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Ecology of subterranean fishes: an overview

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Synopsis

A synthesis of ecological data available for subterranean fishes throughout the world is presented, and comparatively analyzed in an evolutionary context. Methods of ecological research are described, and their potential and limitations for the study of hypogean fishes are discussed. Ecology of troglobitic (exclusively subterranean) fishes is discussed with focus on distribution areas, population densities and sizes, use of habitat and movements, life cycle and feeding. When data are available, these species are compared with their epigean relatives. Putative ecological autapomorphies of troglobitic fishes, including habitat change, adaptations to cope with food scarcity, and precocial lifestyles, are interpreted in ecological and evolutionary contexts. Species interactions among subterranean species, including cases of syntopy and predation are briefly analyzed. Non-troglobitic hypogean fishes, with their ecological importance and evolutionary role, are also addressed. Problems of classification of subterranean fishes according to the Schiner-Racovitza system (troglobites, troglaphiles and troglonexes) are discussed, and a scenario of evolution of subterranean populations is presented.

Introduction

Troglobites, or species restricted to the subterranean habitat, usually show a series of autapomorphies (troglomorphisms), including morphological, physiological, behavioral and ecological features, which can be directly or indirectly related to the hypogean life, being either adaptive or not (for a discussion of theories about character evolution in the cave habitat, see Culver et al. 1995). The most common morphological traits characterizing troglobites are reduction of both eyes and pigmentation. Ecological traits frequently cited for troglobites include low population sizes, restricted geographic distribution, low tolerance to environmental stress, precocial life cycle features (e.g., Culver 1982, Trajano 1997a) related to the life under permanent darkness, few environmental cues, usually restricted space, and frequent food scarcity.

More than 86 species of subterranean troglobitic fishes belonging to 18 families in nine orders have been recorded throughout the world (Weber et al. 1998

among others), the majority being found in caves. Cave fishes are fairly easy to investigate in the field because they are relatively large, generally conspicuous, and not difficult to observe and collect, as many species have lost phobic reactions and show increased activity. Nevertheless, there have been few studies in this area, partly because ecological investigations require long-term permanence in the field and many troglobitic fishes occur in tropical regions, sometimes in caves of difficult access, where there are few local researchers.

The relatively abundant cavefish literature (about 1600 references, G. Proudlove personal communication) is dominated by studies on systematics, genetics, morphology, physiology and behavior in the laboratory and focuses on few taxa, especially the blind Mexican characins, genus *Astyanax*, followed by North American amblyopsids. A low proportion of these publications (fewer than 4%) dealt strictly with ecology of subterranean fishes.

One can trace ecological data scattered in the literature on cave fishes, including habitat descriptions

and comments on habitat use, abundance, reproduction and behavior, back to Eigenmann's (1909) 'Cave Vertebrates of America', or earlier. However, detailed ecological studies with population analyses started with the investigation of the African cyprinid, *Caecobarbus geertsii*, by Heuts (1952). Some years earlier, Pavan (1946) published a population study on the Brazilian blind catfish, *Pimelodella kronei*, but essentially within an evolutionary context. Among the ecological studies published since then, we can mention the comprehensive study on the North American amblyopsids by Poulson (1963), also the object of recent studies by Means & Johnson (1995) and Brown (1996); the rare ecological studies on the otherwise intensively investigated Mexican blind tetras, *Astyanax* spp. (Mitchell et al. 1977, Parzefall 1983); and a series of ecological studies on Brazilian troglotic catfishes published in the last decade (Trajano 1991, 1997a,b, Mendes 1995a,b, Trajano & Bockmann 2000).

These works included information on population sizes and densities, fish movements and life history aspects besides feeding (reproduction, growth rates, etc.). However, few authors studied feeding beyond general diet (as Trajano 1997b, focusing on temporal variation and seasonality). Likewise, few publications included a detailed description of cavefish habitats (as those by Heuts 1952, for *C. geertsii*, and Mitchell et al. 1977, for *Astyanax* spp.) and habitat preferences. Mitchell et al. (1977) made the most thoughtful and comprehensive description of habitats occupied by cave fishes, listing and describing all localities known for Mexican troglotic *Astyanax*, and detailing the geomorphology and hydrology in the so-called Huastecan Province; such a publication provides a solid basis for discussion of the origin and evolution of these populations. The modern tendency is to greatly abbreviate habitat descriptions, which rarely include good maps, and information on fish microhabitats based on careful field and laboratory observation is scarce, making it difficult to get a proper notion of habitat use. Therefore, ecological aspects such as habitat change and specialization are usually overlooked.

Herein I present an overview of results from ecological studies on hypogean fishes throughout the world, comparatively analyzing data on population sizes and densities, use of space (habitat, movements, species syntopy), feeding and life history of different taxa, as a contribution to the knowledge of fish species restricted to this special habitat. When data are available, subterranean populations were compared to those of epigean close relatives living in the same area, in an attempt

to distinguish between plesiomorphic character states and ecological autapomorphies of troglotites, resulting from specialization to the particular conditions in the subterranean habitat. Because few troglotic species, and even fewer epigean relatives, have been studied with focus on ecological aspects, general patterns may be difficult to visualize. The present overview shows how much there still is to be learned about these fascinating animals.

Methods of ecological studies in subterranean fishes: a comparative analysis

Basically, three kinds of methods have been used in studies of the ecology of subterranean fishes: extensive collections of preserved samples, direct observation in the habitat, and capture-mark-recapture programs. Different methods are the most useful for investigating different aspects of ecology, and each one has its advantages and limitations. Therefore, they must be regarded as complementary.

Two methods have been applied to determine population sizes and densities in cave fishes: visual censuses (VC) and mark-recapture (MR) techniques. In visual censuses, 'instantaneous' counts of the number of fish seen in the habitat are made from the surface or during snorkeling or SCUBA diving. These censuses may encompass the total accessible habitat, as done for amblyopsids (Poulson¹, Willis & Brown 1985, Brown & Todd 1987) and the Brazilian catfish, *Taunayia* sp. (Trajano & Bockmann 2000). In other cases, selected sections of the cave habitat are inspected, such as small areas, for *Astyanax* spp. (Parzefall 1983), transects, for an undescribed genus and species of Brazilian heptapterine from NE Brazil (Mendes 1995a – the species is here cited as *Imparfinis* sp.), or stream sectors, for Thai balitorids, *Schistura oedipus* and *Cryptotora thamicola* (Trajano, Borowsky, Mugue & Smart unpublished data).

Visual censuses produce estimates of minimum population densities, from which one can calculate the total population size if: (1) the total habitat area occupied by the fish population is known, and (2) population density remains constant throughout this area. These two conditions are rarely met and such estimates generally provide only a rough comparative notion of minimum

¹ Poulson, T.L. 1969. Population size, density and regulation in cave fishes. pp. 4–5. In: Proc. 4th International Congress of Speleology, Ljubljana.

population sizes. We must keep in mind that VC produce underestimates, especially when done from the surface; as pointed out by Brown & Todd (1987), snorkeling greatly increases accuracy in VC.

Mark-recapture methods produce more accurate population data, but are time-consuming, demanding more visits to the study site and adequate fish marking techniques. In addition to assessment of population sizes, individual marking allows determination of fish movements and home ranges, and estimation of growth rates without the need for large preserved samples, frequently difficult to obtain due to the small size and ecological fragility of many troglobitic populations.

Few MR studies on cavefish have been carried out so far. Medium (one season) to long term (one to several years) studies comprising multiple marking and recapture occasions were done for Brazilian catfishes, *Pimelodella kronei*, in Areias Cave (Trajano 1991) and *T. itacarambiensis* in Olhos d'Água cave (Trajano 1997a), and the North American Ozark cavefish, *Amblyopsis rosae*, in Logan Cave (Means & Johnson 1995, Brown 1996); a study on Mexican ictalurids, *Prietella phreatophila* and *P. lundbergi*, is in progress (Krejca et al. 2000). Two-census MR studies were carried out for the Brazilian armored catfish, *A. cryptophthalmus* in Angélica and Passa Três caves (Trajano 2001), and troglobitic *Astyanax* in Pachon and Yerbaniz caves (Mitchell et al. 1977). Depending on the extension and difficulty of progression along the cave, and on population densities associated with difficulty in capturing fish (determining the number of fish to be marked), the whole accessible cave habitat may be studied, as was the case with *A. rosae* and *T. itacarambiensis*. In other cases, only part of the habitat was investigated (*P. kronei*, *A. cryptophthalmus*, *P. mexicana*). For the latter, estimates from studied sectors in the caves have been extended to the whole cave population, assuming constant population densities; such estimates are, therefore, more subject to errors.

Individual marking has been achieved using subcutaneous marks by, for example, injecting biocompatible pigments (tattooing), as in *P. kronei*, *T. itacarambiensis* and *Ancistrus cryptophthalmus*, or visually implanting tags, in *Amblyopsis rosae*. The fishes were captured in hand nets (*T. itacarambiensis*, *A. cryptophthalmus*, *A. rosae*) or minnow traps (*P. kronei*), anesthetized, measured, weighed, examined for individual natural marks and gonad development (seen by transparency), marked and released in the collection subsections. Usually only fish larger than a certain size (adults and large

juveniles) have been included in this kind of study, either because young fishes are not located and captured, or because they are too small for marking. No methodological details were given for the *Astyanax* study.

This method produces a large amount of ecological data, including population size and density, spatial and temporal distribution of class sizes, weight and condition factor, and also of reduction of eyes and pigmentation (for variable populations), fish movements and home ranges, life cycle parameters (reproduction, growth rates), among other data. However, in some cases MR is not practical, either because population densities are too small to obtain the minimum number of marks needed for mathematical treatment (case of the Brazilian heptapterine, *Taunayia* sp.), or localities are too remote and difficult to access, hampering the necessary periodical visits, especially when there are no local researchers, as in the case with many African and Asian fishes.

In general, for VC and complementary observation on fish distribution inside caves, habitat preferences and behavior, as well as for hand-netting, the specimens were visually located from stream-side, as is the case with *Astyanax* spp. and amblyopsids in shallow habitats (Poulson¹, Parzefall 1983, Brown & Todd 1987), the balitorids *S. oedipus*, *C. thamicola* and *Nemacheilus troglotataractus* (Trajano, Borowsky, Mogue & Smart unpublished data), the catfishes *T. itacarambiensis* (Trajano 1997a,b) and *A. cryptophthalmus* (Trajano 2001); while snorkeling, for *Taunayia* sp. (Trajano & Bockmann 2000), *Astyanax* spp. and *A. rosae* in deeper habitats (Parzefall 1983, Brown & Todd 1987); or SCUBA diving, for the new heptapterine genus from NE Brazil (Mendes 1995a,b).

Most ecological studies were carried out only during dry seasons, because caves located in regions with seasonal climates may become inaccessible during the rainy periods, and there is always the danger of being caught by flash floods during those periods, a general feature of karst drainages. This restriction to part of the annual cycle imposes a limitation to the generalizations that can be taken from ecological studies of subterranean species. Such is the case with *T. itacarambiensis*, *A. cryptophthalmus*, *Astyanax* spp. and cave balitorids. On the other hand, *P. kronei*, which lives in an area with less accentuated seasonality, could be studied throughout the year (Trajano 1991). The same was true for *A. rosae* in Logan Cave (Brown 1996).

Population density is defined as number of individuals per unit area, per unit volume, or per unit of habitat

(Krebs 1994). Ideally, units of volume should be used for fishes, except for those strictly benthic. Many cave fishes, including those belonging to typically bottom-dwelling epigeal taxa, explore not only the bottom but also the midwater (Trajano & Bockmann 1999). Thus, the number of individuals per unit volume is more representative of the real population densities. However, in the absence of precise data on habitat volumes due to the high spatial heterogeneity, with a great deal of variation in depth along the studied caves, population densities estimated for subterranean fishes have been expressed as number of fish per unit area (m^{-2}). This clearly produces a bias that should be taken into account when comparing populations from different caves.

Likewise, if the goal is to evaluate the impact of cavefish populations over the subterranean ecosystems, biomass is another parameter to be considered. Most troglotic fishes are small, less than 10 mm SL (e.g., Greenwood 1967), and do not greatly differ in terms of biomass. The main exception among the species studied with focus on population ecology is *P. kronei*, a relatively large catfish (maximum size around 180 mm SL) showing a mode of weight = 18.0–22.0 g, with maximum weight = 52.0 g (Trajano & Britski 1992). For comparison, the mode of weight distribution in *T. itacarambiensis* (max. size = 83 mm SL) during the dry season was 1.0–2.0 g, max. weight = 6.0 g (Trajano 1997a, unpublished data) and the mode of weight in a small sample of *S. oedipus* from Mae Lana Cave (max. size = 74 mm SL) was 0.4–1.0, max. weight = 5.0 g (Trajano, Borowsky, Mugue, Smart & Krejca unpublished data).

Methodological discrepancies include different methods to estimate population parameters (e.g., VC versus MR) and different collection (hand-netting versus trapping) and marking (more or less permanent marks) techniques, associated with differences in habitat characteristics (more or less accessible and seasonal habitats) and fish behavior (shy, elusive versus non-shy species), which should always be made explicit. Such differences merit special concern when comparing data available for cave fishes.

Securing preserved samples is necessary not only in the faunistic survey step, for recognition of species and determination of distributional ranges, but also for the study of diet and reproduction. Observation of feeding behavior may provide evidence on the kind of food consumed by the fish, but unquestionable identification of items actually ingested depends on analysis of gut contents. Detection of developed gonads seen by

transparency in living fish may produce useful data on reproduction, but limited to the later stages of gonad development and subject to errors due to difficulties in visualization.

Ecology of subterranean fishes

The problem of species and population delimitation

In the context of ecological studies, distinction of species and delimitation of populations is an important issue. When differences in habitat use, population densities and life cycle parameters are observed between localities, one must determine whether they reflect geographic variation in ecological conditions, or are species-specific characteristics. More or less isolated populations may differ in population parameters. For instance, Heuts (1952) detected distinct growth patterns and age-class distributions in samples of *C. geertsii* from different, separate caves located in a relatively small karst area in Congo. Likewise, a first condition to estimate population sizes is to circumscribe such populations based on biologically meaningful criteria.

Caves, defined as natural cavities large enough to be entered by humans (Monroe²), constitute biologically an arbitrary subdivision of the subterranean domain. In many cases, they encompass only a fraction of the total species habitat, and studies in caves only assess a peripheral part of this population, which may be strongly affected by the proximity to large contacts with the surface. This is especially true for species occupying the phreatic habitat, such as typical phreatobites (e.g., *Satan eurystomus*, *Trogloglanis pattersoni*, *Phreatobius cisternarum*, *Uegitglanis zammaranoi*, *Phreatichthys andruzzii*). It is also the case for hypogean fishes occurring in widely distributed caves, such as the troglitic amblyopsids (except *Speoplatyrhinus poulsoni*, known from a single cave), characins, genus *Astyanax*, and the new heptapterine genus from NE Brazil, which are expected to occur in the aquifer(s) between the caves.

In many cases, the delineation of subterranean species is not clear and a detailed taxonomic revision may reveal a set of separate, cryptic species under the same designation. Molecular evidence shows that

² Monroe, W.H. 1970. A glossary of karst terminology. Geological Survey Water-Supply Paper 1899-K. 26 pp.

T. subterraneus is paraphyletic (Bergstrom & Noltie³), with two of its four lineages more closely related to *A. spelaea* than to the two other lineages, and that *A. rosae* correspond to four different lineages (possibly distinct species) because the divergence between populations from four watersheds is equivalent to, or greater than, the divergence among different species and genera in the family. Willis & Brown (1985) state that continuous cave passages linking all the populations of troglobitic amblyopsids is very unlikely, thus each species, and possibly each current population of cavefish, represents a separate evolutionary event. Molecular studies also indicate that *S. oedipus* comprises three separate groups (Borowsky & Mertz 2001).

Morphological, distributional and molecular data suggest that the cave populations of blind tetras, genus *Astyanax*, found in the Huastecan Province, resulted from at least two, probably three or more isolation events (Alvarez 1946, Mitchell et al. 1977, Borowsky & Espinasa⁴, but see Espinasa & Borowsky 2001). Thus, they correspond to different diagnosable, phylogenetic species (sensu Pinna 1999), whose exact number and geographic limits are not yet clear. The cave population of *Poecilia mexicana* from Cueva del Azufre, in Mexico, presents several morphological and behavioral troglomorphisms, at least part of them genetically based (Parzefall 1993). Therefore, much as the troglomorphic subterranean populations of *Astyanax* (see Trajano 1993) deserves the status of separate species, but it is still treated as *P. mexicana*, the name of an epigeal species. These are examples of nomenclature problems reflecting the lack of taxonomic resolution, which affects all areas of research interest.

Pimelodella kronei was recorded in two sets of limestone caves separated by a non-soluble, diabase dyke that prevents subterranean dispersion between those caves. Therefore, this taxon may comprise two distinct, cryptic species (Trajano 1997c). So far, we have been able to study only populations in the set of caves comprising the type-locality, Areias Cave. There is morphological and behavioral evidence that the populations of *A. cryptophthalmus* from Angélica-Bezerra caves and

Passa Três Cave are at least partially isolated (Trajano 2001), and these populations will be treated separately herein.

In conclusion, it is necessary to define the boundaries of populations that operate in a homogeneous, integrated way, which should constitute the basic units for ecological studies. A starting point is to focus on cave systems defined on a hydrogeological basis (conduits extending continuously between the input and output points of a karst rock, including passages too small to be entered by humans, Ford & Williams 1989) as geographic units, until more detailed comparative morphological studies and assessment of genetic differentiation provide a better understanding of population limits, and a more precise view of species distributions.

Distribution and habitat of troglobitic fishes

Troglobitic fishes occur in all continents except Europe, and also in many islands (e.g., Cuba, Madagascar). The highest species richness is observed in China, Mexico, Brazil and southeast Asia, not necessarily corresponding to the areas with greatest total richness ('hot spots' of biodiversity) of aquatic troglobites. Most troglobitic fishes are siluriforms (found in the Americas, especially the tropics, and in Africa, with a few in Asia) or cypriniforms, mostly cyprinids or balitorids (located throughout tropical Asia, some cyprinids in Africa). Hence, these groups of freshwater fishes present a high potential for easy adaptation to subterranean life.

On the other hand, characiforms, other important group of freshwater fishes, are in general poorly represented among the troglobitic fauna: besides the poorly known Brazilian tetra characin, *Stygichthys typhlops*, whose epigeal closest relatives have not been determined (Romero & McLeran 2000), only the Mexican species inhabiting the Huastecan Province, *Astyanax mexicanus* (= *A. fasciatus*), has successfully originated several troglobitic populations, due to preadaptations to the cave life; for example, a chemically stimulated spawning behavior, ability to feed in darkness, and a well-developed lateral line system (Wilkens 1988). Likewise, cichlids, another important group of freshwater fishes, have no troglobitic derivatives, although epigeal specimens may be occasionally found in caves. Among the usually abundant cyprinodontiforms, only one Mexican species, *Poecilia mexicana*, has specialized to cave life, under very unusual conditions: an exceptionally high availability of food (Langecker et al.

³ Bergstrom, D.E. & D.B. Noltie. 1998. The phylogeny, historical biogeography, and evolution of troglobitism in *Amblyopsis rosae* (Ozark cavefish) and *Typhlichthys subterraneus* (southern cavefish). Abstract 185. In: 78th Annual meeting Amer. Soc. Ichthyol. Herpetol., Guelph.

⁴ Borowsky, R. & L. Espinasa. 1997. Antiquity and origins of troglobitic Mexican tetras, *Astyanax fasciatus*. pp. 359–361. In: Proc. 12th International Congress of Speleology, La-Chaux-des-Fonds.

1996). Those are good examples of low potential for subterranean life.

Preadaptation to hypogean life is clear for siluriforms, which are generally nocturnal, chemo-oriented fishes, most omnivores or generalist carnivores, but not so for cypriniforms which, like characiforms, include many diurnal, visually-oriented species. For the latter, preadaptations for subterranean life must be sought among the closest epigean relatives, which could have retained the preadaptive character states shown by the troglobite's ancestors, as in the epigean *A. mexicanus*.

There is a great variation in the extent of geographic distribution of each troglobitic species, without a phylogenetic/taxonomic correlation. Several species have been so far found in a single cave (e.g., *Sinocyclocheilus anophthalmus*, *Triplophysa ayunnanensis*, *Nemacheilus troglotataractus*, *Clarias cavernicola*, *Rhamdia reddelli*, *Taunayia* sp., *Trichomycterus chaberti*, *T. itacarambiensis*, *Ancistrus galani*, *Speoplatyrhinus poulsoni*, *Poecilia mexicana*), while others present a slightly wider distribution area, occurring in a few caves (e.g., *Caecobarbus geertsii*, *Schistura oedipus*, *Cryptotora thamicola*, *Pimelodella kronei*, the new heptapterine genus) to those who inhabit many, more or less widely distributed caves (e.g., *Astyanax* spp., *Lucifuga subterraneus*, *L. dentatus*, troglobitic amblyopsids except *S. poulsoni*). Troglobitic fishes inhabiting non-karst regions include the Brazilian heptapterine, *Phreatobius cisternarum*, found in alluvial fan from a large area around the Amazon delta (Carvalho⁵).

Subterranean karstic habitats occupied by different species of troglobitic fishes are shown in Table 1. This table does not include all known hypogean fishes, because for many species such data are unavailable. My main purpose was to illustrate the variety of habitats where troglobitic fishes may be found. It is also an attempt to detect patterns related to the fish characteristics, such as systematic position, geographic and biological attributes, which could help to understand why and how fishes colonize and speciate in the subterranean biotope. For species occurring in a large number of caves, such as amblyopsids, *Astyanax* spp. and *Lucifuga* spp., it was difficult to define a typical habitat for the 'species'. In such cases, the habitat classification represents the main tendencies detected for the species,

⁵ Carvalho, A.L. 1967. Novos dados para o conhecimento de 'Phreatobius cisternarum' Goeldi (Pisces, Pygidiidae, Phreatobiinae). Atas do Simpósio sobre a Biota Amazônica 3 (Limnologia): 83–88.

and exceptions will certainly be found. I did not include in Table 1 non-karst habitats such as granular, porous aquifers inhabited by *P. cisternarum*.

Three main karst habitat categories may be distinguished: (1) upper phreatic zone, represented by lakes or static water bodies, connecting to the surface through voids varying from impenetrable fissures to large caves, and generally characterized by lentic conditions; (2) zone of seasonal oscillation of water table, that during flooding may form pools and lakes that will remain isolated during the dry season or may contribute water to dramatically increase the discharge of underground streams; and (3) open channel stream passages, usually showing lotic conditions, that include base-level streams (which may or may not represent the phreatic zone) and vadose upper tributaries (A. Auler personal communication). In addition, some species may live in perched aquifers, as those forming water bodies in rimstone dams fed by percolation water and, occasionally, by water from the stream channel during floods.

The upper phreatic zone habitat may include flooded caves – caves formed above the water table which have been posteriorly flooded due to rise of the water table, caused, for instance, by subsidence of the whole region or elevation of the sea level (for caves situated not far from the coast). Elevation of the sea level affected several caves inhabited by *Lucifuga* spp. in Cuba (Juberthie⁶). Regional subsidence is probably the cause of flooding of caves from Mato Grosso do Sul, SW Brazil, inhabited by *Ancistrus formoso* and a new species of *Trichomycterus* (treated as *Trichomycterus* sp. 2 in Trajano 1997d). It is noteworthy that the original hypogean habitat, present when the fishes first colonized the caves, may be quite different from the recently observed. This is possibly the case of the catfishes from Mato Grosso do Sul, which belong to stream-adapted genera.

There is a great variation in the ecological conditions of habitats occupied by troglobitic fishes, from streams with well-oxygenated waters in riffles and rapids alternating with pools, to lentic environments such as water bodies formed by the water table inside caves or inaccessible phreatic habitats. Extreme adaptation to fast-moving waters is observed in the balitorid *Cryptotora thamicola*, generally found in waterfalls over flowstone (see below) in caves from Thailand.

⁶ Juberthie, C. 1973. Notes sur l'écologie des poissons souterrains de Cuba. pp. 285–293. In: Comptes Rendus du 96^e Congrès National des Sociétés Savantes, tome III, Toulouse.

Table 1. Types of subterranean karst habitats occupied by some species of troglobitic fishes. (I) = syntopic species.

Habitat	Species	Country	
Upper phreatic zone	Connected to surface through inaccessible fissures*	<i>Stygichthys typhlops</i>	Brazil
		<i>Trogloglanis pattersoni</i>	USA
		<i>Satan eurystomus</i>	
		<i>Horaglanis krishnai</i>	India
	Connected to surface through resurgences, sinkholes, natural wells, cenotes, flooded caves, etc.	<i>Phreatichthys andruzzii</i>	Somalia
		<i>Barbopsis devecchii</i>	Somalia
		<i>Typhlogarra widowsoni</i>	Iraq
		<i>Caecocypris basimi</i>	
		<i>Iranocypris typhlops</i>	Iran
		<i>Prietella</i> spp.	Mexico
		<i>Uegitglanis zammaranoi</i>	Somalia
		<i>Ancistrus formoso</i>	Brazil
		<i>Lucifuga</i> spp.	Cuba
		<i>Oxyeleotris caeca</i>	Papua/ New Guinea
Connected to surface through caves	<i>Protocobitis typhlops</i>	China	
	<i>Oreonectes</i> sp.		
	New heptapterine genus	Brazil	
Zone of seasonal oscillation of water table	<i>Astyanax</i> spp.	Mexico	
	<i>Indoreonectes evezardi</i>	India	
	<i>Speoplatyrhinus poulsoni</i>	USA	
Open channel stream Passages	Base-level streams	<i>Sinocyclocheilus anophthalmus</i>	China
		<i>Triplophys ayunnanensis</i>	
		<i>Paralepidocephalus</i> aff. <i>yui</i>	
	Vadose tributaries	<i>Nemacheilus troglotataractus</i>	Thailand
		<i>Pimelodella kronei</i>	Brazil
		<i>Rhamdia reddelli</i>	Mexico
		<i>Trichomycterus chaberti</i>	Bolivia
		<i>T. itacarambiensis</i>	Brazil
		<i>Ancistrus cryptophthalmus</i>	Brazil
		<i>Ancistrus galani</i>	Venezuela
		<i>Poecilia mexicana</i>	Mexico
		<i>Schistura oedipus</i>	Thailand
		<i>Cryptotora thamicola</i>	Thailand

*Collected in artificial wells.

Among cave stream-dwellers, habitat preferences have been observed, for instance, in *P. kronei* (Trajano personal observations) and *Rhamdia reddelli* (Miller 1984), that prefer pools to riffles; an opposite tendency is shown by *A. cryptophthalmus*, which prefers rapids to pools (Trajano 2001). In other cases, no habitat preferences were detected: *T. itacarambiensis*, for instance, occurs both in riffles and in pools (Trajano 1997a).

The widely distributed troglobitic amblyopsids may occupy habitats that fall into different categories depending on the locality, but always showing preference to stagnant or slow-moving water, including places in which the upper phreatic zone is connected to

the surface through caves, the zone of seasonal oscillation of the water table, or pools and slowly flowing sectors in open channel streams (Poulson 1963, Romero 1998a,b). Thus, these species were not included in Table 1.

Other species live in typically phreatic waters, such as *Phreatobius cisternarum*, *Satan eurystomus*, *Trogloglanis pattersoni*, *Uegitglanis zammaranoi*, *Phreatichthys andruzzii*, *Barbopsis devecchii* and *Taunayia* sp. Some of these fishes show miniaturization, probably achieved by paedomorphosis (as proposed by Weitzmann & Vari 1988 for miniature epigeal species), as an adaptation to life in small phreatic spaces: *S. eurystomus*, *T. pattersoni*

(Langecker & Longley 1993), *Prietella lundbergi* (Walsh & Gilbert 1995), *Taunayia* sp., and the new heptapterine genus (Trajano & Bockmann 1999). Small size may also be energetically adaptive for hypogean environments (Walsh & Gilbert 1995).

Many fishes living in phreatic waters, or in shallow habitats subject to periodical drought or to special conditions (e.g., a high concentration of bacteria), must be tolerant to hypoxia in view of the low oxygen concentration frequently recorded in these habitats. For instance, very low values of dissolved oxygen (DO), ranging from 0.7 to 2.1 mg l⁻¹, were recorded in the phreatic water body inhabited by *Taunayia* sp. (Trajano & Bockmann 2000), much below the normal values for streams, which is >6.4, frequently 8–10 mg l⁻¹ (S. Buck personal communication, Trajano & Bockmann 2000). Low oxygen content characterizes the sulfur spring cave inhabited by troglobitic *Poecilia mexicana* (Langecker et al. 1996). Low values of DO were recorded in wells where phreatobitic fishes have been collected: *Barbopsis devechii* (1.0–5.0 mg l⁻¹), *Phreatichthys andruzzii* (2.7–3.8 mg l⁻¹) and *Uegitglanis zammaranoi* (5.7 mg l⁻¹) from Somalia (Ercolini et al. 1982); *Trogloglanis pattersoni* and *Satan eurystomus* from Edwards Aquifer in Texas (4.3–5.1 mg l⁻¹ – Longley & Karney 1979).

Putative adaptations to cope with hypoxia include an intense skin irrigation suggestive of cutaneous respiration in *P. cisternarum* (Carvalho⁵) and probably also in *Taunayia* sp. (Trajano & Bockmann 2000). Reduction of respiratory intensity resulting in low oxygen consumption was demonstrated for some troglobitic fishes such as *C. geertsii*, *P. andruzzii*, *B. devechii* and amblyopsids (Ercolini et al. 1987), but not for troglobitic *Astyanax* (Wilkens 1988). Lowered metabolic rates which have been interpreted as an adaptation to low and discontinuous food supply (Poulson 1963), may also aid life in non-cave aquifers. Subterranean populations of *Indoreonectes evezardi*, which lives in small pools with stagnant water during the dry seasons, exhibit air-gulping behavior; the epigeic relatives, that live in permanent hill streams, do not show such behavior (Biswas et al. 1990). *P. mexicana* is reported as exhibiting a remarkable tolerance to low oxygen concentrations, and also to high sulfide contents (Langecker et al. 1996).

Tolerance to depth is highly variable among troglobitic fishes, and some species may be found at great depths in lakes, flooded caves or non-cave aquifers. For instance, the amblyopsid *T. subterraneus* is apparently

adapted to shallow water and seems to be very sensitive to supersaturated conditions (Schubert et al. 1993); individuals observed in a deep lake in Sell's Cave were never seen at depths greater than 2 m (Cooper & Iles 1971). The Brazilian phreatobites, *P. cisternarum* and *S. typhlops*, have been obtained from wells drilled at 10–20 and 30 m, respectively (Carvalho⁵, Romero & McLeran 2000). *Lucifuga subterraneus* and *L. dentatus* are found up to 30 m deep in Cuban flooded caves (Juberthie⁶). The new heptapterine genus from NE Brazil inhabits a big lake in Poço Encantado Cave, with maximum depth around 60 m, but the blind catfishes were observed until 35 m, concentrating between the surface and 10 m (Mendes 1995b). Catfishes living in flooded caves from Mato Grosso do Sul, SW Brazil, were found in sectors as deep as 32 m (*Ancistrus formoso*, Sabino & Trajano 1997) and 46 m (*Trichomycterus* sp. 2 – E.P. Costa Jr. personal communication). However, by far the species known to live at the greatest depths are the ictalurids from Edwards aquifer: *S. eurystomus* was recorded from 610 m deep artesian wells (Longley & Karney 1979). These species have a reduced swimbladder which is replaced by large fat deposits as an adaptation to food scarcity and to help maintain neutral buoyancy, reduced muscles and weak ossification, apparently a pedomorphic trait in *S. eurystomus* and *T. pattersoni*; all probably adaptations to cope with high hydrostatic pressure (Langecker & Longley 1993).

Population sizes and densities

Population densities reported for several cavefish species in different caves are presented in Table 2. For populations studied by MR methods, these numbers were calculated by dividing the estimated population size by total area (from topographic maps) of the studied sections; therefore, these numbers correspond to mean population densities throughout the caves. In the case with VC, some values correspond to total counts in the accessible habitat divided by its area (*Taunayia* sp., *N. troglolactaractus*, amblyopsids), and therefore also represent mean densities, whereas others result from counts in selected small areas (*Astyanax* spp., *P. mexicana*, *S. oedipus*, the new heptapterine genus from NE Brazil) and are more subject to errors due to spatial variation in fish densities. Extreme values recorded by Willis & Brown (1985) were not included in the table, because they may represent very unusual situations (maximum of one individual in 1200 m² surveyed

Table 2. Approximate population densities (individual m⁻²) reported for subterranean fish species, based on mark-recapture studies (MR) or visual censuses (VC) in different caves; in parentheses, maximum densities are recorded.

Species	Country-Cave	Population density	Method	References
Heptapterinae	Brazil			
<i>Pimelodella kronei</i>	Areias	0.04	MR	Trajano (1991)
New genus	Poço Encantado	0.03	VC	Mendes (1995a)
<i>Taunayia</i> sp.	Toca do Gonçalo	0.01	VC	Trajano & Bockman (2000)
Trichomycteridae	Brazil			
<i>T. itacarambiensis</i>	Olhos d'Água	0.15	MR	Trajano (1997a)
		0.05	VC	Trajano (1997a)
Loricariidae	Brazil			
<i>A. cryptophthalmus</i>	Angélica	0.90	MR	Trajano (2001)
	Passa Três	0.50	MR	Trajano (2001)
		0.20	VC	Trajano & Souza (1994)
Characidae	Mexico			
<i>Astyanax</i> spp.	La Chica	(5)	VC	Parzefall (1983)
	Pachon	(5)	VC	Parzefall (1983)
	Micos	(15)	VC	Parzefall (1983)
Balitoridae	Thailand			
<i>Schistura oedipus</i>	Mae Lana	0.02	VC	J. Spies personal communication
		(0.25)	VC	Trajano, Borowsky, Mugue & Smart unpublished data
	Nong Pha Cham	(60)	VC	Trajano, Borowsky, Mugue & Smart unpublished data
<i>N. troglotataractus</i>	Wang Ba Dan	0.01	VC	Trajano, Borowsky, Mugue & Smart unpublished data
Amblyopsidae	U.S.A.			
<i>T. subterraneus</i>	Several caves	0.03	VC	Poulson ¹
<i>Amblyopsis spelaea</i>	Several caves	0.05	VC	Poulson ¹
<i>Amblyopsis rosae</i>	Several caves	0.15	VC	Poulson ¹
<i>A. rosae</i>	11 caves	0.005–0.15	VC	Willis & Brown (1985)
Poeciliidae	Mexico			
<i>Poecilia mexicana</i>	Azufre	(100–200)	VC	Parzefall (1993)

during five visits to Turnback Creek Cave; three individuals in a pool of 1 m² in Jail Cave).

Some of these species are also found in localities other than those included in Table 2. Whereas *Taunayia* sp., *T. itacarambiensis*, *N. troglotataractus* and *P. mexicana* occur only in the studied caves, *P. kronei* was found in six localities (possibly two groups; the Areias group comprises three other localities, Trajano 1997c, unpublished data), the new heptapterine genus in four (Mendes 1995a unpublished data), *S. oedipus* in five (three groups; the Mae Lana group comprises populations from two other caves, Borowsky & Mertz 2001), *Astyanax* spp. in 29 (at least the Micos population corresponds to a separate group comprising three of those 29 caves), and, among the amblyopsids, the three nominal species were recorded

in dozens of caves (Willis & Brown 1985), but these probably correspond to a higher number of phylogenetic species whose distribution was not clearly established yet. In the case of *Astyanax*, population densities greatly vary from cave to cave, but large populations seem to be more common (Mitchell et al. 1977).

Thus, distribution of many cavefishes encompass multiple caves that may be several kilometers distant from each other, presumably including intervening non-cave subterranean habitat. On the other hand, higher population densities are expected to occur in caves with greater food availability due to the larger contacts with the surface. In fact, the highest densities of *Lucifuga* spp. are observed in the twilight zone under cave entrances. Such higher density would be the result of a balance struck between the positive reaction

to food and the negative reaction to light in these bythitids (Eigenmann 1909). Therefore, the values shown in Table 2 are probably close to the highest densities of the studied populations throughout their distribution area.

Non-quantitative data on population densities, based on observations in the cave habitat and on the size of samples obtained, are available for other troglobitic fishes. Among cave species showing apparently low population densities, we can mention the bythitid *O. pearsei*, from cenotes in Yucatan, Mexico (Chumba-Segura 1983); the armored catfish, *Ancistrus galani*, from Venezuela (Perez & Vilorio 1994); the amblyopsid *S. poulsoni*, for which no more than 10 individuals have ever been observed on a single visit to Key Cave, with 3300 m of mapped passages (Romero 1998a).

On the other hand, the Bolivian trichomycterid, *T. chaberti*, is described as numerous (Durand 1968). Apparently, *Lucifuga subterraneus* and *L. dentatus* are also quite abundant. These species have been reported from several caves and may reach high population densities: as many as 10 individuals were observed by Eigenmann (1909) in a well about '6 feet in diameter and 10 feet deep'. According to Yang & Chen (1993a), the cyprinid *Sinocyclocheilus anophthalmus*, from a cave in Yunnan Province, China, has a large population, larger than that of the syntopic *Triplophysa ayunnanensis*.

A great deal of variation in population densities is observed among troglobitic fishes, without a taxonomic correlation. At first sight, such variation could be at least partly attributed to differences in study methods, because the lowest densities were generally recorded in VC. A comparison between the numbers of fish estimated by MR and those seen during visual inspection of the same habitat provide a measure of underestimation produced by VC. Even under the most favorable conditions for fish detection, like those observed at Passa Três Cave (small, shallow stream; non-cryptobiotic, exposed fishes), the population estimated by MR is larger than that seen by the above-water observers. Because, as already mentioned, in many cases it is not possible to carry out MR studies, it may be useful to establish an average proportion expressing the differences between estimated and observed populations which could be used as a correction factor for values obtained in VC. In view of the very limited number of studies using MR, this must be regarded as a first, very preliminary attempt to produce such indices.

The proportions between numbers of estimated and observed fish in different studies varied,

but most were around three estimated for each captured/observed individual. In *T. itacarambiensis* and *A. cryptophthalmus* from Passa Três Cave, such proportions were 3 and 2.5, respectively (Table 2). From Brown's (1996) data on *A. rosae* at Logan Cave, I calculated 2.2 estimated individuals for each captured fish; the mean population size estimated by this author was three times larger than the maximum number of fish seen by Willis & Brown (1985) in this cave. All these fishes are easy to capture in hand-nets (Means & Johnson 1995, Trajano personal observation), therefore the number of captures would closely approach that of observed fishes. About 25% of the *T. itacarambiensis* catfishes observed in the cave escaped our capture attempts, and this has been added to the total number of captures (Trajano 1997a) to produce the value from VC shown in Table 2. In *P. kronei*, the proportion of estimated to trapped fishes, varying from 2.5 to 7.6 among capture occasions (Trajano 1991), also gives an idea of the percentage of the population unseen by observers. Therefore, as a first approach, it seems reasonable to multiply by three the values obtained in VC in order to get numbers more comparable to those produced by MR studies.

Even applying a 'correction factor' of three, population densities still greatly differed among the studied cave fishes, which may be arbitrarily divided into three groups (some species not included in Table 2 were also classified on the basis of literature data on numbers of fishes collected/observed): (1) species with low population densities (<0.1 individuals m^{-2}), for example *N. troglodactylus*, *T. subterraneus*, *Speoplatyrhinus poulsoni*, *Trichomycterus* sp. from El Guácharo Cave, *Taunayia* sp., possibly *P. kronei*, the new heptapterine genus; (2) species with median population densities (0.1–1.0 individuals m^{-2}), *S. oedipus*, *A. spelaea*, *A. rosae*, *T. itacarambiensis*, *A. cryptophthalmus*, and (3) species with high population densities (>1.0 individuals m^{-2}), *Astyanax* spp., *P. mexicana*, *C. geertsi* in some caves. If biomass was used as another correction factor, then *P. kronei* should be ranked with species showing higher population densities.

In the few cases in which comparative data are available, population densities estimated for epigeal close relatives are, as expected in view of the higher food availability in this habitat, higher than that observed for troglobitic species, but not by a huge margin. Population densities of eyed *Ancistrus* sp. in epigeal reaches of streams crossing caves where *A. cryptophthalmus* is found are 50% greater than

Table 3. Population sizes (number of individuals) estimated for some cave fishes using mark-recapture methods. The extension of stream occupied by these population is given in parenthesis.

Species	Cave (extension)	Population size	References
<i>Pimelodella kronei</i>	Areias (5000 m)	900–1200	Trajano (1991)
<i>Trichomycterus itacarambiensis</i>	Olhos d'Água (5000 m)	1500–2000	Trajano (1997a)
<i>Ancistrus cryptophthalmus</i>	Angélica (8000 m)	>20 000	Trajano (2001)
	Passa Três (2000 m)	1000	Trajano (2001)
<i>Astyanax</i> spp.	El Pachón	8500*	Mitchell et al. (1977)
	Yerbaniz	8700**	Mitchell et al. (1977)

*95 percent confidence limits of 1280 to 18280.

**95 percent confidence limits of 1810 to 15530.

those of this troglóbite (Trajano 2001). Densities of 0.043–0.097 individuals m^{-2} were recorded in epigean streams for *P. transitoria* (Gerhard 1999), putative sister-species to *P. kronei* (population density in Areias Cave = 0.04 individuals m^{-2} , Table 2). Also as expected, *P. transitoria* present lower population densities inside caves, about ten times lower than that of *P. kronei* in Areias Cave, where these species are syntopic (Trajano 1991). Another troglóphile, the amblyopsid *Chologaster agassizi*, also presents cave population densities which are lower than the observed densities for this species in the epigean habitat, and lower than the densities shown by its troglóbite relatives (Poulson¹). Maximum densities of epigean *Astyanax mexicanus* recorded by Parzefall (1983, table 1) greatly varied among streams: some were comparable to the highest values reported for cave populations (15 individuals m^{-2} , as in Micos cave), others were much higher (up to 200 individuals m^{-2}); however, the numbers recorded in test areas both in epigean and cave habitats did not greatly diverge (Parzefall 1983, figures 1–2). Epigean *A. mexicanus* co-occur with troglóbite populations in some caves, where they are usually less abundant than eyeless tetras and frequently show signs of starvation (La Cueva Chica, characterized by a high input of energy represented by bat guano, is an exception); even so, extensive hybridization may occur (Mitchell et al. 1977).

Estimates of population sizes based on capture-mark-recapture are in Table 3. These estimates do not include individuals that were too young, too rarely found, and/or too small for marking. Thus, the values correspond to the average adult stock found in each studied cave (i.e. the accessible habitat). In the case of the stream-dweller *T. itacarambiensis*, the study encompassed almost all the cave habitat known for these fishes, and the values obtained probably closely approach the total population sizes. For

P. kronei and *A. cryptophthalmus*, estimates from MR in sectors of the studied caves have been extended to the whole cave populations, assuming constant population densities. Because these populations are probably continuous with those inhabiting other caves nearby (Bombas, Córrego Seco and Águas Quentes, for *P. kronei*, Trajano 1997c, unpublished data; Bezerra for *A. cryptophthalmus*, Trajano 2001), the total populations in the respective cave systems may be a few times larger than that.

The rare studies based on MR of *Astyanax* (Table 3) well illustrate how underestimated population size values may be when based on VC, and the consequences of such errors. Avise & Selander (1972), based on inspection of part of the available fish habitat, estimated the populations from La Cueva Chica, El Pachón and Los Sabinos caves as 200–500 individuals each, founding their evolutionary discussion on these numbers. However, in El Pachón and probably in the other caves as well, the total numbers of fish are many times higher, and may invalidate at least part of Avise & Selander's (op. cit.) conclusions. Even considering the value at the lower limit of confidence (1280 individuals, Mitchell et al. 1977), the population estimated by MR in El Pachon cave is 3–6 times larger than that visually estimated. Likewise, the hybrid population from La Cueva Chica is probably thousands of individuals, in view of the high number of fish captured since the 30s (samples with up to 100 specimens, Romero 1983), apparently without affecting significantly the population.

Cryptobiotic fishes, such as several *Trichomycterus* species, are especially prone to underestimation in VC. From a VC by Romero (1987), a low population density of 0.01 individuals m^{-2} was calculated for the troglomorphic population of *Trichomycterus* (then referred as *T. conradi*) in Cueva del Guácharo (Venezuela), corroborated by the small samples usually

obtained in the cave (Nalbant & Linares 1987, Andreani-Armas 1990). However, as noted by Romero (1987), some individuals tend to bury into the substrate, thus the number present in the cave was certainly higher.

The new species of *Trichomycterus* (treated as *Trichomycterus* sp. 1 in Trajano 1997d) syntopic with *A. cryptophthalmus* in Passa Três Cave illustrates the inadequacy of VC for cryptobiotic cave fishes. In a one-day collection based on visual inspection of the habitat, 15 specimens of *Trichomycterus* and 70 of *A. cryptophthalmus* were captured (Trajano & Souza 1994), suggesting a population density of the former was 4.5 times lower than the latter species. After careful collections, searching also under hiding places for a MR study in progress, M.E. Bichuette raised the proportion of captured specimens of *Trichomycterus* to 30 compared to 100 captured *A. cryptophthalmus*. However, none of 27 marked specimens of *Trichomycterus* sp. 1 were recaptured, whereas recapture rates of *A. cryptophthalmus*, marked using the same method, reached 44% in this cave. Mortality due to marking procedures is highly unlikely because *Trichomycterus* catfishes marked in the laboratory lived normally (Trajano personal observation) and tattooing with biocompatible pigments has been proven to be quite safe for fishes in general (Hill & Grossman 1987, Trajano 1997a). Therefore, absence of recaptures in *Trichomycterus* sp. from Passa Três indicates a population size higher than previously thought (perhaps even higher than that of *A. cryptophthalmus*) and/or frequent movements between the cave and inaccessible spaces contiguous to it.

Likewise, according to Brown (1996), specimens of *A. rosae* may go undetected for long periods, hidden under rocks and in crevices, that may contribute to negative bias in population estimates. *T. subterraneus* has the ability to burrow in interstitial spaces and disappear into the substrate, entering and exiting gravel interstices periodically (Schubert et al. 1993).

Thus, it is advisable to observe the fish behavior before carrying out population studies based on VC. Fortunately, most studied subterranean fishes are not cryptobiotic, even those belonging to typically cryptobiotic epigeal taxa, just like other Brazilian *Trichomycterus* species (*T. itacarambiensis*, *Trichomycterus* sp. 2, from SW Brazil) and the heptapterines *P. kronei*, *Taunayia* sp. and new genus from NE Brazil (Trajano & Bockmann 1999).

Poulson (1963) estimated population sizes for amblyopsids in several caves, based on VC: *T. subterraneus*, around 40 individuals per cave (maximum

150 individuals); *A. spelaea* – 105 per cave (max. 175); *A. rosae*, about 75 per cave (max. 100). According to Willis & Brown (1985), population sizes of about 150 individuals are probably normal for the Ozark cave-fish, *A. rosae*. However, these authors observed much lower numbers in 14 caves visited, finding between one and 12 individuals in 13 of these caves, and 100 in Cave Springs (where Poulson found a similar number). They attribute this to population losses caused by habitat destruction and collection. Mean population size of *A. rosae*, estimated by MR in Logan Cave between 1992 and 1995, was 34 individuals (considered an underestimate, Brown 1996), about three times the maximum number recorded in VC by Willis & Brown (1985).

Monthly fluctuations in the estimated size of the Logan Cave population were interpreted by Brown (1996) as reflecting frequent movements between the accessible habitat and the non-cave aquifer (see below). According to Brown, individuals in the cave are probably members of a large population living in the aquifer. The constant inflow of fish into the cave and the small, fluctuating number of observed fish indicate that the Logan ‘population’ is not self-sustaining. This may also be the case with other caves inhabited by *A. rosae*, explaining, along with their cryptobiotic habits, the low numbers of fish usually seen. As also pointed out by Poulson (1963), the Ozark cavefish exhibits a clear preference for still water: in Logan Cave, *A. rosae* is not found in sections with fast flowing water over bedrock substrate, and, in Cave Spring Cave, the majority of cavefishes are found in a single still, shallow pool. This, along with its occurrence in widely distributed caves, corroborates the notion that the main habitat for the species is the non-cave aquifer. Therefore, the actual total population size is far from being assessed, but may be much larger than currently thought. Such may also be the case of *T. subterraneus* and *A. spelaea*. However, it must be recalled that *T. subterraneus* and *A. rosae* are probably artificial taxa, thus a more realistic picture on population sizes depends on studies delimiting the natural taxa inside these nominal species.

It is noteworthy that epigeal populations of *Chologaster agassizi* estimated by MR in southern Illinois were generally small (18 to 302 individuals per stream). In fact, this species is referred as rare to uncommon throughout most of its range, except for a large spring in Kentucky where it is exceptionally abundant (Smith & Welch 1978).

Parzefall (1993) refers to densities of 100–200 individuals m⁻² for the troglobitic population of

P. mexicana in its only locality, Cueva del Azufre (also known as de las Sardinias or de Villa Luz), a remarkable cave due to the exceptional food availability represented by chemoautotrophic sulfur-bacteria. Such values probably correspond to localized, maximum densities. Short-term MR experiments in some sectors of this cave resulted in values around 1700 individuals in chamber X (~10–15% of the cave stream area) and 100–140 individuals in chamber XIII (see cave maps in Langecker et al. 1996, [Hose & Pisarowicz 1999](#)); a population of approximately 9000 individuals was estimated for the epigeal reach of the spring downstream of the cave (J. Parzefall unpublished data). Assuming constant population densities throughout the cave, total population size of troglobitic *P. mexicana* would be around 15 000 individuals. However, such estimates were made before the annual traditional religious ceremony, at the end of the dry season, when native people collect and eat large quantities of fish (see [Hose & Pisarowicz 1999](#)), greatly depleting the population. This population constitutes an example of extraordinary recovering ability, probably unparalleled among troglobitic fishes.

Heuts (1952) provided estimates of population sizes based on VC of *C. geertsii* studied in seven caves from a small karst area in the Congo. He refers to a population roughly estimated at one thousand individuals in one locality, four thousands in a second one, and several thousands in a third locality. If all these populations are connected, representing a single species, then the total population size for *C. geertsii* is quite large, around tens of thousands of individuals.

Stream-adapted troglobitic species, which tend to be more restricted to fast-flowing waters in cave systems, offer more reliable population data. On the other hand, populations widely occupying the phreatic habitat are particularly difficult to estimate, even when there are estimates of population densities in accessible parts of this habitat (such as for *Taunayia* sp. and the new heptapterine genus, Table 2). The main problem is determining the total distribution area, especially when natural accesses (such as wells, small caves or springs) are rare or nonexistent. It is necessary to assume that population densities throughout wide subterranean areas are similar to those observed at the limited contacts with the surface. Therefore, only rough, highly tentative estimates may be made.

A low population size is referred to for the ictalurid *Prietella phreatophila* by Krejca et al. (2000), who estimated that less than 100 fish live in the accessible parts of Sótano de Amecua, Mexico, where a MR study is

in progress. These authors point to the vulnerability of such a small population to environmental disturbances, which could quickly eliminate this localized population. However, considering that this phreatobitic species is distributed throughout a large area, from the type-locality to 160 km to the north (Hendrickson & Krejca personal communication), the total population may be considerably large.

Indirect estimates of population sizes are available for the phreatobitic North American ictalurids, *Satan eurystomus* and *Trogloglanis pattersoni*, collected in waters pumped from several wells in the San Antonio pool area (103 600 hectares) of the Edwards aquifer. Based on the flow rates in a few artesian wells from a single pump station, Longley & Karney (1979) estimated a loss of about 460 specimens of *T. pattersoni* and 230 *S. eurystomus* from the subterranean population during one year (1977–1978); from pumped flow records for the period 1950 to 1977, a total loss of 3250 *T. pattersoni* and 1650 *S. eurystomus* was estimated. These numbers provide a crude estimate of total population sizes of tens of thousands for both species. Population density in the predatory *S. eurystomus* is, as expected, lower than (approximately half) that of the detritivorous *T. pattersoni*. These data reveal how questionable it is to make inferences on the relative abundance of phreatobites based on small collected samples: before that extensive program of collection in artesian wells and pumping stations with nets attached to the outlets, only six individuals of *T. pattersoni* and three *S. eurystomus* were captured (Langecker & Longley 1993), leading to the faulty conclusion that these species are very rare.

The phreatobitic cyprinid *Barbopsis devechii* also seems to present large populations. As a result of an extensive collecting program in Somalia during the 60s and 70s, more than 500 specimens were obtained. Lower, but still impressive numbers of cyprinids, *Phreatichthys andruzzii* (140 specimens) and clariids, *Uegitglanis zammaranoi* (82 specimens), were captured on those occasions (Ercolini et al. 1982). The latter is probably much more abundant than indicated by this number: Thinès (1958) opened an artificial canal fed by a subterranean stream and found about 150 individuals along 30 m of canal (section 1.5 × 1.0 m; 0.4 m water column). Such exceptionally high population density is explained by the occurrence of a large amount of plant debris as a food source inside the canal.

From the above, it may be concluded that population sizes estimated for troglobitic fishes vary greatly, from hundreds to tens of thousands of individuals, without

a phylogenetic correlation. Based on such estimates, and also on population densities or number of fish collected/seen allied to fish distributions, I tentatively classified several troglobitic species into categories of total population sizes according to three orders of magnitude: (1) Very small populations (10^2 individuals): low population densities and restricted distributions: *C. thamicola*, *Taunayia* sp., *S. poulsoni*, and possibly *N. troglotactaractus*. (2) Small populations (10^3 individuals): low densities and median distributions, or median to high densities and limited distributions: *P. kronei*, *T. itacarambiensis*, *A. cryptophthalmus* in Passa Três Cave, and, possibly, *A. rosae*. (3) Medium-sized to large populations (10^4 individuals): low densities and wide distributions, or median to high densities and limited to large distributions: *Astyanax* sensu lato, *C. geertsii*, *S. oedipus* sensu lato, *A. cryptophthalmus* in Angélica Cave, *S. eurystomus*, *T. pattersoni*, *T. subterraneus*, *P. mexicana*. The latter are within the lower range observed for many epigeic freshwater populations (Trajano 1997b), except for very restricted species living in specialized habitats, such as temporary epigeic pools.

It is interesting to note that species showing very small populations are among the most specialized troglobitic fishes, homogeneously anophthalmic and depigmented (except for pigmentation in *A. cryptophthalmus*), indicating speciation in peripheral isolates. The comparison between the populations of *A. cryptophthalmus* from Passa Três and from Angélica caves is particularly illustrative of a relationship between population size and degree of troglomorphism: the small population apparently isolated in Passa Três shows much more reduced eyes and cryptobiotic habits than that from the Angélica-Bezerra Cave system (Trajano 2001).

Fish movements and home ranges

In view of the contrasting ecological conditions under which epigeic and subterranean populations live, differences are expected in the use of space, including the frequency and extensiveness of movements, home ranges, etc. For instance, food scarcity could determine an increase in movement rates or intensification of territorial behavior. Comparisons between epigeic and subterranean related species, or between subterranean populations living under different conditions as a result of distinct regional climates (e.g., highly seasonal versus non-seasonal climates) may contribute

to answering this question. Unfortunately, very few of such studies have been so far carried out.

The first evidence of movement in subterranean organisms is a temporal variation in the number of individuals observed at given sectors of the habitat (this is particularly evident for soil organisms). Eigenmann (1909) reported a decreasing number of *Lucifuga subterraneus* and *L. dentatus* individuals in the accessible parts of some Cuban caves following successive collections in a period of few months. Therefore, population loss was not compensated for by immigration from inaccessible underground spaces, indicating a low rate of movement within a relatively short period of three months.

Even in the absence of variations in population density, occurrence of movement cannot be ruled out because immigration and emigration rates may be similar, thus fish numbers will not change with time. The most reliable method to study fish movements is MR, which allows detecting and quantifying the movements of individual fish.

Detailed data on cavefish movements is available for Brazilian catfishes living in cave streams: *P. kronei* in Areias Cave (Trajano 1991), *T. itacarambiensis* in Olhos d'Água Cave (Trajano 1997b), *A. cryptophthalmus* in Angélica and Passa Três caves (Trajano 2001); and *A. rosae* from stream-like habitat in Logan Cave (Means & Johnson 1995, Brown 1996). In such studies, the investigated sectors were divided into subsections, inside which the fishes were grouped. The extension of such subsections depended on the total extent of habitat sampled, the number of fish to be marked in each occasion, and the collecting method. These factors determined the maximum number and extension of subsections viable for fieldwork: 5 m for *Amblyopsis rosae* (cave 1300 m long, low population density), 20 m for *Ancistrus cryptophthalmus* at Passa Três (cave 400 m long, high population density), 100 m for *T. itacarambiensis* (cave 5000 m long, medium population density) and *A. cryptophthalmus* at Angélica (cave 8000 m, but only 500 m studied due to the high population density), 200 m for *P. kronei* (cave system 5000 m, but only 800 m studied due to the use of large traps which were difficult to carry into the cave). Therefore, the spatial scales of discrimination of fish movements varied among these studies.

High recapture rates, indicating small population sizes and/or low movement rates, have been obtained in cave stream habitats: total recapture rate of *P. kronei* was 47.7%, varying between 15 and 100% among recapture occasions; total recapture rate of

T. itacarambiensis was 25.7%, with an increase from 13% in the first recapture occasion to 29% in the last one (Trajano 1997a); recapture rates of *A. cryptophthalmus* were 44% at Passa Três Cave and 15% at Angélica Cave (Trajano 2001); in *A. rosae*, recapture rates varied between 25 and 88% among recapture occasions (Means & Johnson 1995). Lower rates were generally obtained for stream-dwelling epigeal species: total rates of 17–20% were recorded for *P. transitoria* in the epigeal habitat (similar rates were also observed for cave populations of this species, Gerhard 1999); rates varying between 3 and 33% in samples with minimum 20 marked fishes were recorded by Hill & Grossman (1987) for three North American species.

Knapp & Fong (1999) obtained similar rates (mean 36%, ranging from 19 to 50%) for troglotic amphipods *Stygobrommus emarginatus* at stream sites. On the other hand, recapture rates were extremely low (3.0%) at mud-bottomed pool sites, situated in the upper reaches of the stream and fed by seeps and by water from the mainstream during high water. These authors interpreted this low value as an evidence of movements between the epikarst and the studied pools, which would represent small windows into the epikarst inhabited by a much larger population of amphipods. M.E. Bichuette (personal communication) also obtained very low recapture rates (4.4%) for *Trichomycterus* species living at similar habitats in caves from São Domingos karst area in central Brazil, probably representing a similar case among cave fishes. Likewise, none of 17 specimens of *S. oedipus* marked in an upper vadose soft-bottomed, slow-moving water tributary in Mae Lana Cave was recaptured a few days later (Trajano, Borowsky, Mogue & Smart unpublished data).

Results obtained for the three studied Brazilian cave stream-dwelling siluriforms indicate a high degree of sedentariness, with small variations between species. The armored catfish, *A. cryptophthalmus*, as expected for a loricariid, is usually observed attached to rocky substrates scraping off the film of detritus covering the substrate. It seems to be very sedentary: within a period of one month, no fish was recaptured at Angélica more than 100 m from its initial capture, and, in Passa Três Cave, maximum movements 20–40 m along the stream were recorded (Trajano 2001).

Trichomycterus itacarambiensis, studied during the dry season, was less sedentary: 34% of recaptures were made in a section other than that of previous capture, corresponding to movements at distances greater than 100 m in periods of one to five months. Active,

non-seasonal movements (both upstream and downstream) were recorded at maximum distances of 600 m; a few longer movements, up to 1500 m along the stream, were considered to be passive since they were always downstream movements. Passive movements are probably more frequent during the rainy season. Contrary to what was expected, *P. kronei*, a larger, potentially more mobile species studied during a one-year period, showed a higher degree of sedentariness, moving less frequently and for smaller distances: 20% of recaptures were made at a site different from the previous one, and only 2% of total recaptures were at distances greater than 300 m (Trajano 1997a).

Such differences may reflect variation in feeding styles associated with differences in the degree of food scarcity and species behavior, illustrating ecological and phylogenetic constraints determining patterns of cavefish movements. Armored catfishes, typically grazers and most territorial, are in general relatively sedentary, at least in short time-scales. *P. transitoria*, putative sister-species to *P. kronei*, is also highly sedentary: 93% of recaptures by Gerhard (1999) were made within the same 50 m long stream sections. *P. kronei* is a solitary, aggressive, possibly territorial fish, tending to stay in the same site for a long time. Because it has reduced cryptobiotic habits (Trajano & Bockmann 2000), defense of territory is probably centered on food resources (as also observed for *A. cryptophthalmus*, Trajano & Souza 1994), and not on hiding places as in *P. transitoria* and many other cryptobiotic fishes. Due to the absence of a well-defined dry season in the area, food availability for this cavefish is constant and apparently not greatly limiting, judging from the high percentage of specimens with stomach contents (Trajano 1989). This would justify the defense of relatively small feeding territories.

On the other hand, the degree of aggressiveness is lower and more variable in the few studied *Trichomycterus* catfishes, including the Brazilian cave species. Territoriality in these fishes seems to be restricted to particular situations, when individuals kept isolated are confronted with intruders. Besides, food scarcity in *T. itacarambiensis* habitat is, at least during part of the year, more accentuated than for *P. kronei*. Probably, the best style for *T. itacarambiensis*, representing the most economically favorable energetic balance between food demand and availability, is to have a relatively large home range, moving more frequently and for longer distances, at least during the dry season, in order to enhance the chances of finding food (Trajano 1997a).

Fluctuations in the estimated population size of *A. rosae*, associated with high recruitment rates at some occasions, with a peak during summer, were interpreted as an evidence of high rate of immigration from the aquifer into Logan Cave (Brown 1996). Inside the cave, the great majority of fish were captured in a 220 m long pool, and few movements of marked individuals upstream or downstream of this section were recorded. On the other hand, most fish moved throughout the pool, and a few individuals tended to remain within the lower 100 m of pool; as expected, larger fish tended to move longer distances and more frequently than small ones. In view of its relatively small size (max. TL = 63 mm), *A. rosae* has relatively large home ranges at Logan Cave when compared to the studied Brazilian cave catfishes. Periodic movements between the accessible habitat and the surrounding aquifer (including gravel interstices) was reported by Schubert et al. (1993) for *T. subterraneus* found in a boxed spring from Missouri.

Feeding

In view of the food scarcity generally prevalent in the hypogean environment, it is expected troglobitic fishes to be generalist feeders. As a matter of fact, hypogean fish species studied with a focus on this aspect are omnivores (e.g., *Astyanax* spp.) or, more frequently, generalist carnivores feeding on an opportunistic basis (amblyopsids, bythitids, siluriforms, etc.). Usual food items for cave fishes include crustaceans from copepods to crayfish, aquatic insects (juveniles and adults), mollusks (mainly gastropods), worms (annelids, nematodes), besides several allochthonous items (arachnids, terrestrial insects, etc.). For instance, *T. subterraneus*, *A. rosae* and small *A. spelaea* feed mainly on copepods, complemented by other crustaceans (cladocerans, isopods, amphipods, crayfish) and insect larvae; cannibalism on young fishes was recorded for *Amblyopsis* spp. (Poulson 1963). *Lucifuga subterraneus* and *L. dentatus* feed largely on crustaceans, including troglobitic shrimps, *Troglocubanus* sp. and *Typhlatya* (Eigenmann 1909, Nalbant 1981). Miller (1984) attributes the rarity of shrimps and mysids in pools inhabited by *R. reddelli* to predation by this catfish. Stream-dwelling trichomycterines such as *Trichomycterus conradi* from Cueva del Guácharo and *T. itacarambiensis*, and the heptapterine *P. kronei*, feed largely on insects, complemented by crustaceans and oligochaetes (Andreani-Armas 1990,

Trajano 1989, Trajano 1997b). *P. mexicana*, which lives in an unusual chemoautotrophically based ecosystem, have an unusual diet, mainly composed of *Beggiatoa* bacteria and subsidiarily of insects (e.g., chironomid larvae) and other invertebrates (Langecker et al. 1996). Some cave species seem to prefer living prey (amblyopsids, *Taunayia* sp.), while others may also scavenge, feeding on both living and dead organisms (most catfishes such as *P. kronei*, *T. itacarambiensis*, etc.). The former have well-developed lateral line systems and probably use mechanical stimuli in the search for food, particularly moving prey.

There are records of cavefish using submerged bat guano as a food source (e.g., *Astyanax*, Parzefall 1993), but in many cases it is not clear whether these fishes are feeding directly on the guano or on the invertebrates living on it. For instance, based on field observations and examination of gut contents by transparency, Mendes (1995b) first concluded that the new heptapterine from NE Brazil fed on bat guano; however, the analysis of stomach contents revealed that this species is strictly carnivorous, preying on invertebrates found near or on the guano. Few troglobitic fishes are truly detritivorous, such as the ictalurid *T. pattersoni* (Langecker & Longley 1993) and the loricariid *A. cryptophthalmus*; the latter probably feeds on the thin film of detritus covering rocks inside caves (Trajano 2001).

The effect of food scarcity is made clear in the high proportion of specimens captured with no or few stomach contents observed in subterranean species like *Caecocypris basimi* (Banister & Bunni 1980), and *T. itacarambiensis* collected during dry season (Trajano 1997b). This, allied to the generally small size of samples, may hamper the investigation of individual, spatial and temporal variations in feeding habits. Small samples also render difficult a detailed analysis of diet allowing to detect more subtle, but nevertheless important, differences between species, especially relevant for syntopic troglobitic fishes (see below). Therefore, feeding is one of the least known aspects of cavefish biology, with a few exceptions.

In spite of the low frequency of *T. itacarambiensis* individuals with stomach contents, the large population size made it possible to get sufficient data for analysis. These data showed a decrease in the frequency of insects and an increase of oligochaetes as food items throughout the pronounced dry period, probably reflecting a decrease in insect availability as the season advanced (Trajano 1997b). Comparison with *P. kronei* illustrates the consequences of living under different climatic regimens: the contribution of allochthonous,

epigean items to the diet was significantly higher for the latter, which is found in a less seasonal area without a typical dry season, in a larger cave stream with higher and relatively constant carrying capacity (Trajano 1997b).

In the few cases where direct comparisons were made (e.g., Poulson 1963, Trajano 1989), it was shown that troglobitic fishes belong to the same trophic guilds as their epigean relatives. This indicates that, concerning general diet, epigean ancestors were already preadapted to feed in the subterranean habitat. Differences in the proportion of items consumed by hypogean and epigean populations were tentatively attributed to differences in prey availability rather than food preferences (Andreani-Armas 1990, Trajano 1997b), although no quantitative analysis of such availability in the habitat was actually made. On the other hand, different foraging styles were observed for the troglobites, as an adaptation to the special conditions in the hypogean environment. For instance, troglobitic heptapterines also feed at midwater, adding surface picking to the behavior usually employed by the typically bottom-dwelling epigean relatives (Trajano 1989, Trajano & Bockmann 1999). Conversely, a stereotyped polarization to the bottom was described for troglobitic *Astyanax* spp. and *Caecobarbus geertsii* (Thinès & Wissocq 1972, Parzefall 1993). Amblyopsids illustrate a higher feeding efficiency in troglobitic species associated with behavioral specializations (Poulson 1963). The number of specimens with stomach contents in *P. kronei* were greater than in its eyed sister-species, *Pimelodella transitoria*, providing another example of high feeding efficiency in cave fishes (Trajano 1989).

Besides sensorial and behavioral specializations increasing feeding efficiency in troglobitic fishes, adaptation to the food scarcity generally prevalent in the hypogean habitat include the low metabolic rates recorded for some species and fat storage helping to survive long starvation periods. Large deposits of adipose tissue in different body parts were observed in many wild caught troglobitic fishes. Ridges of fat tissue along the base of adipose and anal fins are present in the troglobitic heptapterines, *Rhamdia reddelli*, *R. zongolicensis* and *R. macuspanensis* (Weber 1996, Weber & Wilkens 1998), and *P. kronei* (Trajano personal observation), but not in their epigean relatives, respectively *R. laticauda* and *P. transitoria*. The ictalurids *Prietella lundbergi*, *T. pattersoni* and *S. eurystomus* have large lipid deposits in subcutaneous areas and viscera, associated with mesenteries, and in the place of

the reduced gasbladder (Langecker & Longley 1993, Walsh & Gilbert 1995); however, some individuals of *T. pattersoni* and *S. eurystomus* showed signs of starvation. Experiments with troglobitic *Astyanax* from Pachon Cave have shown that these fishes exhibit an improved ability to store fat and build up enormous reserves (Wilkens 1988).

Less specialized species, such as *T. itacarambiensis*, show these adaptations in lower degree or not at all, and may be heavily stressed during long periods of pronounced food scarcity: during the dry season, these fishes exhibit significant loss of weight, stop growing, and many individuals present negative growth – they actually shrink (Trajano 1997a).

Life cycle parameters: reproduction, growth rate and longevity

It is usually stated that many troglobites show a precocial lifestyle (sensu Balon 1981, 1999), including life history traits such as large and yolky eggs, low fecundity, delayed and infrequent reproduction, slow growth rates, and increased longevity, as adaptations to the food-poor subterranean habitat (Culver 1982). However, in the case with subterranean fishes, little has been done after the classical study on amblyopsids by Poulson (1963), and no other author encompassed all features, from reproduction to longevity, in such a comprehensive way. This author compared one epigean species, one troglophilic species, and the three troglobitic species known at that time, based on large preserved samples, and demonstrated that the latter present a more precocial lifestyle (similarly analogous to K-selected life cycle) when compared to their eyed relatives. This study became a paradigm for life cycle adaptation in subterranean organisms.

Other authors obtained data on reproduction of additional troglobitic fishes, including frequency and periodicity of reproduction and number and size of eggs. A few species have been studied with a focus on growth rates: *C. geersti*, *P. kronei*, *T. itacarambiensis*, *A. cryptophthalmus*, and *A. rosae*. The preliminary data available also point to precocial lifestyles in these populations, with low proportions of reproductive females producing relatively large eggs, slow individual growth rates and high longevity. These data indicate that precocial development may be indeed a common feature of troglobitic fishes. However, they are not necessarily autapomorphic character states representing specializations to the subterranean habitat. A precocial

lifestyle may be a characteristic already present in epigeal species and favoring the colonization of the hypogean environment, as seems to be the case with the Brazilian catfishes, *Pimelodella transitoria* and *P. kronei* (see below).

The study of reproduction in troglobitic fishes poses several problems. As already mentioned, many subterranean habitats are not accessible during the rainy periods, thus it is not possible to follow the whole annual cycle. Moreover, low population densities and infrequent reproduction result in small samples with very low numbers of mature individuals. Therefore, in contrast to epigeal fishes, for which reproduction is one of the most intensively studied aspects of their biology, reproductive data for troglobitic fishes are limited.

Seasonal reproduction, with well-defined annual cycles, was reported for several species and seems to be more frequent than non-seasonal breeding in cavefishes. *A. spelaea*, and possibly *A. rosae* as well, breed during high water from February through April (Poulson 1963). *Ogilbia pearsei*, from Yucatan, which is viviparous like all other bythitids, display a reproductive period from December to February (Ilfie 1993). The Cuban bythitids, *L. dentatus* and *L. subterraneus*, seem to breed throughout the year, but a reproductive peak may occur in March; reproduction is also infrequent in these species (Eigenmann 1909). Epigeal and troglobitic *Astyanax* show spawning peaks which differ among populations in the laboratory and this data are reinforced by sparse observation in the field: March for the epigeal species, April for the La Cueva Chica population, May for the Sabinos population and August for the Pachón population (Sadoglu 1979). *U. zammaranoi* presumably reproduces during the dry, hot season from January to March (Ercolini et al. 1982).

A small proportion (18%) of specimens of the new heptapterine taxon from NE Brazil had developed gonads (infrequent reproduction), and all mature females were found at the end of the rainy season in March (Mendes 1995b). In *T. itacarambiensis*, studied during the dry season, the highest proportion of mature females (18%) was also observed at the end of the rainy season (March), dropping to less than 3% in the subsequent months; this points to seasonal reproduction with a peak during or just at the end of the rainy period (Trajano 1997b). Both *T. itacarambiensis* and the new heptapterine genus live under seasonal climates, subject to pronounced dry periods. The low proportion of ripe fish, which is expected in view of the food scarcity prevailing in the subterranean habitat, indicates that

not all individuals reproduce every year, as observed by Poulson (1963) for troglobitic amblyopsids (see below).

Non-seasonal reproduction was suggested for the syntopic *Typhlogarra widdowsoni* and *Caecocypris basimi* (Bannister & Bunni 1980). A very low number of *P. kronei* catfishes with mature gonads was found (Trajano 1991), hampering any conclusion about reproductive patterns.

Fewer and larger eggs were observed for the troglobitic amblyopsids, *Typhlichthys subterraneus* (~50 mature ova, size 2.0–2.3 mm, per female), *Amblyopsis spelaea* (~70 ova, 2.0–2.3 mm) and *A. rosae* (23 ova, 1.9–2.2 mm), than in the troglomorphic *Chologaster agassizi* (~150 ova, 1.5–2.0 mm) and in the epigeal *C. cornuta* (93 ova, 0.9–1.2 mm). On average, these species first reproduce at ages of 24, 40, 37, 12 and 12 months, respectively, and the estimated proportion of females breeding every year is 50, 10, 20, 100 and 100% respectively, resulting in infrequent reproduction by a small proportion of troglobitic females. Therefore, the effective stock, which is the part of the population genetically contributing to the next generation, determining the rates of genetic drift (Futuyma 1986), is much smaller than the total populations estimated by MR or VC (see above).

Eggs with an increased amount of yolk, producing larger embryos, were reported for several troglobitic populations of *Astyanax* (Wilkins 1988). Large eggs have been observed for *A. cryptophthalmus* (L. Finley personal communication). Production of a small number of eggs (23–28 oocytes ready for spawning), which may be retained for long periods (up to six months), was described for *Horaglanis krishnai* (Mercy et al. 1982). Such retention ability indicates that favorable conditions for spawning occur only during limited periods.

Low individual growth rates and high longevity are other related life cycle traits of troglobitic amblyopsids. Based on examination of marks on scales regarded as annual growth annuli, Poulson (1963) estimated maximum ages of 4.2 years for *T. subterraneus* (maximum size = 62 mm SL), 7.0 years for *A. spelaea* (max. size = 85 mm) and 4.8 years for *A. rosae* (max. size = 52 mm), in contrast to 2.3 years for *C. agassizi* (max. size = 61 mm) and 1.3 years for *C. cornuta* (max. size = 57 mm). Growth rates calculated based on the greatest lifespans and sizes recorded (Poulson 1963; table 5) and on growth curves (Poulson 1963; figures 1 and 2) were around 1.0–1.25 mm month⁻¹ for *T. subterraneus*, 1.0 mm month⁻¹ for *A. spelaea*, and

0.9 mm month⁻¹ for *A. rosae*; such values are lower than those calculated for *C. agassizi* (1.7 mm month⁻¹ calculated from growth curves, 2.2 mm month⁻¹ as calculated from max. lifespan) and much lower than the calculated growth rate for *C. cornuta* (2.4 and 3.8 mm month⁻¹, respectively). Differences in life history result in distributions of age frequencies skewed towards older age classes in *A. rosae* and *A. spelaea*. Differences in growth rates and allometry would also account for differences in morphology (e.g., size of head, cerebellum and inner ear, fin length) between these species.

Mean growth rates estimated for *A. rosae* studied by MR in Logan Cave (Brown 1996) corresponded to values lower than those recorded by Poulson (1963) for this species: for size class 30–39 mm TL, mean growth rate = 0.7 mm month⁻¹; size class 40–49 mm TL, 0.3 mm month⁻¹; size class 50+ mm TL, 0.06 mm month⁻¹. Thus, it would take 3.9 years for a 30 mm fish to attain 50 mm. However, some individuals exhibited much higher growth rates, of 1 mm month⁻¹ or more (that may be the case of the largest individuals examined by Poulson 1963). Growth spurts were not necessarily correlated with the increase of food availability represented by bat guano during the summer. Therefore, growth could be controlled by other factors, such as age, sex and reproductive condition, in addition to exogenous factors (Brown 1996).

Smith & Welch (1978), who carried out an MR study of epigeal *C. agassizi* in southern Illinois, obtained growth rates varying during the spring studied, but they were generally low (overall growth = 0.8–1.7 mm month⁻¹). Some individuals were found to attain relatively large sizes (more than 70 mm SL), which were probably older than three years.

Annual growth in pulses was indirectly recorded for *T. itacarambiensis*. Very low rates were recorded in a MR study carried out during the dry season: mean growth rate was 0.06 mm month⁻¹ for the whole studied population (30–83 mm SL) and 0.17 mm month⁻¹ for size class 30–45 mm SL (immatures); several cases of negative growth were recorded (Trajano 1997a). This was followed by a significant decrease in condition factor during the studied dry period (Trajano personal observation), demonstrating the role of food limitation in the life history of this species. Growth rates under laboratory conditions that simulated the rainy season as regards food availability (food ad libitum) were much higher: 1.2 mm month⁻¹ for adult catfishes, 2.1 mm month⁻¹ for young ones. Based on these rates, longevity of seven years or more was

estimated for the species. Comparison with a few studied Chilean trichomycterids suggests a precocial lifestyle for *T. itacarambiensis* (Trajano 1997a).

Average growth rate of adult individuals of *P. kronei* (more than 70 mm SL) from Areias Cave, Upper Ribeira karst area, was 1.0 mm month⁻¹. Based on this, longevity of 10–15 years was estimated for the species, considered high when compared to the few other catfishes studied at that time (Trajano 1991). However, average growth rates similar to those reported for *P. kronei* were calculated by Gerhard (1999) for its putative sister-species, *Pimelodella transitoria*, in epigeal streams of that karst area during the rainy season (1.0 mm month⁻¹), and lower rates were recorded during the dry season (0.5 mm month⁻¹). Growth rates of 0.7 to 0.9 mm month⁻¹ were observed for individuals of *P. transitoria* living in caves. Cases of negative growth were recorded for this species, suggesting that feeding stress may also occur in epigeal habitats. Longevity estimated for *P. transitoria* was 4.1–12.4 years. *Rhamdioglanis frenatus*, another heptapterine syntopic with *P. transitoria*, shows higher growth rates (3.2 mm month⁻¹ in the rainy season; 0.8 mm month⁻¹ in the dry season) and lower estimated longevity (4.0–8.4 years) (Gerhard 1999).

Therefore, a precocial lifestyle is already present in *P. transitoria*, possibly as a preadaptation to the cave life. This may be a species-specific characteristic. *Pimelodella pappenheimi*, that also lives in a stream from the Atlantic rainforest to the south of the Upper Ribeira Valley, presents a less precocial lifestyle: with similar maximum lengths, average growth rates were higher and maximum longevity recorded (four years) was lower in *P. pappenheimi* than in *P. transitoria* (Amaral et al. 1999). In this case, the low growth rates and high longevity reported for *P. kronei* may be not a consequence of isolation and further specialization to the subterranean habitat, but just a plesiomorphic trait inherited from the epigeal ancestors.

Some records in laboratory confirm the high longevity for cavefishes: three years for males and five years for females of the small-sized and rather unspecialized *P. mexicana*, 10 years for *Astyanax* spp. (J. Parzefall personal communication), at least ten years is estimated for *T. itacarambiensis* (specimens collected 7.5 years ago with 50–60 mm SL are still alive), 18 years for *P. kronei* (a specimen collected when 115 mm long lived more than 10 years in laboratory) (Trajano personal observation), more than 15 years for *U. zammaranoi* and more than 23 years

for *P. andruzzi* (specimens of these species collected respectively in 1985 and 1977 are still alive, R. Berti personal communication).

Heuts (1952) performed a detailed study of growth in *C. geertsii* based on examination of scale rings of preserved samples, presuming that such rings were real year-rings due to seasonality of the hydrological system. Longevities of 9 to 13 years were estimated for fishes attaining 80–90 mm, with mean growth rates varying among populations from 0.25 to 0.60 mm month⁻¹. Compared to the epigeal *Barbus holotaenia*, found in the neighborhood of the studied caves (four years to attain 80 mm, growth rates 250–300% higher than those recorded for *C. geertsii*), *C. geertsii* has a precocial lifestyle.

Heuts (1952) detected a variety of growth patterns among populations of *C. geersti*, associated with pronounced differences in the distribution of age classes. One of the studied populations exhibited a constant, but very small geometric growth rate, while the others showed deviations from this simple type, by accelerations and retardations in given periods of life. Such differences would reflect local ecological conditions. Growth patterns in *C. geersti* differ from the usual patterns observed for epigeal fishes. Heuts interprets these unusual patterns as a result of heterochronic development, hypothesizing that regressive character states are a consequence of retardation of body growth.

Heterochrony seems to be a frequent phenomenon in the evolution of subterranean fishes and may explain at least part of the special morphological and behavioral traits of troglobites: longer fins, larger heads and greater exposure of sense organs in amblyopsids (Poulson 1963); small size and weak ossification in *T. pattersoni* and *S. eurytomus* (Langecker & Longley 1993); small size, reduction of cryptobiotic habits and increased midwater activity in Brazilian heptapterines (Trajano & Bockmann 1999). However, each of these character states have different adaptive meanings, and were probably achieved by different processes: progenesis in the case of ictalurids and heptapterines (Trajano & Bockmann 1999) and neoteny in amblyopsids (Poulson 1963), or possibly hypermorphosis (sensu Chaline 1987), at least in *A. spelaea*. The latter exhibits a particularly extended lifespan, attaining much larger sizes. For example, there are records of individuals 200 mm long (Greenwood 1967), while other amblyopsids do not surpass 70 mm. Therefore, those traits are not the result of a common causal phenomenon.

Species interactions: syntopy of troglobitic fishes and predators

Among more than 86 species of subterranean troglobitic fishes known throughout the world, there are 15 cases of coexistence of troglobitic fishes in the same cave system (Proudlove⁷, personal communication): 13 cases involve two species and two involve three syntopic species. Differences between these figures and those reported by Proudlove are due to the fact that the existence of a second, undetermined species, troglomorphic *Rhamdia* catfish syntopic with *R. reddelli* in Mexico could not be confirmed afterwards (A. Weber personal communication), and that the Brazilian *A. cryptophthalmus*, *Trichomycterus* sp. 1 and *Eigenmannia vicentespelaea* were reported as syntopic by mistake in the São Vicente system (Trajano 1997d); only the former two are really syntopic in Passa Três Cave, part of that system (Trajano 2001). Half the cases of syntopy correspond to species belonging to the same families, ecologically close. The case of the bythitid *Lucifuga* is particularly interesting: three species of this genus are reported as syntopic in one cave and two in a second cave from Cuba.

If all these cases actually correspond to syntopy and all the species recorded are valid and truly troglobitic, almost 40% of the troglobitic fishes share at least part of their habitat with other troglobitic fish species, and a higher proportion share habitat with any fish species if we also consider non-troglobitic fishes that may coexist with the troglobites (see below). Therefore, a considerable proportion of troglobitic fishes may interact with other fish species.

Habitat partitioning or differences in diet, allowing coexistence with minimum competition, may explain some of the well-documented cases of syntopy of subterranean troglobitic fishes. Different habitat preferences have been observed for the cave balitorids, *S. oedipus* and *C. thamicola*, which are syntopic in Mae Lana Cave in NW Thailand. In this cave, *S. oedipus* occurs in slow moving waters over silty substratum in two upper tributaries of the base-level stream and in rimstone dams atop flowstone; *C. thamicola*, on the other hand, is found in waterfalls formed by runoff waters from those tributaries, which cascade over flowstones, and in one section with rapids on limestone bedrock of the mainstream (Trajano, Borowsky,

⁷ Proudlove, G.S. 1997. A synopsis of the hypogean fishes of the World. pp. 351–353. In: Proc. 12th International Congress of Speleology, La-Chaux-des-Fonds.

Mugue & Smart unpublished data). The occurrence of *C. thamicola* in specialized, highly discontinuous habitats in two different caves (Tham Mae Lana and the type-locality, Tham Susa; Kottelat 1988) poses an interesting question about the fish dispersion and connectedness of populations.

On the other hand, *A. cryptophthalmus* and *Trichomycterus* sp. 1, syntopic at Passa Três Cave, central Brazil, present different feeding habits: while *A. cryptophthalmus* is detritivorous, *Trichomycterus* sp. 1 is a generalist carnivore (Trajano & Bichuette unpublished data), much as their respective epigeal relatives. Unfortunately, for the majority of syntopic fish species, there is no detailed data on diet and microhabitat occupation for an analysis of mechanisms allowing coexistence. In some cases of closely related hypogean species that are syntopic in some caves, such as *Lucifuga* spp., morphology and biology are so similar that they are treated together (e.g., Eigenmann 1909, Juberthie⁶) suggesting direct competition when these species meet each other.

Some syntopic species present similar population densities, but the majority seem to differ. Based on the size of collections, population density of the carnivorous *S. eurystomus* is half that of the detritivorous *T. pattersoni* (Longley & Karney 1979). The same is true for *C. basimi* in relation to *T. widdowsoni* (Banister & Bunni 1980). The Chinese *S. anophthalmus* has a larger population size (the proportion is not given) than *T. ayunnanensis* and *Paralepidocephalus* aff. *yui* (Yang & Chen 1993a). On the other hand, similar population densities are reported for *Protocobitis typhlops* and *Oreonectes* sp., also from China (Yang & Chen 1993b).

There is a general notion that, as a consequence of food scarcity, subterranean food pyramids would not support more than one level of predators (e.g., Mohr & Poulson 1966). Therefore, hypogean fishes, usually predaceous, would not generally be subject to important predation pressures, and some specializations of troglobitic fishes have been interpreted in this context, such as the absence of generalized phobic reactions and reduction of cryptobiotic habits allied to increased midwater activity in Brazilian siluriforms (Trajano & Bockmann 2000), and reduction of dorsal aculeum in *P. kronei* (Trajano & Britski 1992) and some *Rhamdia* species (Weber 1996). Refractoriness to disturbing stimuli, probably related to lowered metabolism (energy economy), and increased activity in troglobitic amblyopsids and *T. widdowsoni* (Poulson 1963) are specializations that

can develop in the absence of important predation pressures.

As a matter of fact, there are few cases of potential cavefish predators identified in the natural habitat, and rare confirmed reports of predation on cave fishes. Epigeal fishes were pointed out as potential predators of amblyopsids such as *A. rosae* (Brown 1996, Poly & Boucher 1996) and *Taunayia* sp. (Trajano & Bockmann 2000). The erythrinid *Hoplerethrinus unitaeniatus* was observed preying on the troglobitic armored catfish, *Ancistrus cryptophthalmus*, in a cave in central Brazil (M.E. Bichuette personal communication). Langecker & Longley (1993) suggested that *Satan eurystomus* may be a predator of *Trogloglanis pattersoni*, which, if confirmed, would constitute the first example of such kind of interaction between troglobitic fish species. Crabs, *Epilobocera* sp., were observed attacking *Lucifuga* spp. in Cuban caves (Díaz-Pérez 1988), and, according to Romero (1998a), crayfishes are known predators of cave fishes. Decapod crustaceans, frequently co-inhabiting caves with fishes, could be important predators, especially of juvenile fishes. Conversely, young decapods are food for *L. dentatus* (Eigenmann 1909), *P. kronei* (Trajano 1989) and other cavefishes, configuring a complex food web.

Extensive fieldwork showed that fish predators are actually absent for the great majority of studied species or, if they do exist, these predators are so rare that their impact on the resident fish population is negligible. This is the case for *Astyanax* spp., *P. mexicana*, *P. kronei*, *T. itacarambiensis*, the new heptapterine genus from NE Brazil, and amblyopsids, among others.

On the other hand, cannibalism, observed for amblyopsids (Poulson 1963) and *Taunayia* sp. (Trajano & Bockmann 2000) but possibly more common among subterranean fishes (the scarcity of feeding data for most species may account for the absence of additional records), may be an important ecological factor regulating population densities.

Non-troglobitic cave fishes

Non-troglobitic fishes regularly found in the subterranean biotope, although rarely forming large populations in this habitat, also deserve a place in this synthesis. Most importantly, these are also hypogean fishes and are subject to the same ecological constraints as troglobites. In addition, they may coexist and interact with troglobitic fishes, as predators, prey, competitors, or simply sharing space. Finally, they illustrate the kind of fish community that can be

isolated in the subterranean habitat, originating troglobitic species. These fishes may be troglaphiles, organisms able to complete their life cycle both in hypogean and in epigeal habitats (Holsinger & Culver 1988), troglonexes, organisms found regularly in the subterranean habitat, but which must return periodically to the surface to complete their life cycle (op. cit.), or just transient occurrences in the subterranean environment.

Such an emphasis has been understandably given to the troglobitic fauna that little attention is paid to non-troglobitic fishes, and little data are available for such communities beyond species records. As a consequence, there is little evidence allowing classification of most of these fishes as troglaphiles, troglonexes or accidentals. Rare presumed troglaphiles have been studied in detail and compared to troglobitic relatives. For instance, the troglaphilic amblyopsid *C. agassizi* is so frequent in caves from south-central United States that it received the same emphasis as troglobitic amblyopsids (e.g., Poulson 1963, Smith & Welch 1978). *C. agassizi* is clearly preadapted to the hypogean life, not only in relation to behavior and sense organs (much as the exclusively epigeal *C. cornuta*), but it is also adjusted endocrinologically to live under permanent darkness (in contrast to *C. cornuta*). The heptapterine *P. transitoria*, putative sister-species of *P. krontei* and syntopic with the latter, was object of studies by Pavan (1945, 1946) and Trajano and colleagues (Trajano 1989, 1991, 1994, Hoenen & Trajano 1995, Trajano & Gerhard 1997); this species also exhibits several preadaptations to the cave life, as discussed above. *Synocyclocheilus* cyprinids, with five troglobitic species in China (Proudlove⁷), are described as having 'half-cave-dwelling' habits, usually occurring and breeding in underground rivers or caves connected to epigeal rivers or lakes (Chen & Yang⁸), thus are typical troglaphiles.

On the other hand, the status of eyed tetra characins *Astyanax mexicanus* found in caves is unclear, especially when they co-occur with troglobitic populations, hybridizing to a greater or lesser extent (Mitchell et al. 1977). In the literature, it is implied that epigeal tetras are frequently introduced in caves, possibly during high water. However, if such fishes are able to breed with blind forms, they could also breed among themselves. The point is: how self-sustained must these cave populations of eyed tetras be in order to fit into the

troglophile category? (Self-sustainability is not mentioned in any definition of troglaphilic populations, but it seems to be a logical inference.) A similar situation is observed in Brazilian caves: groups of normally eyed and pigmented *Astyanax* fishes, sometimes very large (dozens to hundreds of individuals), have been found in caves from Mato Grosso do Sul, SW Brazil (E.P. Costa Jr. personal communication) and central Brazil (see below). The status of these groups remain undetermined, but no troglobitic *Astyanax* was found in these areas (although troglobitic siluriforms do exist in both areas, indicating that there were opportunities for isolation), suggesting that such groups do not form self-sustained populations.

I will illustrate non-troglobitic ichthyofaunas with three examples showing how diverse this fauna may be under certain circumstances, and the kind of community that can be isolated in the subterranean habitat and originate troglobitic populations: fish communities in caves from western Thailand and central Brazil (unpublished data) and non-troglobitic fishes in caves from West Virginia, U.S.A, where troglobitic species are absent (Poly & Boucher 1996). Although generally not numerous in caves, those large animals may exert a considerable impact on subterranean communities, preying on invertebrates including troglobitic species, such as the endangered crayfish *Cambarus aculabrum* from Arkansas, possibly also on troglobitic fishes, and conversely as an abundant food source for cavernicoles.

A considerable number of fish species belonging to different families and orders were found in streams crossing caves from West Virginia (and in other North American caves as well), at distances of hundreds of meters from the known entrances, but only a few were found on a regular basis and in reasonable numbers (constituted by several dozen): *Cottus* spp. (Cottidae), *Semotilus atromaculatus* and *Pimephales notatus* (Cyprinidae), *Lepomis cyanellus* (Centrarchidae), *Catostomus commersoni* (Catostomidae). *Cottus* spp. are one of the non-troglobitic fishes most commonly found in caves throughout the United States. In other regions of North America, catfishes such as *Ameiurus*, which are rare in the caves studied in West Virginia, may be quite common; 100 individuals were found in a cave in Florida.

Poly & Boucher (1996) mention the occurrence of depigmentation, including albinism (albinos may comprise 2–3% of the subterranean populations), and other morphological abnormalities in non-troglobitic fishes occurring in North American caves. They suggest

⁸ Chen, Y. & J. Yang. 1993. Species and origin of cave-dwelling *Synocyclocheilus* fishes. pp. 123–124. In: Proc. 11th International Congress of Speleology, Beijing.

that such abnormalities, and also the appearance of out-of-season reproductive features, may be a consequence of hormonal imbalance. This hypothesis was based on authors like [Rasquin & Rosenbloom \(1954\)](#), who failed to rear epigean *Astyanax mexicanus* in permanent darkness for months, although this could not be confirmed by later studies ([Wilkens 1988](#)).

Cavers in western Thailand are familiar with non-troglobitic fishes frequently seen in caves crossed by large streams, characterized by high water volumes and, in many cases, strong currents. These fishes, mainly cypriniforms, are found all the way through most caves, often many kilometers from the nearest entrance, in the typical aphotic subterranean habitat. They are observed swimming in isolation or in small groups, up to ten individuals. Such fishes include the cyprinids *Garra* sp., *Danio* sp., *Tor* sp. and *Poropuntius* sp., the balitorids *Schistura* sp., *Homaloptera* sp., *Balitora* sp., and *Hemizyon* sp., plus a sisorid, *Glyptothorax* sp., and an unidentified silurid ([Borowsky⁹](#)). The cyprinids, including large bodied species, were usually seen in slow-moving water of variable depths; both adults and juveniles were recorded. Collected specimens seemed to be well fed and in good healthy condition. The eyed balitorids found inside caves were in habitats typical for these fishes – swimming over or maintaining position on rocks in fast-flowing, turbulent water. We never observed epigean fishes and troglobitic balitorids in syntopy. Representatives of other fish taxa, such as siluriforms and synbranchids were rarely seen during our visits ([Trajano, Borowsky, Mugue & Smart unpublished data](#)).

A similarly rich fauna of non-troglobitic fishes was recorded in São Domingos karst area, Goiás State, central Brazil, in caves crossed by large streams similar to those studied in Thailand. This area harbors the richest subterranean ichthyofauna in Brazil, including at least four (possibly six) troglomorphic species and several non-troglobitic ones. This may be partly due to the fact that the area is part of the Tocantins River basin, with a diversified Amazonian epigean fauna as source of potential colonizers of the hypogean environment, and partly because many cave entrances are sinkholes favoring energy input. As a matter of fact, large amounts of detritus are observed inside these caves, so food does not seem to be a limiting factor.

⁹ Borowsky, R. 1998. Survey of the cave fishes of south-western and peninsular Thailand. Report to the Thai Royal Forest Department, Web version <<http://pages.nyu.edu/~rb4/thaicave.htm>>.

Several non-troglobitic species were regularly found in São Domingos caves since the 80s ([Dessen et al. 1980](#), [Trajano 1987](#), [Trajano & Bichuette unpublished data](#)), including characiforms such as *Hoplerythrinus unitaeniatus* (Erythrinidae), *Brycon* spp. and *Astyanax* sp. (Characidae), siluriforms as *Imparfinis hollandi*, *I. minutus* and *Rhamdia quelen* (Pimelodidae, Heptapterinae), *Pseudocetopsis plumbeus* (Cetopsidae), *Hypostomus* sp., *Loricaria* sp., *Rineloricaria* sp. (Loricariidae), gymnotiformes as *Apteronotus* sp., *Sternachorhinchus* sp. and *Sternopygus* sp., and the cichlid *Cichlasoma araguaiensis*; semi-aquatic tetrapods such as alligators and turtles were also occasionally found in these caves. A small population of *Pimelodella* catfishes apparently showing some reduction of eyes, pigmentation and phobic reactions (a character state also observed for *P. kroni* – [Trajano 1989](#)), was found in a small tributary in one of those caves. The commonest non-troglobitic fish species in São Domingos caves are *H. unitaeniatus*, *Imparfinis* spp., *Astyanax* sp. and gymnotiforms. There is a record of a small group formed by the same individuals of *B. brevicauda* living for at least three years in the same site in São Mateus Cave ([R.H. dos Santos personal communication](#)), demonstrating that these fishes are able to survive in healthy conditions for long periods inside a cave.

Non-troglobitic fishes co-occur with troglobitic species in Angélica-Bezerra Cave system (*A. cryptophthalmus*), in Passa Três Cave (*A. cryptophthalmus* and *Trichomycterus* sp. 1), where a considerable number of *H. unitaeniatus* is found in pools in the small stream crossing the cave (see [Trajano 2001](#)), along with *Astyanax* sp. (a depigmented specimen was found in 1988, [Trajano & Souza 1994](#)), and in São Vicente I Cave (*Eigenmannia vicentespelaea*). A study based on the analysis of stomach contents of those non-troglobitic fishes is in progress to determine their possible role as predators of troglobitic organisms. Nevertheless, in view of their relative abundance and diversity, there is little doubt that non-troglobitic fishes are important components of the subterranean ichthyofauna at the São Domingos karst area.

General discussion

According to [Vandel \(1964\)](#), Schiner originally defined troglobites as organisms exclusively found in caves. However, because caves constitute an artificial subdivision of the hypogean domain based on human

parameters, this category must be redefined to encompass all subterranean habitats, for example, interconnected spaces of subsoil characterized by permanent darkness and tendency to climatic stability (Juberthie 1983), which determine the most important ecological traits of strictly hypogean species. More recently, the term 'stygobite' came into use to designate aquatic troglobites. Considering that, in accordance with the expanded definition of troglobites comprising species restricted to subterranean habitats in general, 'aquatic troglobites' and 'stygo bites' are synonyms, and to maintain coherence with the term 'troglomorphisms' for the autapomorphisms shown by such species, I herein use the term troglobites for exclusively hypogean fish species.

Because applying the geographic criterion of exclusion from epigean habitats is frequently unfeasible, particularly in poorly studied tropical regions, the presence of troglomorphisms, especially reduction of eyes and/or pigmentation in relation to epigean relatives, is commonly used to deduce the status of troglobite for subterranean species. Although 'troglomorphic traits' may occur in species living in epigean habitats which share important ecological characteristics with the hypogean ones (e.g., deep, turbid river waters) (see Thinès & Proudlove 1986 and Trajano 1997d for lists of troglomorphic fishes including non-hypogean species), the presence of troglomorphisms is generally a useful criterion to recognize troglobites and has been used in the case of species discussed herein.

Representatives of epigean fish species found in the subterranean environment are more difficult to accommodate into the Schiner-Racovitza classification (cf. Holsinger & Culver 1988), as pointed out by Poly & Boucher (1996). Few eyed and pigmented species, such as *C. agassizi* and probably *P. transitoria*, have been recognized as troglophiles. For the great majority of non-troglomorphic fishes found in caves, there is no indisputable evidence allowing their classification as troglophiles, troglaxenes or accidentals. Many appeared to be quite healthy, although it was usually impossible to determine the length of time these fishes had been in caves, indicating that they are able to orient themselves and to get some food under permanent darkness and food scarcity. In the case of Mexican tetras, *A. mexicanus*, epigean individuals entering some caves may reproduce with the resident troglobitic tetras, producing hybrid populations (Mitchell et al. 1977, Romero 1983). However, evidence of establishment of reproductive, self-sustained populations, defining the troglophilic condition, is usually lacking. It

is also unclear how sensitive each one of these non-troglotic species are to the absence of photoperiods and how they cope with hormonal imbalance and other physiological consequences of life under constant darkness. Inability to adjust endocrinologically to such conditions may explain the absence in caves of fish apparently preadapted to the hypogean life, as seems to be the case with *C. cornuta* (Poulson 1963), and *T. bifasciata* (epigean sister-species of the troglotic *Taunayia* sp.), that survived shortly under constant darkness in laboratory (Trajano personal observation).

Regardless of their status as troglophiles, troglaxenes or accidentals, non-troglomorphic fishes in general are not numerous in caves, frequently showing population densities lower than those of troglotic fishes. This is probably because few individuals among the epigean populations are able to cope with the harsh ecological conditions in the subterranean biotope, and accidental introduction of fishes into this habitat is a relatively rare event.

Population data on non-troglotic fishes, although scarce and rarely quantitative, indicate that most cave-fish populations, when first isolated in the subterranean habitat, are small and prone to genetic drift due to bottleneck effects. Such founding populations are expected to be small because they had not yet acquired the special adaptations to cope with food scarcity, as those shown by most troglobites, and many of them were probably even more food-limited and habitat-restricted than now. Several authors hypothesize that isolation may occur during dry periods, as a consequence of paleoclimatic changes, when previously continuous epigean/hypogean water bodies fragmented due to breakdown of hydrological continuity (Willis & Brown 1985, Trajano 1995, Cobolli-Sbordoni et al. 1996). During these periods, energy input to caves would decrease due to the interruption of epigean drainage, and aquatic communities would be isolated in discontinuous hypogean water bodies. Some of these isolated populations may survive periods of climatic stress, accumulating significant changes that may be eventually recognized as distinct phylogenetic troglotic species. The others may survive without significant change, or simply not survive such periods at all.

In isolation, genetic drift and other evolutionary processes would lead to transformation of characters such as eyes and pigmentation, resulting in troglotic speciation. After the appearance of derived character states that improve efficiency of orientation and feeding in the hypogean environment, the new troglotic populations may increase, attaining the densities herein recorded

for several fish species. However, effective population sizes may remain low due to a decrease in reproductive rates, a common specialization of troglobites, which may be associated with a decrease in the proportion of individuals reproducing at least once during their lifespans.

Therefore, effective population sizes of epigean or trogliphilic fishes phylogenetically related to the troglobitic species would constitute the best approximations for the initial 'N' modeling the evolution of troglomorphic characters (see, for instance, Culver 1982). Unfortunately, there are no reliable estimates of effective population sizes either for non-troglobitic or for troglobitic fish species.

As aforementioned, most of the 86+ species of troglobitic fishes so far recorded are siluriforms or cypriniforms, found in all continents but Europe. The highest species richness is observed in karst areas from China, Mexico, Brazil and southeast Asia. Such areas do not necessarily correspond to regional or local hotspots of biodiversity of troglobites. For instance, no other confirmed troglobites, aquatic or terrestrial, were found in São Domingos karst area, in the Brazilian region with highest richness of troglobitic fishes.

Interestingly, only three out of 20 caves and wells identified by [Culver & Sket \(2000\)](#) as local hotspots of biodiversity (those with 20 or more troglobitic species) harbor troglobitic fishes: Shelta (*T. subterraneus*) and Mammoth (*T. subterraneus* and *A. spelaea*) caves, in the U.S.A., and Gua Salukang Kallang, in Indonesia. However, 14 of these caves are located in Europe, where no troglobitic fish has ever been found. The scarcity of high diversity tropical caves can be explained by the short history of biospeleology in the tropics, and related to the paucity of specialists dedicated to the taxonomy of tropical subterranean groups. With the progress of biospeleological surveying and taxonomic studies in tropical localities, many more hotspots of biodiversity are expected to be identified in these regions. The real puzzle is the absence of troglobitic fishes from Europe, especially from the Dinaric karst, which has a high diversity of other hypogean fauna. Considering the extension of this karst area and its rich geological history explaining the occurrence of hotspots of biodiversity ([Culver & Sket 2000](#)), and the presence of troglobitic aquatic salamanders (ecologically close to fishes), at least in theory, conditions are good for colonization of caves by fishes and for isolation ultimately originating troglobitic species in this and other European karst areas.

No strong phylogenetic/taxonomic or geographic correlation was found for population parameters in troglobitic fishes: related species may differ considerably in relation to the extent of distribution, habitat, population density and size, etc. Apparently, such traits correspond mostly to responses to local conditions, as exemplified by the comparison between the Brazilian catfishes, *P. kronei* and *T. itacarambiensis*, which live in karst areas which are quite distinct climatically. Local ecological conditions would determine the kind and extent of specializations in troglobitic fishes, limited by biological constraints proper to each group; detritivores are not expected to become carnivores while adapting to the subterranean habitat, just as the not usually numerous heptapterines are not expected to show high population densities in caves. Nevertheless, some amazing cases of high degree of evolutionary modification affecting a large number of characters have been described, especially among species that managed to adapt to extreme conditions in deep phreatic habitats (e.g., *T. patterni*, *S. eurystomus*, *U. zammaranoi*, *P. cisternarum*).

In some cases, habitat and habitat preferences observed in troglobitic fishes correspond to plesiomorphic character states retained from epigean ancestors, in others there was an evolutionary change after speciation in the subterranean biotope. Epigean *Trichomycterus* catfishes are typical stream-dwellers, as are the troglobitic *T. chaberti*, *T. itacarambiensis*, *Trichomycterus* sp. 1, from central Brazil; on the other hand, *Trichomycterus* sp. 2, from SW Brazil, inhabits flooded caves, a specialized habitat. Habitat preferences of *P. kronei* and *A. cryptophthalmus* are similar to those of their respective epigean close relatives: *P. transitoria*, sister-species to *P. kronei*, is also found preferentially in pools ([Gerhard 1999](#)), whereas epigean *Ancistrus* prefer rapids, like *A. cryptophthalmus* ([Trajano 2001](#)).

Probable cases of habitat change were reported for *Taunayia* sp. and the new heptapterine genus ([Trajano & Bockmann 1999](#)), *S. oedipus* ([Trajano, Borowsky, Mugue & Smart unpublished data](#)), and possibly also *Ancistrus formoso* and *Trichomycterus* sp. 2, all of them found in the phreatic zone habitat. These fishes belong to the stream-adapted epigean taxa (the subclade *Nemuroglanis* for the two former, balitorids for the latter), but have secondarily adapted to lentic conditions.

Precocial phenotypes are products of stability and the resulting competition, or specialization or both ([Balon 1981, 1993](#)). Eggs with a larger amount and

density of yolk develop longer but directly into juveniles that are comparatively advanced at the time of the first feeding. This represents a clear survival advantage, especially important in food-poor and stable habitats such as caves. There seems to be an evolutionary trend to shorten the vulnerable larva period in competitive environments (Balon 1990, 1999). Therefore, a precocial lifestyle is probably an adaptive specialization shown by troglobitic fishes.

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