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Population ecology of cave armoured catfish, *Ancistrus cryptophthalmus* Reis 1987, from central Brazil (Siluriformes: Loricariidae)

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Abstract – The population ecology of *Ancistrus cryptophthalmus* (Reis 1987) was studied by mark–recapture technique in caves from the São Domingos karst area, State of Goiás, northeastern Brazil. Total population sizes estimated for Angélica and Passa Três Caves were 20,000 and 1000 individuals, respectively. Densities around 1.0 individuals per m^2 in Angélica, Bezerra and São Vicente I Streams, and 0.6 individuals per m^2 in the smaller Passa Três Stream may be considered high for cavefish standards, as well as for epigean loricariids. As expected for benthic grazers, cave catfish are highly sedentary. The distribution of size classes did not differ among caves and within the same cave throughout the studied dry seasons; on the contrary, the condition factor decreased throughout this period probably because of the progressive depletion of organic matter available as food. Low proportions of mature individuals, low growth rates (average = 0.5 mm month^{-1}) with cases of negative growth and high longevities (8–10 years) point to a precocial lifestyle, typical of troglobitic species.

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Introduction

The remarkably rich and diverse subterranean ichthyofauna from South America includes at least 26 troglobitic (exclusively subterranean) species. This troglobitic fauna is composed of representatives from few taxa, which show a high potential for adoption of the hypogean life, especially among siluriformes: mainly Heptapteridae (several genera), Trichomycteridae (e.g., *Trichomycterus*, *Ituglanis*) and Loricariidae (*Ancistrus*). The latter encompasses three nominal species: *Ancistrus cryptophthalmus*, from the State of Goiás, central Brazil; *Ancistrus formoso* Sabino & Trajano 1997, from the State of Mato Grosso do Sul, NW Brazil and *Ancistrus galani* Perez & Viloria 1994, from NW Venezuela (Trajano 1997a; Weber *et al.* 1998).

A great deal of variation in morphological, physiological and behavioural specialisation, besides ecological traits, is observed among these species. For example, the commonest traits are the reduction of eyes and dark pigmentation. These traits likely resulted from genetic isolation in the subterranean environment. Historical (phylogenetic constraints) and ecological factors (adaptation to a perpetually dark, usually food-limited environment) interact to produce the particular ecology of troglobites. Among subterranean fish, very few species have been studied in detail for population parameters such as population sizes and densities, individual movements and home range, individual growth (as a lifestyle parameter) and other ecological characteristics (Trajano 2001a). Such knowledge is not only scientifically relevant but also fundamental for the establishment of efficient

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conservation policies, much needed in view of the intrinsic fragility of subterranean ecosystems and the threats to troglobitic fish observed around the world (Proudlove 2001).

The São Domingos region, State of Goiás, central Brazil, is the Brazilian karst area harbouring the richest subterranean ichthyofauna, including both troglomorphic and nontroglomorphic components; the latter are isolated individuals or groups of specimens belonging to normal-eyed epigean (surface) species, which are regularly found in caves (Bichuette & Trajano 2003). With seven troglomorphic species, the São Domingos karst area is a hotspot in diversity of troglobitic fish on a worldwide scale. This diversity includes *Eigenmannia vicentespelaea* Triques 1996 (Gymnotiformes, Sternopygidae), *Pimelodella spelaea* Trajano *et al.* 2004 (Siluriformes: Heptapteridae) and four species of *Ituglanis* [Siluriformes: Trichomycteridae: *Ituglanis bambui* Bichuette & Trajano 2004, *Ituglanis epikarsticus* Bichuette & Trajano 2004, *Ituglanis passensis* Fernández & Bichuette 2002 and *Ituglanis ramiroi* Bichuette & Trajano 2004, corresponding to one of the highest number of different troglobitic fish belonging to the same genus in a single geographically restricted area], in addition to *A. cryptophthalmus*. Except for the latter, found in four caves (two cave systems), all these species are known from a single cave each.

We present herein the results of a 2-year population study based on mark–recapture of armoured catfish from three caves (*A. cryptophthalmus*) and an epigean stream reach (*Ancistrus* sp.) of the São Domingos karst area, central Brazil; part of these data, gathered during the first study year, are in Trajano (2001b). There are very few studies on the ecology of loricariid catfish, such as those by Power (e.g., Power 1984, 1990), focusing on *Ancistrus* and others. The present study is a contribution to the knowledge of these important components of neotropical ichthyofaunas, and contains valuable information on the generally fragile subterranean ecosystems.

This study provides field data allowing for addressing general questions pertaining to subterranean biology, such as: are low population densities and tendency to a precocial lifestyle patterns for troglobites, as generally stated in the literature (Trajano 2001a)? Do different populations of the same species, or closely related species, consistently present similar population densities? How stable are such populations?

Study sites

The São Domingos karst area, which encompasses about 110 km^2 and includes 66 known limestone caves, is part of the Bambuí geological group (Auler & Farrant 1996). It is situated in the Cerrado domain (savannah-like vegetation), characterised by a tropical semi-humid climate, with 4–5 dry months (Nimer 1979). The studied caves are located within the limits of the Terra Ronca State Park, São Domingos County, Goiás State.

Specimens assigned to *A. cryptophthalmus* have been found in four caves belonging to two different cave systems (conduits extending continuously between the input and output points of a karst rock – Ford & Williams 1989): Angélica and Bezerra Caves, which form the Angélica-Bezerra system, and São Vicente I Cave and its tributary Passa Três Cave, part of the São Vicente system. These streams, with epigean and hypogean reaches, run parallely westwards, contributing to form the Paranã River, one of the main tributaries of the Tocantins River, in the Amazon basin. An epigean species of *Ancistrus*, probably new (Sonia Muller pers. comm.), is widespread in surface streams of the São Domingos karst area.

Differences in body shape and condition of the eyes and pigmentation among the four cave populations, which present a mosaic distribution of character states in these populations, indicate that they evolved rather independently in recent times (Reis *et al.* 2006). This justifies a separate treatment of such populations.

The present study focused mainly on the large and easily accessible populations from Angélica and Passa Três Caves, which are contrasting in terms of habitat dimensions. The Angélica is a large stream, of the same stream order (sensu Mattheus 1998) as the São Vicente Stream. The large entrance of Angélica Cave (13 °21′S, 46 °23′W) is the sinkhole of the Angélica Stream. The cave presents 13,800 m of mapped passageways; the stream conduit is about 8000 m long, average width is 5 m and depth varies from 0.5 to 2+ m. In most of its extension, it is a fast-flowing stream with a strong current, running over a rocky substrate (blocks, gravel and sand), with a discharge of 2.27 $m^3{\cdot}s^{-1}$ at the sinkhole during the dry season (Guyot et al. unpublished report). As a result of cave size and the large number of catfish found throughout it, our study was limited to sections in the first 2000 m downstream from the sinkhole (main entrance).

The Passa Três Stream is a small tributary of the São Vicente system (13 °25′S 46 °22′W). After an epigean course, this stream sinks into a 2000-m subterranean conduit, herein referred to as Passa Três Cave (mean width around 1.0 m; discharge at the sinkhole 0.02 $m^3{\cdot}s^{-1}$). Approximately, 100 m from the cave entrance, there is a waterfall – 5 m high during the dry season. Upstream and downstream from this waterfall, the stream is nearly horizontal, with shallow riffles and moderate water current over a rocky and gravelled bottom, alternating with some deep, soft-bottom pools. A short underwater passage separates the first 400 m from the remaining 1600 m reach, which joins the large São Vicente Stream inside São Vicente I Cave. The population study in Passa Três Cave was carried out in the 400-m long reach upstream from the underwater connection. A short reach of São Vicente I Cave at the sinkhole end (water discharge = 4.91 $m^3 \cdot s^{-1}$), at ca. 3000 m from the connection with the Passa Três conduit and separated from it by several strong waterfalls, was visited for study in March 2001.

Population data were also gathered in Bezerra Cave. The Bezerra Cave stream conduit is approximately 8000 m long, but mean width is half of Angélica and discharge at the sinkhole is lower, around 0.24 $m^3 \cdot s^{-1}$ (Guyot et al., unpublished report). The Angélica and Bezerra Caves meet at their resurgence ends, 100 m from each other in a common twilight zone gallery (transition between surface and cave environments).

Ancistrus cryptophthalmus is usually found on rocky substrates, from large pebbles to boulders and rocky walls, in fast-flowing, well-oxygenated waters (Trajano 2001b). These catfish are syntopic with *I. passensis* in the Passa Três Cave, where they share the same habitat. They are sympatric but not syntopic (different habitats) with *I. bambui* in the Angélica Cave (*A. cryptophthalmus* in the main, base-level stream, *I. bambui* in upper, vadose tributaries). No *Ancistrus* catfish were found in other caves.

Methods

The São Domingos karst area was visited for a mark–recapture programme in the Angélica and Passa Três Caves on five occasions during the dry seasons of 1999 and 2000: May, July and September 1999 (40-day interval both between May and July and between July and September), and April/May, July and September 2000 (90- and 40-day intervals, respectively). Bezerra Cave was visited for mark–recapture in July and September 2000. Additional fieldtrips, without marking, were carried out in May 2001 and March 2004 (end of the rainy season). As a result of the occurrence of flash floods, it was not safe to enter the caves to extend the population study to the peak of the rainy period (November to February).

The studied 2000 m reach of the Angélica Cave was divided into 100-m long sections, numbered from 1 to 20. Among these sections, we selected five (sections 1, 2, 3, 5 and 7) in 1999 and three (sections 5, 7 and 20) in 2000, for the population study – in the second study year, the sections closer to the cave entrance were excluded, and a deeper section, 2000 m from the entrance, was included. Armoured catfish were captured in two 50-m long contiguous sections in the Bezerra Cave. The 400-m long stream reach studied in the Passa Três Cave was divided into 20-m long sections, also numbered from 1 to 20, and we hand-netted and marked all fish captured in these sections. All catfish captured in the same section were handled together.

In May 2001, 20 specimens were collected and measured in a 100-m long reach inside the São Vicente I Cave, situated ca. 400 m from the cave entrance; these catfish were preserved for morphological studies. In March 2004, catfish were measured and released without marks in two sections of the Angélica Cave, 500–700 m from the cave entrance, and near the entrance of the Passa Três Cave. For comparison, epigean *Ancistrus* catfish were captured using electric fishing in a 100-m^2 stream reach situated about 500 m upstream from the Angélica Cave sinkhole.

We used subcutaneous injection of biocompatible fluorescent pigments (‘Photonics marking’; New West Tech., Santa Rosa, CA, USA) to mark the armoured catfish. Injection of the pigments through the bony armour was difficult and only four positions were possible: the softer posterior ventral area around the anal-fin base (right and left) and the lateral caudal peduncle (right and left). The combination of different colours and position of marks allowed for individual recognition. Specimens were anesthetised by MS-222 or a benzocaine solution, measured (standard length, SL), weighed, examined for individual natural marks and gonad development (observed by transparency), marked and released in the same collection sections. As a result of technical difficulties, only specimens larger than 20 mm SL were marked. Smaller catfish were measured, weighed and released. Population sizes were estimated by the triple-catch method and also using the Petersen estimator (Lincoln index) (Begon 1979; Blower *et al.* 1981).

Standard length and weight data were used to calculate allometric condition factors ($K = 100W\mathrm{SL}^{-b}$; Le Cren 1951). The power coefficient (b) for the growth equation was estimated from the slope of the regression of log weight on log SL using the pooled data for each year. Histograms and boxplots show distributions of the following statistical parameters throughout the years: frequencies, medians, standard deviations and extreme values of SL and K.

For each studied cave, SL and K values from samples examined in different months were compared by ANOVA. In addition, Angélica, Bezerra and Passa Três populations were compared with regard to SL and K values obtained in July 2000 (a month in the mid-dry season with average values for all populations). When ANOVA detected significant differences in the set of data, pairs of samples were compared using the Dunn *a posteriori* test. For comparisons of two samples, e.g., data from 1999 versus 2000, we used the two sample *t*-test (for parametric data) or the Mann–Whittney test (*T*-test, when data was nonparametric), with $\alpha = 5\%$ (SigmaStat version 2.0, 1992–1995, Jandel Corporation). The Mann–Whittney test was also used to compare samples collected near entrances (sinkholes) and deeper in the caves, in both the Angélica (pooled data from sections 1–7 vs. 20) and the Passa Três (sections 8–15 vs. 16–20) caves, in order to verify whether the average condition factors were influenced by food availability, which decreases with the distance to the epigean habitat.

To calculate individual growth rates and longevities in the Angélica and Passa Três Cave populations, size increments [$\Delta SL = $ (SL at recapture − SL at previous capture)/time between consecutive captures, in days] were calculated for the pooled data relative to 1999 plus 2000. To exclude measurement errors from calculations, an error propagation equation was used [$s_v = \pm (s_a^2 + s_b^2)^{1/2}$, where s_v is the final propagated error and s_a and s_b are the measurement errors] (Yamamura & Watanabe 1992). The calculated propagated error was ±0.14 mm, thus ΔSL values within this interval were considered as null growth. Scatter plots showing the individual growth rates related to mean sizes were compounded, and the average growth rates for each population were calculated. These data were also used to calculate the parameters of the von Bertalanffy equation (von Bertalanffy 1938).

Precipitation data were obtained from INMET-Brazil (Instituto Nacional de Meteorologia http://www.inmet.gov.br).

Results

Population ecology

Mark–recapture data for 1999 are in Trajano (2001b). Data for 2000 are shown in Table 1, with estimated population sizes based on the triple-catch method. The three sections studied in 2000 in the Angélica Cave totalled 300 m along the stream; average stream width was 5 m^2, thus the total area sampled corresponded to 1500 m^2. In the Passa Três Cave, we sampled an area of 400 m^2 (400 m along the stream, on average 1 m wide). The Lincoln–Petersen method resulted in the following values for 2000: Angélica Cave, May–July, $N = 2230.0$, $SE = 415.6$, July to September, $N = 1659.5$, $SE = 310.1$; Passa Três Cave, May to July, $N = 250.8$, $SE = 36.7$, July to September, $N = 257.7$, $SE = 34.8$. High recapture rates, between 40% and 50%, were obtained in Passa Três. Lower recapture rates, around 10%, were obtained in the Angélica Cave, which is expected in view of the large number of individuals in this cave.

In the dry season of 1999, the population size estimated for a 2500-m^2 study area in the Angélica Cave (five sections) was 2236.6 individuals, $SE = 502.7$, and the population estimated for a 400-m^2 area in Passa Três (same area as in 2000) was 192.8 individuals, $SE = 19.3$ (Trajano 2001b). For the Angélica Cave, adjusting the estimated values to differences in the studied areas, the population size estimated by the Lincoln–Petersen method for July to September 1999 was close to the values estimated for this period in 2000; a higher value was obtained for May 2000. For the Passa Três Cave (same area studied in 1999 and 2000), the population size estimated for July to September 1999 was similar to that estimated for May 2000, with higher values estimated for the two subsequent sampling occasions (July and September 2000).

Nevertheless, confidence intervals widely overlap. Moreover, visual censuses of catfish densities in the studied caves and the number of specimens captured per unit of collecting effort, i.e., number of catfish captured per hour by three collectors, which did not visibly differ among the months (the lower number captured in September 2000 was due to the rains that started in the area, thus interrupting work inside the cave), indicate that populations did not visibly fluctuate between sampling occasions, both within the same year and between the two consecutive study years. Differences in the estimated values of population sizes may be artefacts or may reflect less important fluctuations. It is interesting to note that the number of catfish seen and collected in the Passa Três Cave in July 1988 (Trajano & Souza 1994) was consistent with the figures herein presented for 1999–2000, suggesting a relatively long-term stability for this cave population.

Values around 1500 and 250 individuals are a reasonable estimate for the studied sectors in the Angélica and Passa Três Caves, respectively. Taking into account the studied areas, average population densities would be around 1.0 individuals per m^2 in Angélica and 0.625 individuals per m^2 in Passa Três, these being close to those estimated for 1999, 0.9 and 0.5 individuals per m^2 (Trajano 2001b), respectively.

Table 1. Mark-recapture data for *Ancistrus cryptophthalmus* from Angélica and Passa Três caves, São Domingos karst area, Central Brazil: triple-catch method, May to September 2000. N = estimated population size; ϕ = survival rate.

	ANGÉLICA (1500 m^2)			PASSA TRÊS (400 m^2)		
	May	July	September	May	July	September
Captured		237	170		97	85
Marked in May		22	14		29	17
Marked in July			21			31
Released	207	205		75	94	
N	2089.3	1584.2*	1468.0	193.5	259.6*	385.3
ϕ	0.7396	0.8757		1.0596	1.0389	
	*SE_{N2} = 536.9			*SE_{N2} = 51.3		

In July 2000, 47 individuals were marked and released in two 50-m long sections (3 m wide, on an average) inside Bezerra Cave. Three of them were among the 27 specimens captured in September. This low recapture rate (11%) points to a numerous population (around 290 individuals) and a high population density (1 individual per m^2), comparable to that in the Angélica Cave. A visual census carried out in May 2001 in a 100-m long stream reach inside the São Vicente I Cave resulted in the same value, around 1 individual per m^{-2}, for population density.

The numbers of epigean *Ancistrus* catfish captured using electric fishing in a 100 m^2 area situated about 500 m upstream from the Angélica Cave sinkhole are as follows: May 2000, 75 specimens captured, 40 marked and released; July 2000, 47 captured (no recapture), 36 marked and released; September 2000, 88 captures, including one recapture. As a result of the extremely low recapture rate, no mark–recapture estimator could be used. Nevertheless, the high numbers of captured specimens point to high population sizes and densities for the epigean species, in accordance with the conclusions drawn from visual censuses [average population densities up to 50% higher than those of *A. cryptophthalmus*, reaching maximum values of 10 individuals per m^2 (5–6 for *A. cryptophtalmus*)] (Trajano 2001b).

Movements of marked individuals between sections were more frequent in the second study year. In the Angélica Cave, 2 of 47 recaptures obtained in sections situated 500 and 700 m inside the cave were carried out in sections different from that of the previous capture, but adjacent, corresponding to maximum movements of 100 m along the stream. All other recaptures were carried out in the same section where the catfish were marked (no movement was recorded in 1999 – Trajano 2001b). In the Passa Três Cave, which was divided in shorter, 20-m long sections, 24 of 70 recaptures were carried out in a section different from that of the previous capture. Among these, 13 were carried out in adjacent sections (movements up to 40 m along the stream), and the remaining ones in more distant sections, with recorded maximum movements of 100–120 m along the stream (four cases), within periods of 40 or 90 days. Less frequent movements were recorded in 1999 (seven of 44 recaptures, maximum distances of 60 m within 40-day periods).

Distribution of classes of length and condition factor

The monthly frequencies of distribution of SL classes in *A. cryptophthalmus* from the Angélica, and Passa Três Caves are shown in Figs 1 and 2, respectively. Medians, standard deviations and 95% confidence intervals of SL and *K* of *A. cryptophthalmus* from the Angélica and Passa Três Caves are shown, respectively, in Figs 3 and 4.

For the Bezerra population, significantly lower SL values were observed only in July 1999 in relation to September 1999 ($Q = 4.13$, $P < 0.05$). No differences were detected for 2000.

In relation to the condition factor (*K*), ANOVA analysis showed some tendencies throughout the studied years. Significant differences in the condition factor between months were observed for the Angélica population, for both 1999 ($H = 10.571$, $P = 0.005$) and 2000 ($H = 14.152$, $P < 0.001$), and the Passa

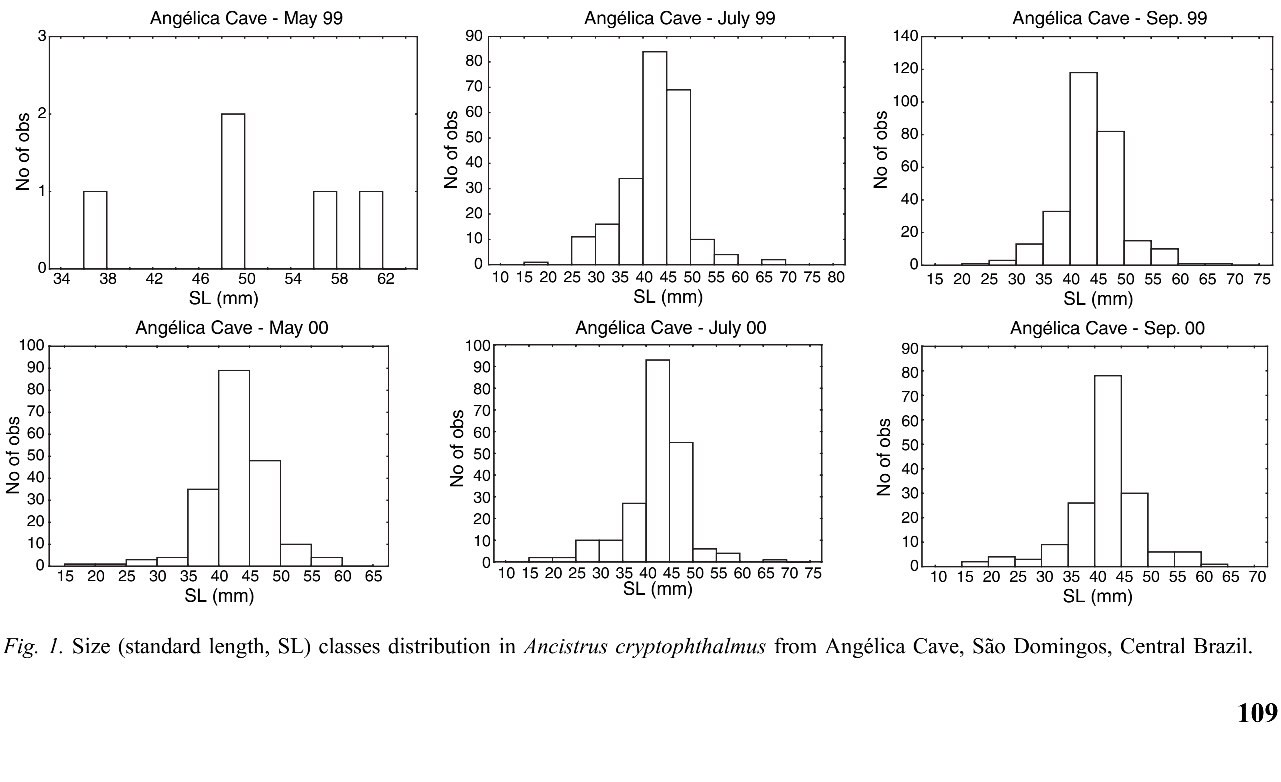

Fig. 1. Size (standard length, SL) classes distribution in *Ancistrus cryptophthalmus* from Angélica Cave, São Domingos, Central Brazil.

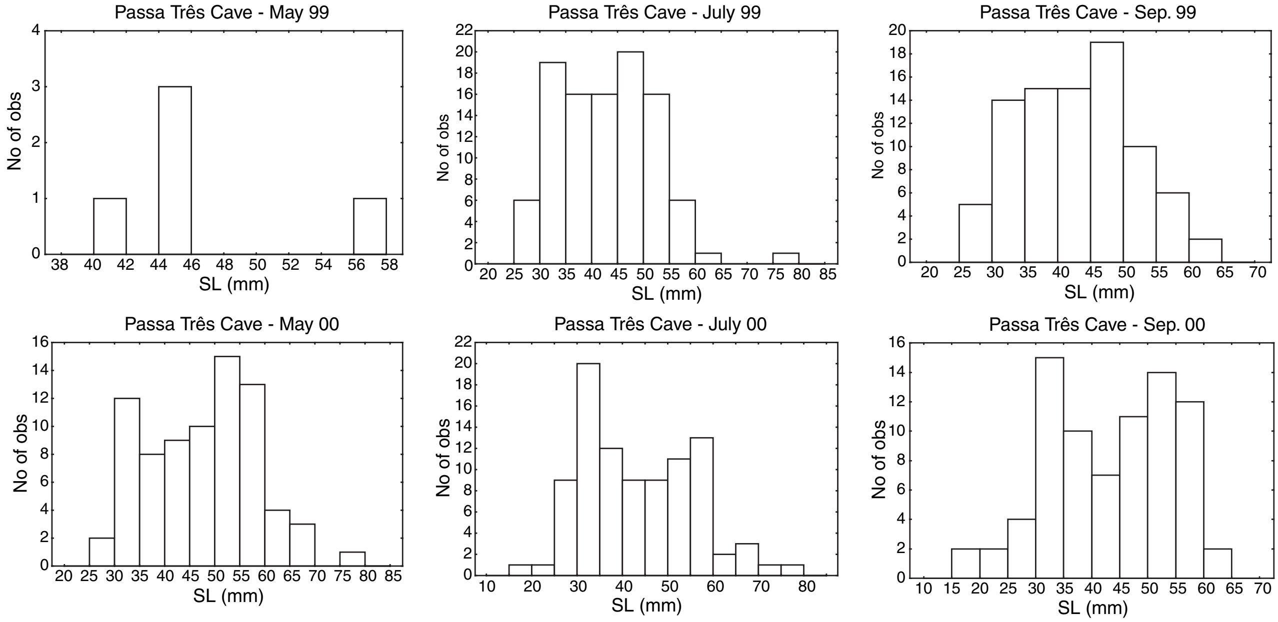

Fig. 2. Size (standard length, SL) classes distribution in *Ancistrus cryptophthalmus* from Passa Três Cave, São Domingos, Central Brazil.

Três population, for 2000 ($H = 7.949$; $P = 0.019$). The Dunn test revealed significant differences between May and July (decrease; $Q = 2.422$, $P < 0.05$), May and September 1999 (decrease; $Q = 2.417$, $P < 0.05$) and between May and September 2000 (decrease; $Q = 3.726$, $P < 0.05$) for the Angélica Cave, and between May and September 2000 (decrease; $Q = 2.487$, $P < 0.05$) for the Passa Três Cave. An increase in the average condition factor was detected for the Bezerra population from July to September 1999 ($T = 483.0$, $P = 0.003$). The Mann–Whitney test did not show any statistical differences between years (1999 and 2000) either for Angélica ($T = 273129.9$, $P = 0.07$) or for Passa Três ($T = 40369.0$, $P = 0.323$).

Comparing SL and K data from Angélica and Passa Três populations obtained in 1999, 2000 and 2001 with the respective values recorded in March 2004, the Angélica population showed no significant values for length and lower values for condition factor in 2004 (May 1999 vs. March 2004, $Q = 3.586$, $P < 0.05$; May 2000 vs. March 2004, $Q = 5.201$, $P < 0.05$). For Passa Três Cave, no differences were found for SL, and lower values were observed for condition factor in 2004 (May 1999 vs. March 2004, $Q = 3.138$, $P < 0.05$, May 2000 vs. March 2004, $Q = 5.041$, $P < 0.05$; July 2000 vs. March 2004, $Q = 4.100$, $P < 0.05$; September 2000 and March 2004, $Q = 4.097$, $P < 0.05$). In this case, the results may be cautiously interpreted as only five individuals were measured in the Passa Três Cave in March 2004.

No significant differences in SL and K values were observed when comparing data from Angélica, Bezerra and Passa Três populations relative to July 2000 (for SL, $H = 4.634$, $P = 0.099$; for K, $H = 2.223$, $P = 0.327$). SL and K values recorded in May 2001 in the Angélica Cave were significantly lower than those recorded in the São Vicente I Cave on this occasion (for SL, $T = 290.0$, $P < 0.001$; for K, $T = 256.0$, $P < 0.001$).

Significant differences between the average condition factors at cave sections located at different distances from the epigean habitat were detected only in 2000, for the Angélica ($T = 57315.0$; $P < 0.001$) and Passa Três ($T = 6405.0$; $P = 0.001$) populations, with higher mean values unexpectedly observed for those sets of sections located farther from cave entrances (sinkholes) in both caves.

Individual growth, maximum size and longevity

Figs 5 and 6 show individual size increments (ΔSL) related to mean sizes of *A. cryptophthalmus*, respectively, from the Angélica and Passa Três Caves. As a result of the small number of individuals recaptured in the Bezerra Cave (only three), it was not possible to estimate growth rates and longevities for this population.

During the studied dry seasons, Angélica Cave catfish smaller than 42.0 mm SL grew, on an average, 0.0237 mm·day^{-1} (0.7 mm·month^{-1}) and the larger ones 0.0117 mm·day^{-1}(0.35 mm·month^{-1}). Passa Três Cave catfish grew, in average, 0.0167 mm·day^{-1} (0.5 mm·month^{-1}). It is noteworthy that higher growth rates in smaller individuals (as is usual for vertebrates with continuous growth) were observed for the studied

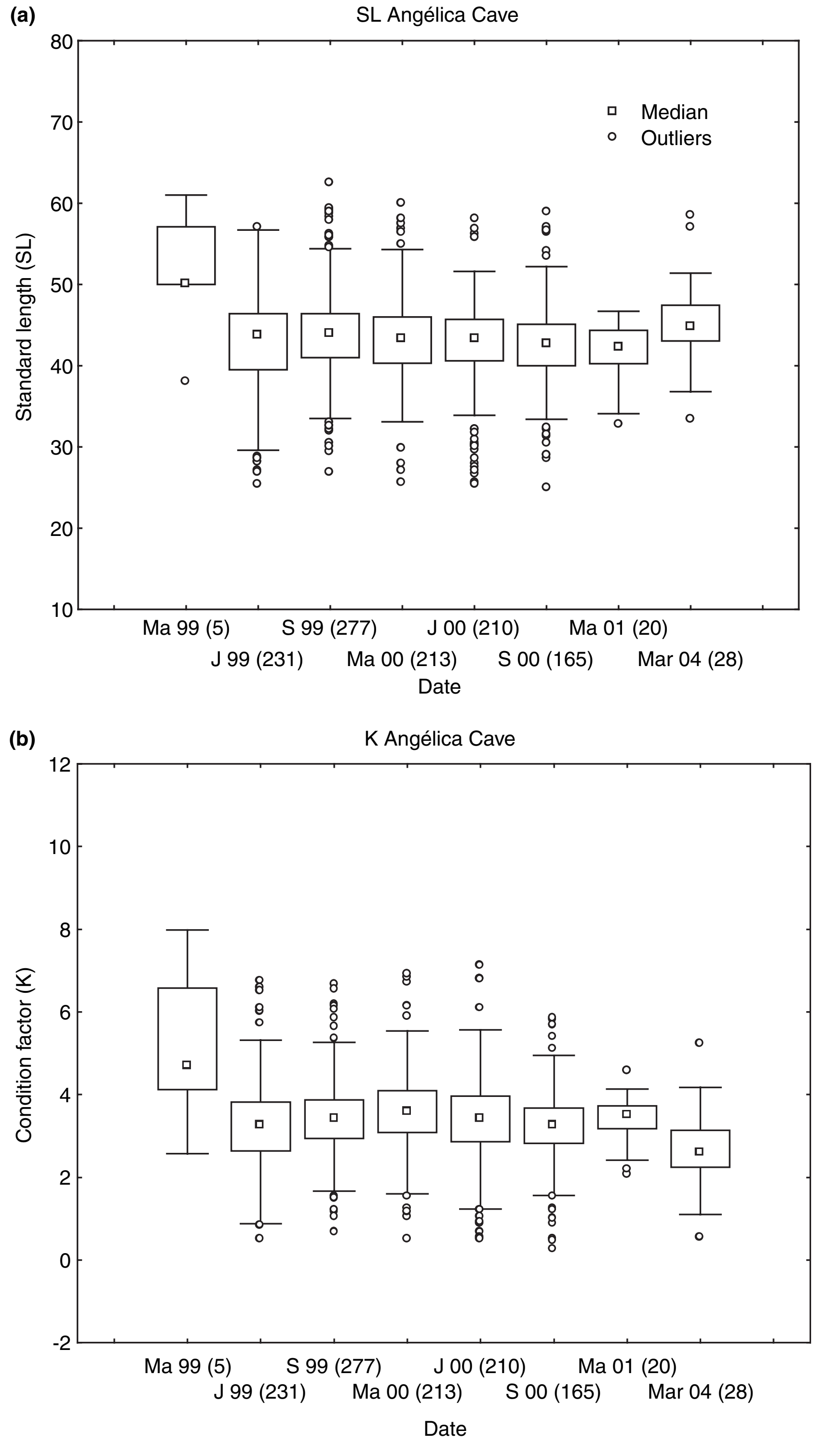

Fig. 3. Medians, standard deviations and confidence intervals of SL (a) and K (b) in *Ancistrus cryptophthalmus* from Angélica Cave. SL in mm. Ma, May; J, July; S, September; M, March. In parenthesis, number of individuals measured and weighed.

Angélica population, but not for the Passa Três population, for which no age/size-related tendency was visible. In fact, growth rates similar to those observed for both young and adult individuals in the cave habitat were observed for very young catfish (until 25 mm SL) from the Passa Três Cave raised in laboratory and fed *ad libitum*: 0.5 mm·month^{-1} (S. Secutti pers. comm.).

The von Bertalanffy parameters estimated for the pooled yearly data (1999 plus 2000) were, respectively: Angélica, $SL\infty = 72.89$, $K = 0.010744$; Passa Três, $SL\infty = 70.92$, $K = 0.011350$ (t in months, SL in

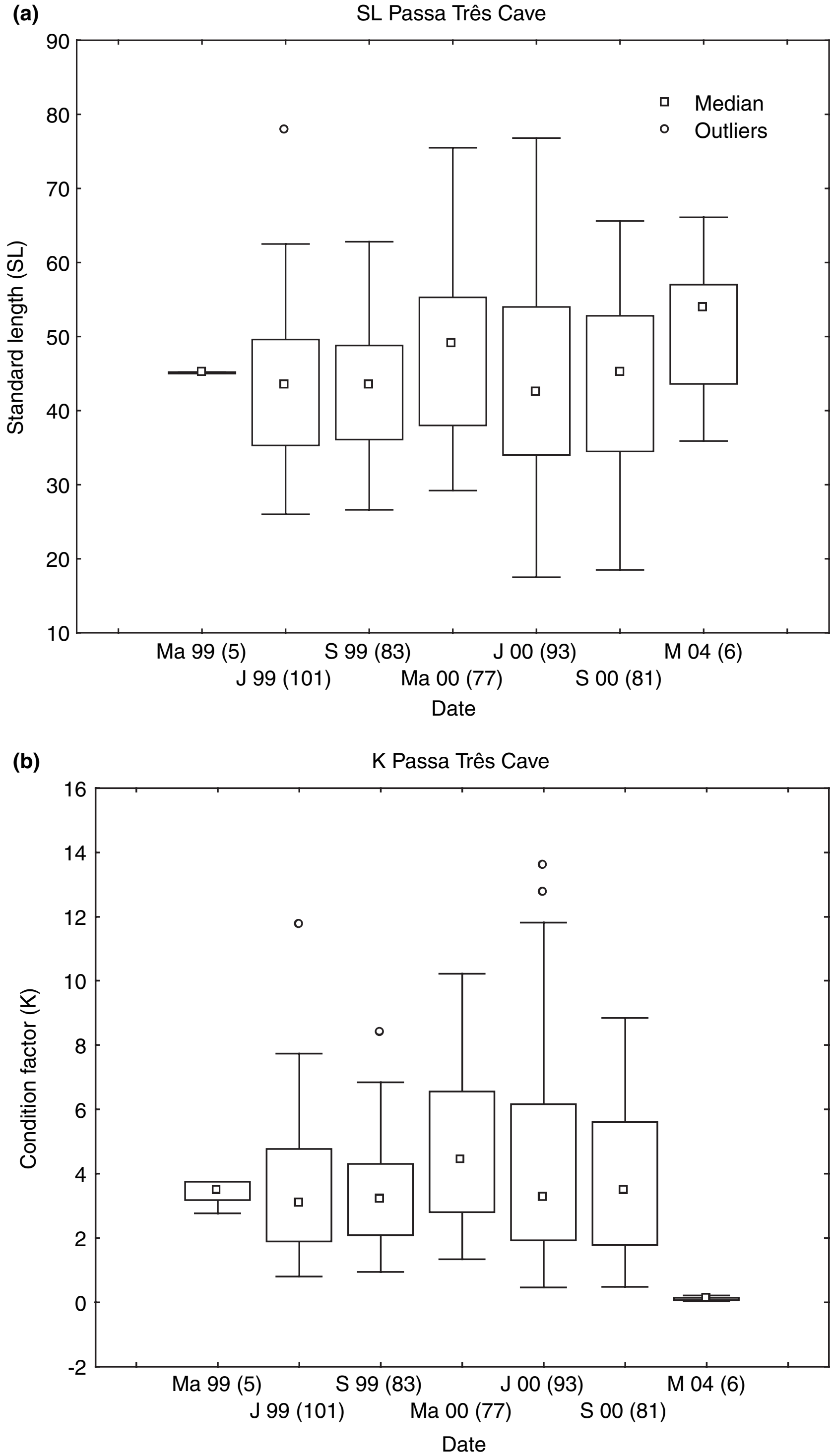

Fig. 4. Medians, standard deviations and confidence intervals of SL (a) and K (b) of *Ancistrus cryptophthalmus* from Passa Três Cave. SL in mm. Ma, May; J, July; S, September; M, March. In parenthesis, number of individuals measured and weighed.

millimetre). Longevities of 8–10 years were calculated for the cave populations.

Gonad development

In the Angélica Cave, the proportion of individuals with developed gonads, seen by transparency, remained constant around 8–9% between July and September 1999, increased from 8% to 15% between May and July 2000, then decreased to 6% in September 2000. Contrary to expected, the sample studied in the Angélica Cave in March 2004 (end of the rainy season, theoretically a favourable period because of presumed higher food availability) did not include a higher proportion of individuals with developed gonads: only 2 of 28 examined specimens certainly had developed gonads, and three additional specimens had possibly developed gonads.

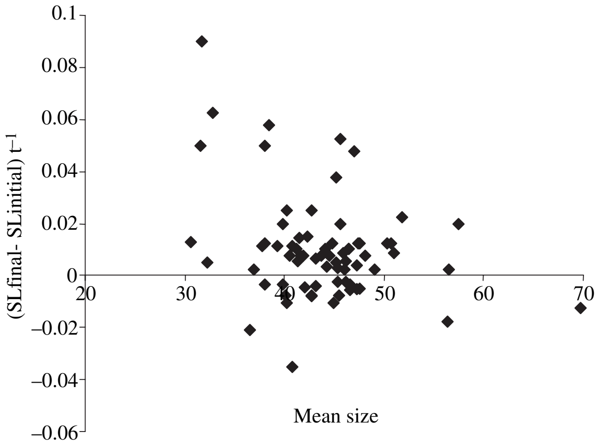

Fig. 5. Individual size increments related to mean sizes (SL) in *Ancistrus cryptophthalmus* from Angélica Cave during the dry seasons of 1999 and 2000 (n = 70). SL final, SL at recapture time; SL initial, SL at previous capture; t, time (in days) between samples collections.

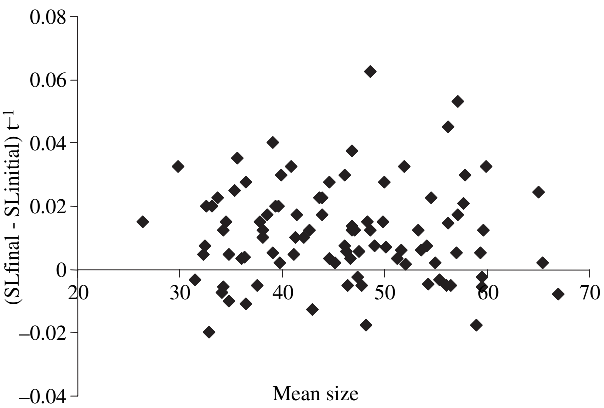

Fig. 6. Individual size increments related to mean sizes (SL) in *Ancistrus cryptophthalmus* from Passa Três Cave in dry seasons of 1999 and 2000 (n = 94). SL final, SL at recapture time; SL initial, SL at previous capture; t, time (in days) between samples collections.

The proportions of individuals with developed gonads were generally much lower in the Passa Três population: 1% in July, 7% in September 1999, 6.5% in May, 4.5% in July and 5% in September 2000.

Discussion

The mark–recapture data associated to visual censuses pointed to a relatively stable population in Angélica (around 20,000 individuals for the whole cave; Trajano 2001b) and Passa Três (around 1000 individuals) Caves. Long-term stability (10+ years) is evident for the Passa Três population. When compared with other cave catfish studied throughout the world (Trajano 2001a), these populations represent two extremes in the range of variation in population sizes, the Angélica population being among the largest recorded and Passa Três population among the smallest.

On the contrary, for all four known populations of *A. cryptophthalmus*, population densities that varied from 0.5 to 1.0 individuals per m^2 may be considered high by hypogean fish standards (Trajano 2001a). These densities are rather constant among caves, around 1.0 individuals per m^2 for the large Angélica, Bezerra and São Vicente I Caves. The lower densities observed in the Passa Três Stream, which is a tributary of the São Vicente Stream, are probably because of the lower water volume.

When compared with epigean loricariids, population densities of *A. cryptophthalmus* may not be considered low. As already mentioned elsewhere (Trajano 2001b), densities of the epigean *Ancistrus* species in the studied stream reaches of the São Domingos karst area are not much higher than those of *A. cryptophthalmus*: on an average up to 50% higher, with maximum densities (10 individuals per m^2) close to that observed in cave reaches where troglobitic catfish concentrate. Buck & Sazima (1995) recorded maximum monthly densities of 0.49 individuals per m^2 in open stream reaches and 0.22 individuals per m^2 in shaded reaches, for a set of four species of loricariids (including one undescribed *Ancistrus* species) living in an Atlantic forest stream from southeastern Brazil. Average densities of all loricariids [*Ancistrus spinosus* Meek & Hildebrand 1916, maximum SL of 20 cm, accounting for 74% of all sightings] observed on grazing platforms of the Frijoles Stream, Panamá, were 1.9 individuals per m^2 in Limestone Flats Pools and 2.9 individuals per m^2 at the Bat Rocks Pool; maximum densities, observed during the dry season, were six loricariids per m^2 (Power 1990). The estimated mean densities of *A. cryptophthalmus* in the Angélica Cave are close to that observed for small-sized *A. spinosus* kept in heavily sedimented enclosures (1.2 and 2.5 individuals per m^2, respectively, in two enclosures), whereas the densities of *A. cryptophthalmus* in Passa Três are closer to those of *A. spinosus* in moderately sedimented enclosures (0.30, 0.44 and 0.34 individuals per m^2, respectively, in three enclosures) (Power 1990). Therefore, the notion of low population densities as characteristics of troglobites does not apply to *A. cryptophthalmus*, possibly because their food (mainly detritus) is not as limiting as usual for subterranean populations.

Seasonal fluctuations may occur, as indicated by the higher population size estimated for the Angélica Cave for May 2000. In fact, January to April precipitation was higher in 2000 (671.3 mm) when compared with 1999 (579 mm), possibly resulting in a higher food input in the form of organic debris carried by water into caves.

The progressive decrease in the average condition factor observed in the Angélica, Passa Três and Bezerra (this latter only in 2000) Caves may be attributed to a progressive decrease in food availability throughout the studied dry seasons. Seasonal variation in the condition factor was reported by Power (1984) for the epigean *A. spinosus* in a Panamanian Stream, which tended to loose or just maintain their mass during the dry season, when grazing areas are limited; whereas these fish would quickly recover mass during the rainy season, when they gain access to areas previously too shallow to graze.

Negative growth has also been reported for other cavefish: the Brazilian catfish, *Trichomycterus itacarambiensis* (Trichomycteridae) (Trajano 1997b) and *P. spelaea* (Heptapteridae) (Trajano *et al.* 2004), and the North American *Amblyopsis rosae* Eigenmann 1898 (Amblyopsidae) (Brown & Johnson 2001). For *T. itacarambiensis* and *P. spelaea*, studied during the dry season, when the input of food transported by water is mostly cut, it has been suggested that the instances of negative growth are a consequence of extreme feeding stress. In fact, *T. itacarambiensis* adult catfish kept in the laboratory and fed *ad libitum* grew, on an average, 1.2 mm·month^{-1}, whereas those studied in the cave habitat grew, on an average, only 0.06 mm·month^{-1} during the dry season (Trajano 1997b).

On the contrary to expectation, the mean condition factor calculated for *P. spelaea* at the end of the rainy season (E. Trajano & M. E. Bichuette unpublished data), in theory a period of higher food availability, was even lower than that for the dry period (Trajano *et al.* 2004), as reported here also for the sympatric (but not syntopic) *A. cryptophthalmus*. This indicates that the rainy season may also be a stressful period for the fish.

Our cumulative data on Brazilian cavefish indicate that negative growth is a real, biological phenomenon, not an artefact. As a component of total fish growth, instances of negative growth must be included in calculations of growth parameters, in order to produce biologically realistic models. The removal of such data, as performed by Brown & Johnson (2001) for *A. rosae*, most probably produces biased results, with overestimated mean growth rates.

Data on the condition factor of *A. crytophthalmus* at the end of the rainy season provides no evidence that this would be a more favourable period for weight gain and growth. Therefore, we believe that growth rates estimated for *A. cryptophthalmus* during the dry season may be extrapolated for the whole year. The slow growth observed for well-fed individuals kept in the laboratory indicate intrinsically low growth rates, corroborating our results for populations studied in the natural habitat.

Considering maximum fish sizes (around 70 mm), longevities estimated for *A. crytophthalmus* (8–10 years) are slightly superior to the observed for a few other studied cavefish – e.g., longevities of 10–15 years were estimated for *Pimelodella kronei* that reaches double the size of *A. crytophthalmus* (Trajano 1991), 7 years for *T. itacarambiensis* (maximum sizes around 80 mm; Trajano 1997b) and 4–5 years for *A. rosae* (Brown & Johnson 2001), although the latter is probably underestimated.

We found no evidence of seasonal reproduction in *A. crytophthalmus*, similar to that observed for *P. kronei* and in contrast to *T. itacarambiensis* and the new heptapterid catfish from Chapada Diamantina (NE Brazil), that live in areas with a highly seasonal climate (well-defined, accentuated dry seasons) and for which higher percentages of mature individuals have been recorded at the end of the rainy period. Seasonal reproduction, with well-defined annual cycles, was reported for several other hypogean fish, and seems to be more frequent than nonseasonal reproduction (Trajano 2001a).

Low individual growth rates associated to low fertility and high longevities indicate a precocial lifestyle (sensu Balon 1981), a common feature of troglobitic species, usually interpreted as an adaptation to a food-limited environment (Trajano 2001a). Although food availability for grazing fish such as *Ancistrus* catfish was not directly measured in the studied caves, it is quite clear that it is much lower than in epigean habitats: in the latter, periphyton may cover large portions of aquatic substrates and be food for grazing fish, while, in cave habitats, only a film of finely particulate organic matter is available. This explains the low growth rates and relatively high longevity observed for *A. cryptophthalmus*. However, in the absence of comparable data for the epigean *Ancistrus* species from São Domingos, it is not possible to decide whether this precocial lifestyle is actually an adaptation of *A. cryptophthalmus*, acquired after the differentiation in the cave habitat, or a feature already characterising epigean ancestors (retained by epigean species currently living in the area), which could have favoured the colonisation of the food-limited hypogean environment.

So far, no recognisable disturbance has been detected for the Passa Três population caused, for instance, by human visitation (which is currently infrequent) or water pollution. However, its small size imposes the need for more effective protection. On the contrary, the Angélica population, in spite of its large size, is a matter of concern in view of increasing touristic visitation, poorly controlled by the Terra Ronca State Park authorities.

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