0	1	2	3	4	5	6	7	8
50–69	2	100								
70–89	3	100								
90–109	10	100								
110–129	9	100								
130–149	4	100								
150–169	4	100								
170–189	0									
190–209	5		80		20					
210–229	10	10	60	20	10					
230–249	16		50	32	18					
250–269	28		32	43	19	3	3			
270–289	30		7	33	43	17				
290–309	22		4	37	37	18	4			
310–329	32			25	56	16	3			
330–349	14			29	35	29	7			
350–369	11			9	36	36	19			
370–389	34				50	35	9	3		3
390–409	20			5	20	55		20		
410–429	5					40	40	20		
>430	2						50			50

TABLE 3. Candidate models for TL as a function of age for male and female Giant Cichlids in Lake Yaxhá, incorporating the von Bertalanffy growth parameters of asymptotic length ( $L_{\infty}$ ), Brody growth coefficient ( $k$ ), and theoretical age at zero length ( $t_0$ ). A “2” next to a parameter symbol indicates separate parameters for males and females; a “1” indicates a combined parameter for males and females. The model chosen based on a low Akaike’s information criterion (AIC) score is highlighted in bold ( $\Delta AIC$  = AIC difference between the specified model and the best-performing model).

Model	df	AIC	$\Delta AIC$
2 $L_{\infty}$ , 2 $k$ , 2 $t_0$	7	2,588.6	2.1
1 $L_{\infty}$ , 2 $k$ , 2 $t_0$	6	2,626.9	40.5
2 $L_{\infty}$ , 1 $k$ , 2 $t_0$	6	2,598.8	12.2
<b>2 <math>L_{\infty}</math>, 2 <math>k</math>, 1 <math>t_0</math></b>	<b>6</b>	<b>2,586.7</b>	<b>0.0</b>
1 $L_{\infty}$ , 1 $k$ , 2 $t_0$	5	2,689.4	102.8
1 $L_{\infty}$ , 2 $k$ , 1 $t_0$	5	2,660.2	73.6
2 $L_{\infty}$ , 1 $k$ , 1 $t_0$	5	2,620.6	34
1 $L_{\infty}$ , 1 $k$ , 1 $t_0$	4	2,689.3	102.7

TABLE 4. Candidate models for TL as a function of age for male and female Giant Cichlids in Lake Petén Itzá, incorporating the von Bertalanffy growth parameters of asymptotic length ( $L_{\infty}$ ), Brody growth coefficient ( $k$ ), and theoretical age at zero length ( $t_0$ ). A “2” next to a parameter symbol indicates separate parameters for males and females; a “1” indicates a combined parameter for males and females. The model chosen based on a low Akaike’s information criterion (AIC) score is highlighted in bold ( $\Delta AIC$  = AIC difference between the specified model and the best-performing model).

Model	df	AIC	$\Delta AIC$
2 $L_{\infty}$ , 2 $k$ , 2 $t_0$	7	2,197.4	0.0
1 $L_{\infty}$ , 2 $k$ , 2 $t_0$	6	2,218.6	21.2
2 $L_{\infty}$ , 1 $k$ , 2 $t_0$	6	2,205.9	8.5
<b>2 <math>L_{\infty}</math>, 2 <math>k</math>, 1 <math>t_0</math></b>	<b>6</b>	<b>2,197.8</b>	<b>0.4</b>
1 $L_{\infty}$ , 1 $k$ , 2 $t_0$	5	2,230.9	33.5
1 $L_{\infty}$ , 2 $k$ , 1 $t_0$	5	2,226.3	28.9
2 $L_{\infty}$ , 1 $k$ , 1 $t_0$	5	2,213	15.6
1 $L_{\infty}$ , 1 $k$ , 1 $t_0$	4	2,229	31.6

and Micha (1996) only sampled during 5 months of the year, and their sampling did not extend into the months when the translucent zone was completed. Our study underscores the need to validate the deposition of the macro-zones in fish otoliths on a system-specific basis (Bwanika et al. 2007).

The Giant Cichlid shows sex- and lake-specific growth. Males were consistently larger than females in Lake Yaxhá. Although sexual dimorphism is relatively common for tropical fish with parental care (Magurran and Macias-Garcia 2000; Egger et al. 2004), it was previously unknown for Giant Cichlids. In Guatemala, females tend to be larger in other fish families (e.g., Poeciliidae and Atherinidae), probably because fecundity is related to female weight. However, because the cichlid mating

TABLE 5. The von Bertalanffy parameters estimated for Giant Cichlids by lake and sex ( $L_{\infty}$  = asymptotic length [mm];  $k$  = Brody growth coefficient;  $t_0$  = theoretical age [years] at zero length).

Parameter	Lake Yaxhá		Lake Petén Itzá	
	Male	Female	Male	Female
$L_{\infty}$	406	297	362	277
$k$	0.51	0.97	0.59	0.94
$t_0$	-0.49	-0.49	-0.58	-0.58

system is based on nest site protection, males have a reproductive advantage if they are large (Magurran and Macias-Garcia 2000). In cichlids from Africa, Bwanika

et al. (2007) found that males had greater growth rates, and the authors attributed this to a size advantage conferred upon males defending a territory. Egger et al. (2004) found differential growth between sexes and observed that size dimorphism increased with age. Similarly, size differences in older Giant Cichlids were evident in Lake Yaxhá, where the population age structure was older and where larger individuals were common in the sample. The male size advantage was less evident in Lake Petén Itzá, possibly because the advantage attributed to sexual selection for larger males was countered by fishing pressure on large, potentially faster-growing individuals (Berkeley et al. 2004; Carlson et al. 2007; Allendorf and Hard 2009).

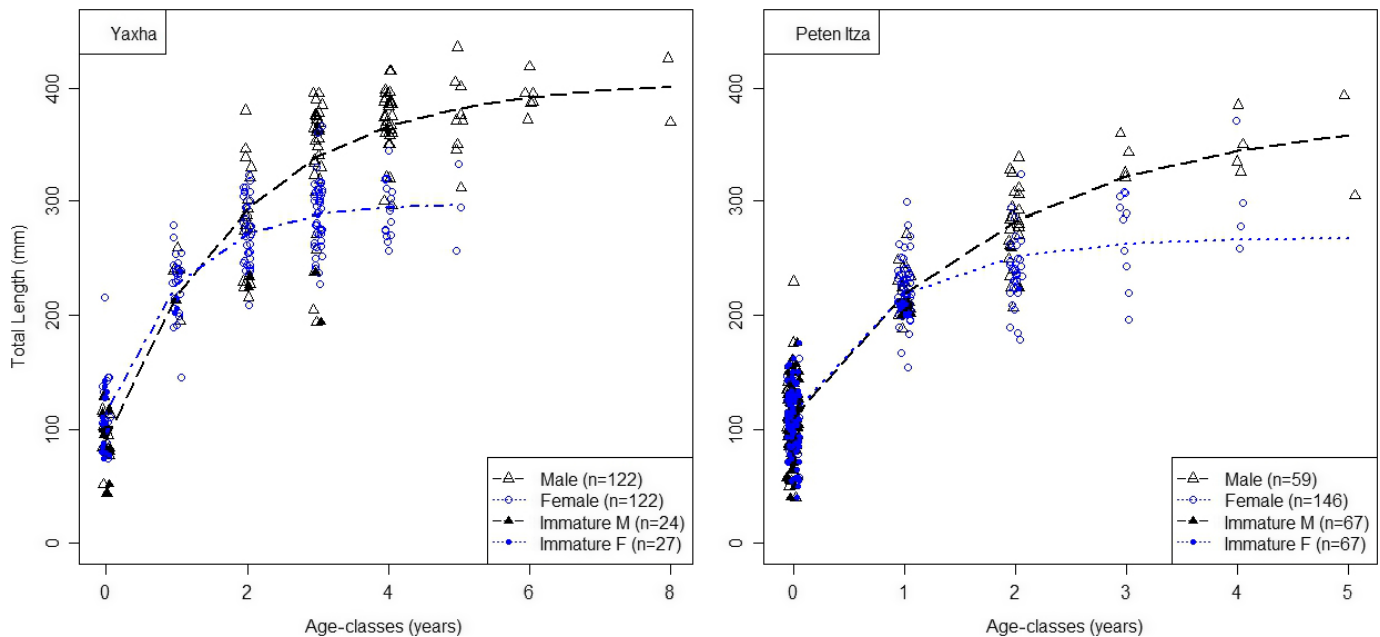


FIGURE 9. The von Bertalanffy growth model fitted to observed TL at observed age for male and female Giant Cichlids sampled in Lake Yaxhá and Lake Petén Itzá, Guatemala. [Color figure can be viewed at [afs.journals.org](http://afs.journals.org).]

TABLE 6. Average observed TL (with SE) at observed age of Giant Cichlids from Lake Petén Itzá ( $n = 339$ ) and Lake Yaxhá ( $n = 327$ ), Guatemala.

Age	Lake Yaxhá				Lake Petén Itzá			
	Male		Female		Male		Female	
	Mean TL (mm)	SE	Mean TL (mm)	SE	Mean TL (mm)	SE	Mean TL (mm)	SE
0	195		186	30.07	209	29.69	182	20.67
1	232.0	14.29	230.3	6.34	233.8	6.83	223.1	3.67
2	292.7	11.87	271.5	4.86	278.0	6.71	239.9	5.38
3	349.8	7.32	288.5	4.36	337.3	8.96	270.6	12.49
4	368.9	5.03	294.3	6.21	349	12.92	301.8	18.84
5	374.1	12.25	295		349			
6	392.7	6.28						
8	398							

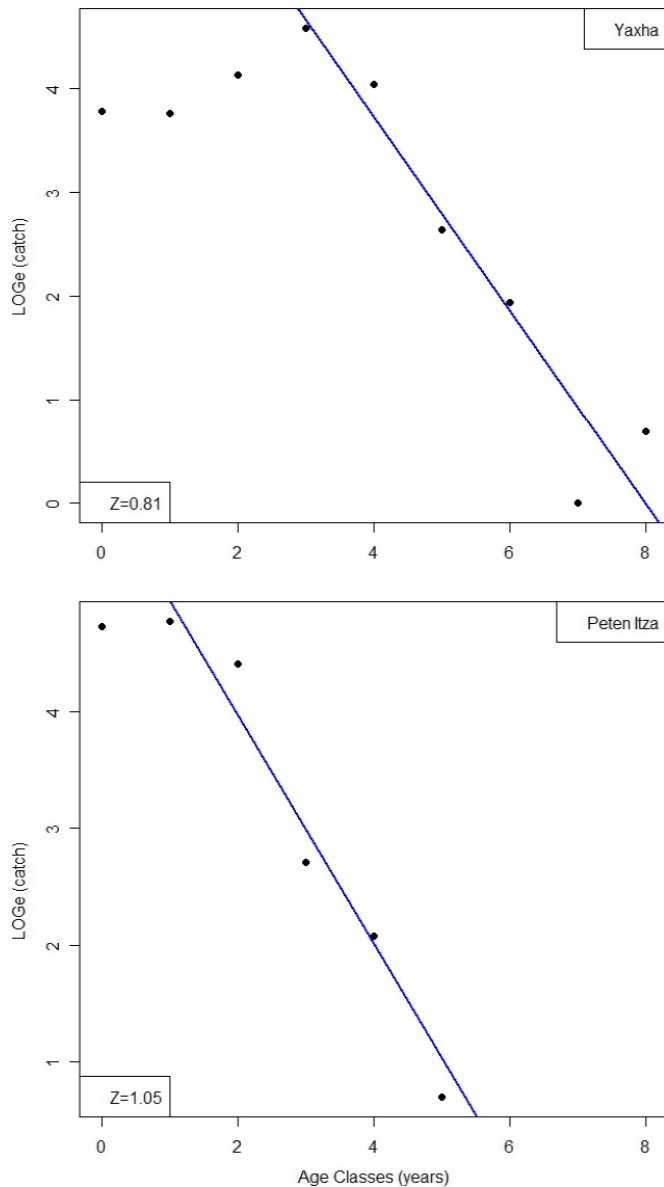


FIGURE 10. Catch curve analysis for Giant Cichlids from Lake Yaxhá and Lake Petén Itzá, Guatemala. Data from age-0–2 fish in Lake Yaxhá and age-0 fish in Lake Petén Itzá are included here for comparison but were not used in the calculation of total mortality ( $Z$ ). [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]

Growth studies focused on Giant Cichlids are rare. Noiset and Micha (1996) fitted data from fish sampled in the San Pedro River, Mexico, using three different methods (Electronic Length Frequency Analysis [ELEFAN], scales, and otoliths) to obtain parameters for the von Bertalanffy growth curve. They found  $L_{\infty}$  ranging from 431 to 452 mm TL and  $k$  ranging from 0.30 to 0.38 when using ELEFAN and scale ages. A lack of older individuals was a problem for fitting the growth curve from otoliths because it did not reach an asymptote. In our

TABLE 7. Natural mortality ( $M$ ), total mortality ( $Z$ ), annual survival rate ( $S$ ), and annual mortality ( $A$ ) of Giant Cichlids captured in Lake Petén Itzá and Lake Yaxhá, Guatemala ( $t_{max}$  = maximum observed age). Fishing mortality ( $F$ ) was estimated as  $Z - M$ .

Estimation method	Variable	Lake Petén Itzá	Lake Yaxhá
Hewitt and Hoenig (2005)	$t_{max}$ (years)	5	8
Catch curve	$M$	0.84	0.53
	Age range (years) used	1–5	3–8
	$Z$	1.05	0.81
	$S$	0.35	0.45
	$M$	0.81	0.81
	$A$	65%	55%
	Estimated $F$	0.24	0.00

study, the von Bertalanffy model provided a good fit for the different sexes of Giant Cichlids in Lake Yaxhá. Fit, however, was not as good for Giant Cichlids in Lake Petén Itzá, probably because of the age-class truncation due to the effects of fishing. Our  $k$ -values for both lakes were greater (range = 0.51–0.97) than those obtained by Noiset and Micha (1996;  $k$  = 0.30–0.38), indicating that the Giant Cichlids in our study were approaching their  $L_{\infty}$  faster than those in the earlier study.

Estimates of  $Z$  for Giant Cichlids were the same for both lakes in the range of ages (2–5 years) that overlapped in the two lakes. This result was surprising given our expectations based on the negligible fishing pressure in Lake Yaxhá. However, the overall age structure in Lake Petén Itzá indicated that fish were experiencing mortality at much younger ages (i.e., ages 0 and 1) compared to fish in Lake Yaxhá (ages 3 and older), and  $Z$  over all ages of fish fully recruited to the fishing gear in Lake Petén Itzá was noted to be higher than that in Lake Yaxhá. To our knowledge, there is no other estimate of mortality rate based on age for Giant Cichlids in any other part of the species' distribution. Using the Length Frequency Distribution Analysis (LFDA) package for Giant Cichlids in Lake Petén Itzá, Ixquiac-Cabrera et al. (2010) estimated  $Z$  at 0.87, which is much lower than our estimate of 1.05. Ixquiac-Cabrera et al. (2010) reported an  $A$ -value of 58% in Lake Petén Itzá, whereas our estimate was 65%, which was higher than the estimate for Lake Yaxhá (54%). Lake Yaxhá is an unfished lake that presented an age structure based primarily on age-2 and age-3 individuals rather than on age-0 and age-1 fish as in Lake Petén Itzá. Comparison of age composition between lakes suggests that such a low value of  $A$  would be less likely in Lake Petén Itzá. Age data provide better estimates of mortality and are preferred to LFDA for stock assessment (Walters and Martell 2004). Underestimation of mortality using LFDA could be misleading and



could inappropriately enable fishing effort to be increased in management plans, eventually resulting in overfishing. Conversely, our mortality estimation could have been influenced by the fish not being equally susceptible to the gear in each lake, although it was not intuitively obvious why this would be the case given that the lakes were sampled over similar habitat and depth on the same day or adjacent days. Finally, our  $M$  estimate for Lake Yaxhá generated by the Hewitt and Hoenig (2005) method was lower than our estimate of  $M$  based on catch curves and based on the fact that Lake Yaxhá does not have any fishing (i.e.,  $Z = M$ ).

Our study presents the first estimates of age, growth, and mortality for Giant Cichlids in Guatemala and the first such estimates in lentic ecosystems, thus providing an important first step toward appropriate fishery management in the region. The results also provide life history parameters needed to inform the fish population dynamics models that are used to test management actions. Our sampling design included two large areas in the MBR under different management regimes, enabling study of baseline conditions in an unfished lake with better longevity and a distinctive size structure. Growth of Giant Cichlids can be modulated from lake to lake, and selection may be possible by favoring small, slow-growing fish (as in Lake Petén Itzá) or larger, faster-growing individuals (as in Lake Yaxhá; Carlson et al. 2007; Edeline et al. 2007; Allendorf and Hard 2009). This is important to consider in light of the recent interest in using the Giant Cichlid as an aquaculture species (Arredondo-Figueroa et al. 2013). The Guatemalan government is now stocking Giant Cichlids in Lake Petén Itzá, and it will be important to understand the growth patterns and choose a parent generation of fish that show high growth rates. Further exploration of growth in regional Giant Cichlid populations will be needed to manage the species in different ecosystems (e.g., lakes and rivers) across its wide distributional range. Like other artisanal fisheries, the Giant Cichlid fishery is spatially structured and small in scale and targets sedentary stocks (Orensanz et al. 2005), but it supports the livelihoods of thousands of families, so it is necessary to manage such fisheries at the local level, with explicit management goals and regulations.

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