A population study of epigean and subterranean *Potamolithus* snails from southeast Brazil (Mollusca: Gastropoda: Hydrobiidae)

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Abstract

Population and reproductive biology of four *Potamolithus* species, two epigean (*P. ribeirensis* and *Potamolithus* sp. 1) and two subterranean (*P. troglobius* and *Potamolithus* sp. 2), from the Upper Ribeira Valley, southeast Brazil, were studied, from June 1996 to June 1997, using 1 m^2 quadrats and counting all individuals found in these quadrats. *P. ribeirensis* showed the highest variation in population densities (from 0 – after floods – to 467 ind.m^{-2}), with average ranges from 16.0 to 284.8 ind.m^{-2}. The densities of the two troglobitic species (average ranges for *Potamolithus* sp. 2 and *P. troglobius*, from 17.6 to 58.4 and from 0 to 61.5 ind.m^{-2}, respectively), higher than those of *Potamolithus* sp. 1 (average from 0 to 9.3 ind.m^{-2}), were high for cave organisms. *P. ribeirensis* and the two troglobitic species showed higher densities in warmer, wetter months, while *Potamolithus* sp. 1 showed higher densities in cooler, less rainy months. The troglobitic species were non-seasonal, since high percentages of mature females were observed throughout the year. In the epigean species, the reproductive periods showed no detectable pattern: in 1996 *P. ribeirensis* had a peak in winter and in the next year (1997) in spring and summer. *Potamolithus* sp. 1 had reproductive peaks in fall and winter.

Introduction

The subterranean, or hypogean environment is characterized by permanent darkness and tendency to environmental stability. Photoautotrophic organisms are absent and subterranean organisms are mainly dependent of allochthonous food items, frequently scarce (Culver, 1982; Howarth, 1983). Among organisms regularly found in the subterranean habitat, troglobites evolved in isolation in this habitat, developing character states that differentiate them from epigean (surface) relatives. Cave-related autapomorphies ('troglomorphisms') usually include reduction of melanin pigmentation and eyes (Wilkens, 1976).

Due to the spatial limitation of subterranean habitats when compared to the epigean ones, and to food scarcity, their populations are generally small (Poulson, 1964; Barr, 1968; Sbordoni, 1982; Trajano,

1991). Although some troglobitic populations may be abundant (e.g. Moracchioli, 1994; Trajano, 1997a).

Troglobites are intolerant of environmental stress and have a precocial lifestyle, low fertility rates, late maturation, and high longevities (Poulson, 1963, 1964; Culver, 1982; Wilkens, 1988; Trajano, 1991).

Low or no reproductive seasonality was observed for some troglobitic species, as a consequence of the relatively stability of the hypogean environment (Barr, 1968; Juberthie, 1975). For instance, Thompson & Moracchioli (1996) observed reproduction throughout the year for a cave polydesmid diplopod from the Upper Ribeira Valley, southeast Brazil. However, many caves are subject to pronounced seasonality related to rainy cycles, and seasonal reproductive peaks exist in cave populations, mainly in aquatic species (Poulson, 1964; Juberthie, 1975; Moracchioli, 1994; Mendes, 1995; Trajano, 1997b).

Gastropoda and Bivalvia are widespread in continental subterranean waters, with many species to be formally described. Among gastropods, the subclass Prosobranchia is best represented, especially mesogastropods (Archaeogastropoda is represented by only one genus and species). The Bivalvia are represented by a few genera of Eulamellibranchia (Bole & Velkovrh, 1986). Among subterranean gastropods, 'hydrobioids' (*sensu* Davis, 1979, in an informal sense, not to be confused with the superfamily Hydrobioidea Nordsieck, 1972) encompass 97% of the troglobitic species, most of them belonging to Hydrobiidae (Bole & Velkovrh, *op. cit.*). The small sized hydrobiids are extremely diverse, with more than 1000 recent species (Boss, 1971; Hershler & Ponder, 1998), generally occurring in freshwaters, some living in brackish water and a few terrestrial (Thiele, 1931, Taylor, 1988). Cave hydrobiids include troglophiles and troglobites. In accordance with Hershler & Longley (1986), hydrobiids are common in many karst regions of the World, including Europe, North America, Africa, Japan, Australia and New Zealand. For South America, there are records of *Andesipyrgus sketi* Hershler & Velkovrh, 1993, in caves from Ecuador and Colombia, and *Potamolithus troglobius* Simone & Moracchioli, 1994 and *P. karsticus* Simone & Moracchioli, 1994, in caves from the Upper Ribeira Valley, Brazil.

Population data for hydrobioids are scarce and mainly restricted to species from temperate regions. A large variation in population density was reported for *Hydrobia totteni*, from dozens to thousands individuals.m^{-2} in Lawrencetown Marsh, Nova Scotia (Wells, 1978). Maximum densities of the Bithyniidae, *Bithynia tentaculata* (thousands ind.m^{-2}) were observed in the springtime (Fretter & Graham, 1962). A population decrease was observed in *Potamopyrgus antipodarum* during the winter (cited as *P. jenkinsi* – Heywood & Edwards, 1962). In estuarine regions of Spain, *Hydrobia ulvae* showed population densities reaching thousands ind.m^{-2} in spring, with decrease in the winter (Sola, 1996).

A faunistic survey in the Upper Ribeira karst area, southeast Brazil, resulted in 14 species of *Potamolithus* recorded, including two epigean, seven troglophiles and five troglobites (Bichuette, 1998). Here, we compare population and reproductive data of two epigean (*Potamolithus ribeirensis* Pilsbry, 1911, *Potamolithus* sp. 1, from Betari river) and two subterranean species (*P. troglobius* and *Potamolithus* sp. 2, from Alambari de Cima Cave). We test the following hypo-theses: 1 – subterranean populations of *Potamolithus* spp. are smaller than epigean ones and, 2 – subterranean species do not present accentuated reproductive seasonality.

Study area

The study area is situated in the Upper Ribeira Valley karst area, Iporanga County, São Paulo State, southeast Brazil. It is geologically inserted in the Açungui group, composed of Upper Pre-Cambrian metasedimentary rocks. Four NE-SW limestone lenses, from 1 to 8 km widths and extending over 20 km, intercalate with non-soluble detritic rocks (Trajano, 1991).

The Upper Ribeira Valley is located in the transition between the Tropical Atlantic and Araucaria Forest domains (Ab'Saber, 1977). The climate in the presently studied area is type "Cfa", defined as tropical wet without a dry season, with temperatures in the warmest month (January, in the Upper Ribeira) above 22 °C and total precipitation in the drier month (July) above 30 mm (Köeppen, 1948). Total precipitation in the region is around 1500 mm. The study area is mostly covered by perennial subtropical humid forest (Hueck, 1972), and crossed by typical well-oxygenated headwater streams, with rocky beds and rapids intercalating with some soft-bottomed pools.

The population and reproductive study focused on four species of *Potamolithus*, two from epigean direct tributaries of the Upper Ribeira river (Betari and Iporanga rivers) and two from cave streams which are tributaries of the Betari river (Águas Quentes and Alambari de Cima Caves), located in the Parque Estadual Turístico do Alto Ribeira (PETAR) and surroundings (Fig. 1).

Study localities

Iporanga river
Locality of *P. ribeirensis*. This river is about 30 km long with many riffles (0.5–0.8 m depth) and pools. Four collecting sites were established in a 70 m long reach, where the streambed was mainly formed by boulders. These study sites were situated 700 m upstream of the Iporanga river discharge into the Ribeira river. Water current was low in sites 1 (depth = 0.1 m), 3 (depth = 0.3 m) and 4 (depth = 0.4 m), and medium to strong in site 2 (depth = 0.6 m).
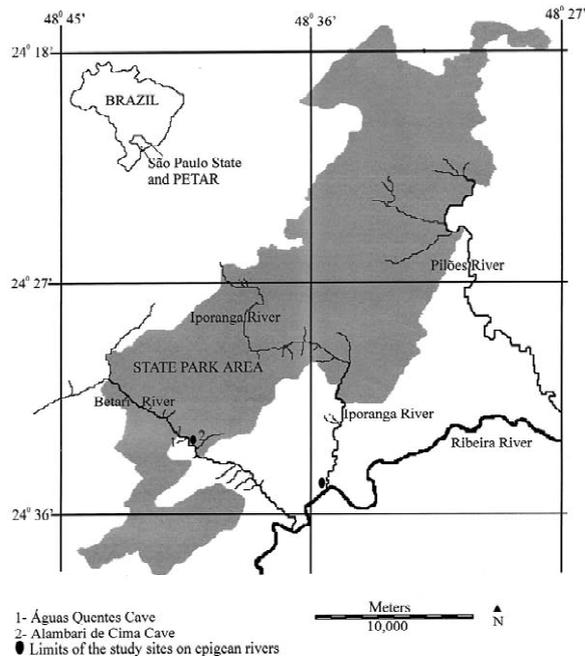
Figure 1. Study area of *Potamolithus* species, Iporanga County, southeast Brazil. In detail is shown São Paulo State and PETAR.

Figure 2. Part of Águas Quentes Cave map, showing the studied stream reach, Iporanga County, southeast Brazil.
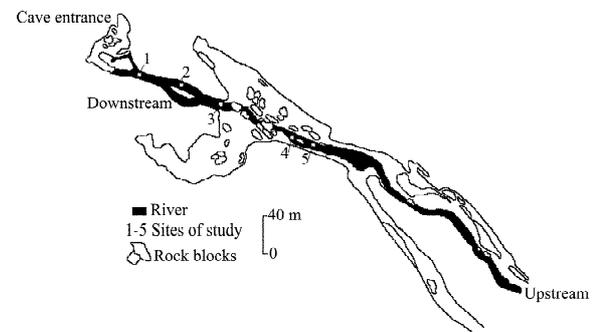
Figure 3. Part of Alambari de Cima Cave map, showing the studied stream reach, Iporanga County, southeast Brazil.

Betari river

Locality of *Potamolithus* sp. 1. This river is about 20 km long, average width 10 m, depth in riffles between 0.5 and 1.0 m, some pools 2.0 m deep. Collecting sites were selected in a 1000 m long reach situated outside the boundaries of the Park (see Fig. 1). For the population study, four equidistant sites were established along a 100 m long reach. These sites had depths varying between 0.1 and 0.3 m, low water current, and bottom formed by boulders (sizes between 63 and 16 mm).

Águas Quentes Cave (Iporanga Co., São Paulo State – 24° 35′ S, 48° 40′ W)

This cave is located in the neighborhood of the Park and is part of the Areias cave system, type-locality of *P. troglobius*. The stream conduit is 370 m long and the accessible cave entrance is situated 20 m above the stream resurgence. After a 500 m long course, the epigean reach joins the right margin of Betari river. Four sites were established in Águas Quentes Cave. Sites 1, 2 and 3 were located in complete darkness. The streambed was formed by blocks and boulders in sites 1 (average depth around 0.2 m) and 3 (depth between 0.10–0.15 m), and by large blocks in site 3 (average depth around 0.15 m); water velocity was low in these three locals. Site 4 was located near the cave entrance,

with some influence from the epigean environment (indirect illumination); the streambed was formed by large blocks, sand and silt, depth was around 0.4 m and moderate water current (Fig. 2).

Alambari de Cima Cave (Iporanga Co., São Paulo State – 24° 33′ S, 48° 40′ W)

Locality of *Potamolithus* sp. 2. This cave is 1580 m long, formed by a main gallery crossed by the Alambari stream plus some dry lateral galleries. The small cave entrance is also located 20 m above the stream level, near the inaccessible resurgence. Due to the occurrence of a low ceiling passage (70 m long, 1 m high) near the entrance, the cave cannot be visited during rainy periods. Five collecting sites were established in the streambed, formed mainly by small boulders, sand and silt; water current low; and depth varying between 0.1 and 0.2 m (Fig. 3).

Materials and methods

The population study focused on four *Potamolithus* species. *P. ribeirensis* is an epigean species from Iporanga river, characterized by a globose shell, conspicuously larger than that of the other studied species (<5.7 mm of shell length), with black periostracum,

pigmented body and well-developed eyes. *Potamolithus* sp. 1 is an undescribed epigean species from Betari stream, up to 2.0–3.0 mm shell length, with an elliptical brown shell. *P. troglobius*, a troglobitic species from Águas Quentes Cave, is small (<2.8 mm shell length) and has a globose shell with transparent periostracum, unpigmented body, and no visible eyes. *Potamolithus* sp. 2, an undescribed troglomorphic species from Alambari de Cima Cave, has a globose and transparent shell, and no visible eyes (Bichuette, 1998).

Population study and environmental variables

Monthly field trips were carried out between June 1996 and June 1997, except for January and April 1997 when severe floods prevented fieldwork. In order to assess population densities, 1.0×1.0 m quadrats were distributed along epigean and subterranean streams. Boulders, pebbles, logs and other submerged substrates were carefully inspected and the total number of individuals found inside the quadrats was counted. The sediment was also sifted. After this, all specimens were returned to the same place. Dislocation of boulders and blocks did not appear to cause significant perturbation of the populations, since densities did not decrease during the study. The study sites were marked with plastic color bands in epigean streams and aluminum stakes in the caves; quadrats were delimited by aluminum frames.

From June to September 1996, water temperature was measured monthly with a mercury thermometer (0.5 °C precision). From September 1996 to June 1997, temperature, pH, dissolved oxygen and conductivity were measured with a digital HORIBA apparatus (model U-10). Monthly precipitation was obtained from a pluviometric station in Serra de Motas District, Iporanga Co., southeastern Brazil; these data were provided by the Departamento de Águas e Energia Elétrica – DAEE/CTH from São Paulo State.

Mean values with respective standard-deviations and coefficients of variation were calculated for monthly population densities and environmental variables. Spearman's test was used for correlation between density and temperature, and, for cave populations, between density and distance to the cave entrance. Cave and epigean population densities were compared by Mann-Whitney and Kruskal-Wallis tests. In addition, to test whether variations in the densities of the *Potamolithus* species were significant or not along the year, an analysis of variance by ranks was applied (Kruskal-Wallis) (Sprent, 1993).

Reproductive biology

For studying reproduction, 20 specimens from each cave and from Iporanga river and 10 specimens from Betari river were collected monthly, in sites situated 20–30 m from those established for the population study.

Adults were distinguished from juveniles by a thickened, folded shell overture associated with a thick shell (L.R.L. Simone, pers. comm.). The specimens were collected and fixed in 70% ethanol, and were dissected in the laboratory to determine their sex (males have a penis behind the right tentacle) and whether females were mature or not (palial oviduct turgid or wilted).

Shell length was measured with a digital caliper (SYLVAC, Fowler model, 0.01 mm precision) to characterize young and adult size ranges. Proportions of juveniles to adults, males to females, and immature to mature females over the study period were compared, in order to detect reproductive peaks.

Results

Monthly precipitation in Serra de Motas District is shown in Figure 4. The study period corresponded with a typical year, with wetter months in summer (November–March), but without an accentuated dry season. Measurements of pH, dissolved oxygen, temperature and conductivity in the studied localities are in Figure 5. As expected, annual fluctuations were more accentuated in the epigean sites, especially for temperature and dissolved oxygen.

Mean population densities recorded along the study period in the four studied localities are presented in Table 1. The highest densities (up to 280 ind.m^{-2}, in average) were shown by *P. ribeirensis*, and the lowest (2–10 ind.m^{-2}) by the epigean *Potamolithus* sp. 1 from Betari river. The average population density of *P. ribeirensis* was significantly higher than that of the troglobitic species, *P. troglobius* and *Potamolithus* sp. 2 (T = 88.50; $p = 0.014$ and T = 65.00; $p = 0.028$, respectively). On the other hand, that of *Potamolithus* sp. 1 was significantly lower than the observed for the two cave species (T = 76.00; $p = 0.001$ and T = 144.00; $p < 0.001$, respectively). Thus, density of the cave species was intermediate between the two epigean spe-
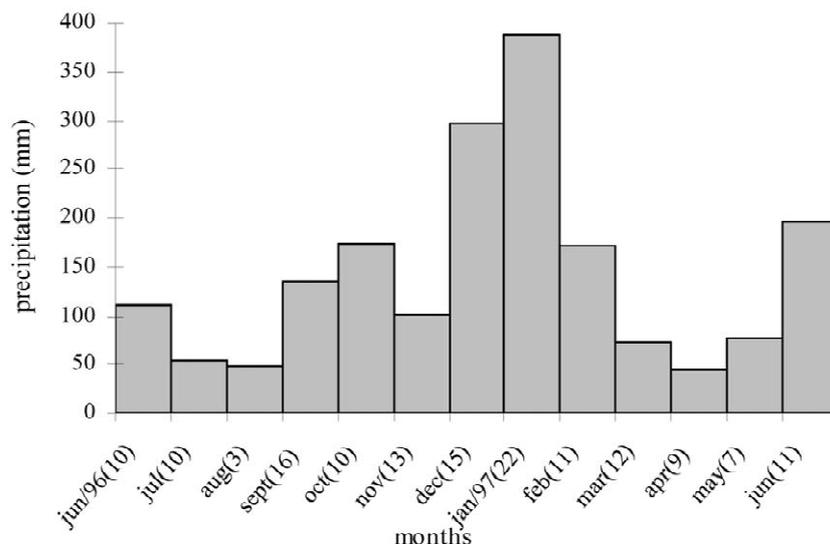
Figure 4. Monthly total precipitation between June 1996 and June 1997 in Iporanga County, São Paulo State, Brazil. In parenthesis, number of days with rainfall in every month.

cies, and similar to each other (30–40 individuals.m^{-2}, an average).

The high standard-deviation and coefficient of variation may due to heterogeneity between collecting sites (e.g., water flow, depth, and proximity of the cave sites to the epigean environment). For instance, the population densities of both *P. troglobius* and *Potamolithus* sp. 2 varied significantly among sites, increasing with distance from the stream resurgence ($r_s = 0.655$, and $r_s = 0.494$, respectively).

No significant differences in population density of *P. troglobius* were found among months (H = 12.764; $p = 0.237$), indicating that this cave population remained relatively stable. The isolated density peak observed in August 1996 may be a sampling artifact. The sharp decline observed in February was clearly a consequence of the flash floods of January. In spite of floods also in April, the studied *P. troglobius* population quickly recovered from March on, regaining its previous densities in June.

Some variation in population density during the study period was observed for *Potamolithus* sp. 2, from Alambari de Cima Cave, without seasonal correlation: higher values were observed in November 1996 and lower values (less than half the maximum ones) in June 1996 and March 1997 (Table 1). As in *P. troglobius*, such differences were not statistically significant (H = 3.503; $p = 0.899$).

Fluctuations statistically significant in density were observed for both epigean populations. After the floods of January, these gastropods completely disappeared, with a re-establishment beginning in March 1997 (Table 1). Differences among monthly densities were significant (H = 26.307; $p = 0.003$), but no correlation was found with temperature ($r_s = 0.0636$; $p = 0.839$). Interestingly, an opposite tendency was observed in the other epigean species, *Potamolithus* sp. 1, from Betari river, which presented by far the lowest densities among the four studied populations: the highest values (5–9 ind.m^{-2}) were observed during cool months (May–June), and the lowest (around 2 ind.m^{-2}), in warm months (October–December). Such differences were significant (H = 22.805; $p = 0.011$), but again no correlation with temperature was found ($r_s = -0.159$; $p = 0.631$).

Reproduction

Females were more frequent than males, reaching percentages higher than 80% on some occasions (see Fig. 6). No seasonal pattern was clear for any of the studied populations.

Mature females were found in almost every month, indicating extended reproductive activity, with peaks in the cool, 'dry' period (June–July) – Figure 7. *Potamolithus* sp. 1 was the only species exhibiting a clear seasonal cycle, with a well-defined reproductive period in the cool season (see Fig. 7A). The absence of mature females in October may be an artifact of our small sample sizes. This pattern may not apply
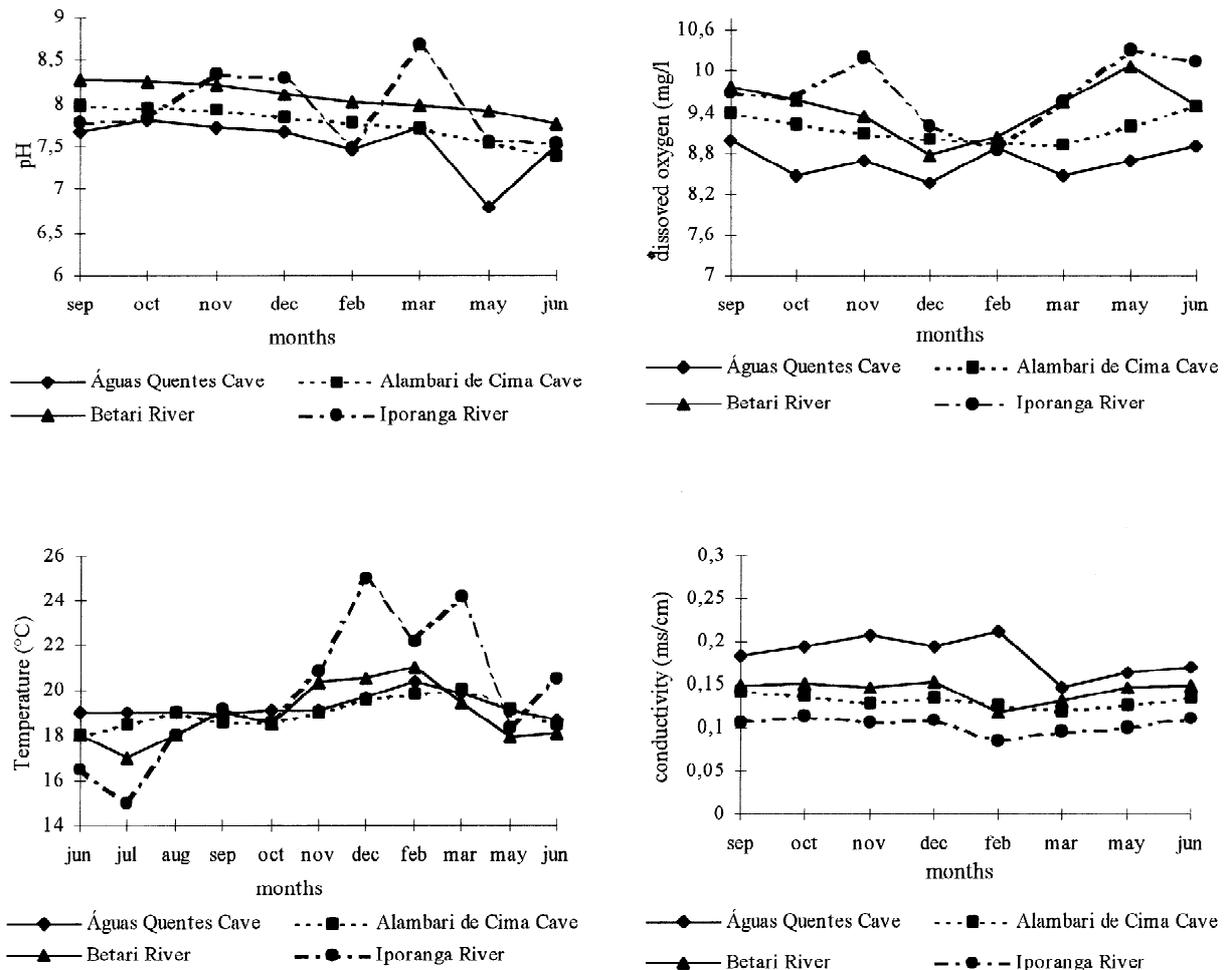
Figure 5. Chemical and physical water variables from the studied localites between June 1996 and June 1997.

to the epigean *P. ribeirensis*, from the Iporanga river basin, since the occurrence of a reproductive peak in June, as observed in 1996, could not be confirmed in 1997 (see Fig. 7B). However, the increase in the proportion of juveniles observed in July–September 1996 (see below) suggests an increased reproductive activity in the preceding months. It is possible that the disturbance caused by the floods of January affected the reproductive cycle during 1997. A second, conspicuous reproductive peak was observed during the warm, rainy period (October–March). Accordingly, in October–November 1997 eggs were found on the walls of an aquarium where *P. ribeirensis* specimens were kept.

A second reproductive peak, suggestive of bimodal activity, was observed for *P. troglobius* at the transition between cool and warm season (September–

November, see Fig. 7C). In September, three pairs of *P. troglobius* gastropods were observed copulating in Águas Quentes Cave (study site 2). On the other hand, *Potamolithus* sp. 2 seems to present an extended reproductive period, with some decrease in activity (which never ceases completely) between September and November (see Fig. 7D). Therefore, no common pattern was found, neither for the troglobitic populations, nor for the epigean ones.

The proportion of juveniles in *P. ribeirensis* increased just after (one to three months later) the reproductive peaks indicated by the increased proportions of mature females (see Fig. 7B). Such an expected relationship was not observed for *Potamolithus* sp. 1. For instance, the highest proportion of juveniles (100%, in November) fell after the occasion in which no mature female was recorded. Likewise, few ju-

Table 1. Monthly average population densities (number of individuals.m^{-2}) registered for Águas Quentes and Alambari de Cima Caves, and for Betari and Iporanga rivers, between June 1996 and June 1997. x = average; s = standard-deviation; CV = coefficient of variation, – no collected data

Months	Águas Quentes Cave (*P. troglobius*)	Alambari de Cima Cave (*Potamolithus* sp. 2)	Iporanga river (*P. ribeirensis*)	Betari river (*Potamolithus* sp. 1)			
	$x \pm s$	CV (%)	$x \pm s$	CV (%)	$x \pm s$	CV (%)	$x \pm s$	CV (%)
June 1996	38.8±24.7	63.6	26.2±15.8	60.4	56.3±64.1	114.0	9.3±5.2	56.1
July	37.5±22.1	59.0	38.8±36.5	94.0	62.5±27.5	44.0	2.3±2.6	116.9
August	61.5±62.3	101.3	40.8±46.3	113.4	73.5±52.3	71.2	2.5±3.7	147.9
September	42.5±27.6	64.9	37.4±32.0	85.7	110.5±55.4	50.1	3.5±3.1	88.8
October	40.0±27.4	79.2	35.2±35.4	79.2	228.3±141.5	62.0	1.8±1.5	85.7
November	41.0±13.8	33.7	58.4±65.5	112.1	276.3±154.7	56.0	3.8±2.2	59.1
December	37.0±12.7	34.3	35.2±35.4	100.5	284.8±164.4	57.7	1.8±1.7	97.6
February 1997	0	0	–	–	0	0	0	0
March	26.5±11.1	41.5	17.6±19.5	110.6	16.0±17.2	109.9	0	0
May	34.8±20.9	60.2	–	–	80.3±58.7	73.1	5.5±2.1	38.6
June	38.0±11.9	31.4	41.2±43.7	106.0	48.0±27.5	57.3	5.0±2.8	56.6
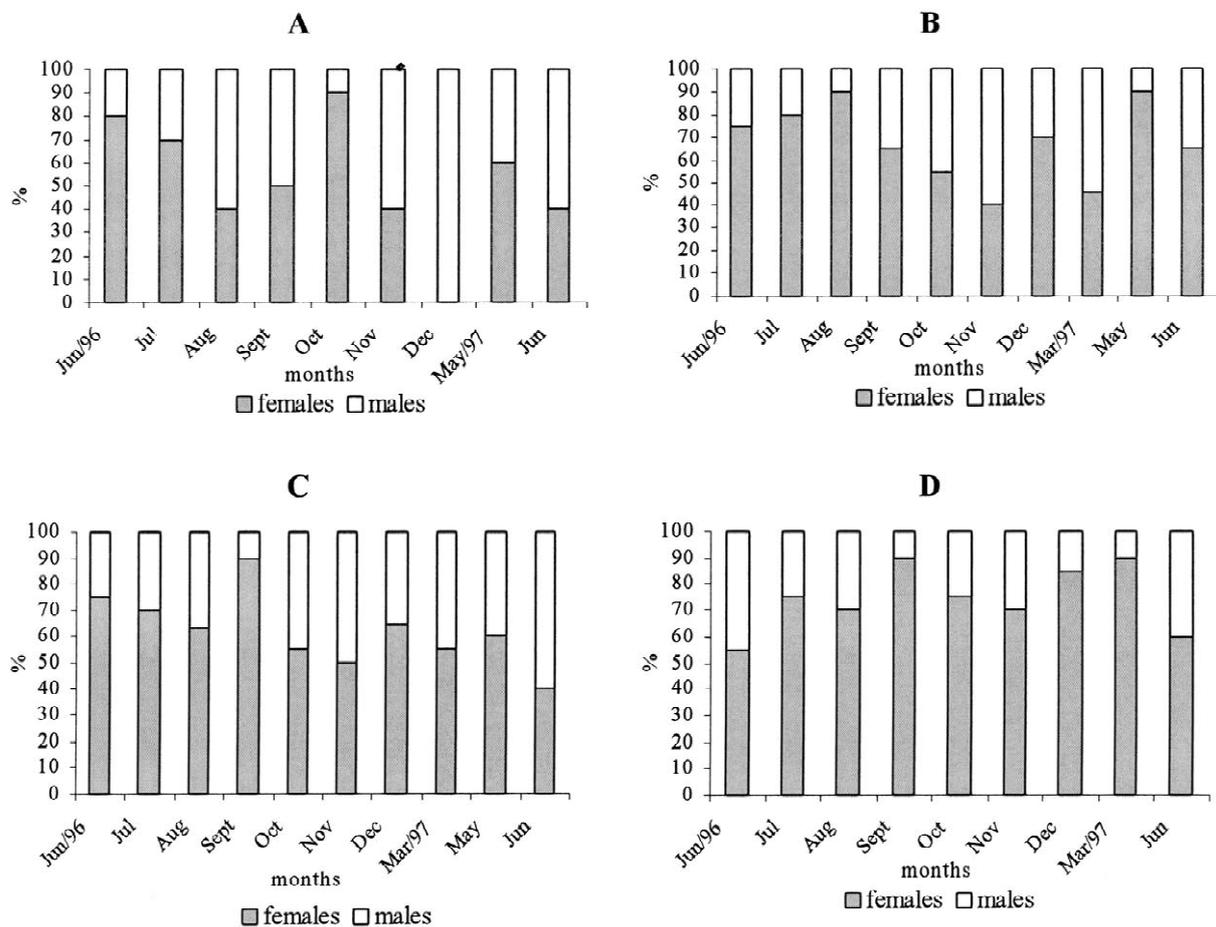
Figure 6. Percentages of females and males for two epigean (*Potamolithus* sp. 1 and *P. ribeirensis* – A and B) and two troglobitic (*P. troglobius* and *Potamolithus* sp. 2 – C and D) populations of Hydrobiidae snails.
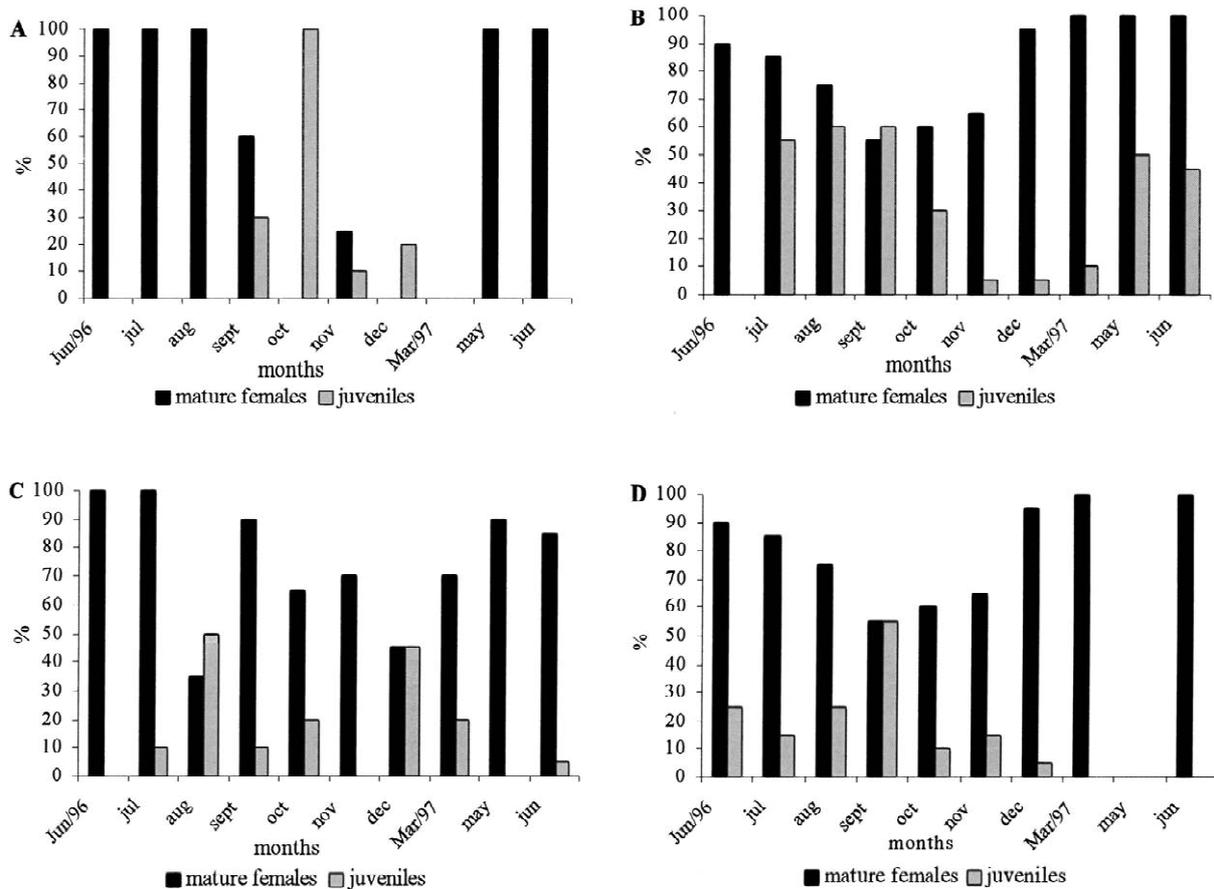
Figure 7. Percentages of mature females and juveniles for two epigean (*Potamolithus* sp. 1 and *P. ribeirensis* – A and B) and two troglobitic (*P. troglobius* and *Potamolithus* sp. 2 – C and D) populations of Hydrobiidae snails.

veniles were found during the cool, 'dry' months, a period of increased reproductive activity as indicated by the high proportion of mature females. We have no explanation for this other than sampling artifacts.

In general, few juveniles were found (see Fig. 7), probably because of their small sizes. The high proportions of *P. troglobius* juveniles in August and in December were expected, in view of the reproductive peaks of May–July and September–November (see Fig. 7C). Likewise, the increase in *Potamolithus* sp. 2 juveniles in September corresponds to the end of the major reproductive period in this population (see Fig. 7D).

Discussion

The values presently recorded in Águas Quentes and Alambari de Cima Caves (temperatures between 18.0

and 20.0 °C, pH between 7.88 and 8.16) are within the range reported for the area (e.g., Trajano, 1991; Karmann, 1994), and the pH values correspond to the expected for subterranean streams crossing limestone terrains (Culver, 1982). High, similar concentrations of dissolved oxygen were measured in both epigean and cave localities, corresponding to well-oxygenated headwater streams.

Population densities of cave species are frequently small (e.g., Poulson, 1964; Culver, 1982). However, this is not always the case, as shown for hypogean fish (Trajano, 1997a, 2001), amphipods (Knapp & Fong, 1999) and decapod crustaceans (Hobbs III, 1977, 1978, 1981; Moracchioli, 1994). Population densities of troglobitic *Potamolithus* may be considered high when compared to the epigean relative living in the same stream basin. On the other hand, in view of the limited extension of subterranean stream habitats, the total population sizes of troglobitic species of *Potamo-*

lithus are probably small compared to those of epigean species, distributed along longer stream reaches. In fact, morphological differentiation of cave populations suggestive of separate species status (12 populations, probably different species, have been reported for the Betari river basin – Bichuette, 1998) indicate that these gastropods have a limited capacity of dispersion, and are mostly restricted to separate microbasins or cave systems.

Potamolithus, reaching a maximum of 467 ind.m^{-2} in *P. ribeirensis*, are much below comparing with those of hydrobioids from temperate regions: up to 3200 ind.m^{-2} in *Bithynia tentaculata* (Fretter & Graham, 1962), 8000 ind.m^{-2} in *Hydrobia ulvae* (Sola, 1996), and 19 000 ind.m^{-2} in *Hydrobia totteni* (Wells, 1978). However, these studies were carried out in swampy areas or estuaries, and their higher food availability could explain such differences. Unfortunately, there are no comparative data for species living in habitats similar to those occupied by *Potamolithus*, e.g., headwater streams.

Temporal fluctuations in population densities of epigean hydrobiids may be an indirect consequence of fluctuations in water temperature, which varied seasonally between 17.0 and 21.0 °C in the Betari river and 15.0 and 25.0 °C in the Iporanga river. Although no direct correlation was found between water temperatures and population densities, increasing temperatures from October to December could have resulted in increased primary productivity and, consequently, in progressively higher food availability for gastropods (periphyton, detritus).

Increasing density of troglobitic *Potamolithus* with distance, relative to stream resurgence is related to the *status* of troglobite (organisms restrict to the subterraneam environment) of these gastropods snails.

The small size of *Potamolithus* species from the Betari river basin may be a preadaptation favoring colonization of the food-poor cave environment, and explaining the wide distribution of these gastropods in the Upper Ribeira caves. Studying cave bivalves, Hayami & Kase (1996) discuss that most species are small (less than 6 mm in adult size) and could result from two different processes: the invasion of subterranean environment by species belonging to clades characterized by small body size or as a result of adaptation to a sheltered and small spaces.

Some authors state that, in the absence of photoperiods, environmental factors such as pH, temperature and precipitation, have a major influence on reproduction of subterranean organisms. During the rainy period, large amounts of organic matter may be carried into caves, preparing the animals for reproduction. This is known as the flood-factor (Hawes, 1939; Poulson, 1964; Husson, 1971). Consequently, aquatic cave organisms living in karst areas subject to pronounced seasonality present well-defined reproductive peaks, generally at the transition between the rainy and the dry periods, as observed in Brazilian troglobitic catfishes (Trajano, 1997b). On the other hand, no evidence of reproductive seasonality was found for the blind catfish, *Pimelodella kronei*, also found in the Betari river basin, syntopic with *P. troglobius* in the Areias cave system.

Maturation of gametes in freshwater prosobranchs is directly influenced by food availability (Boolootian et al., 1962). In temperate zones, seasonal temperature fluctuations could be controlling gametogenesis. In warmer regions, these temperature fluctuations are not so critical (Fretter, 1984). As proposed for *P. kronei*, the occurrence of an extended reproductive period in the studied species of *Potamolithus*, with mature females found across the year, is probably related to the absence of a well-defined dry period, with some rain in each month. Therefore, fluctuations in food availability are not accentuated. However, reproductive peaks were observed in some cave organisms, for instance, Moracchioli (1994) registered a reproductive peak in cooler and less rainy months in the crustacean decapod *Aegla* population from Upper Ribeira valley, southeast Brazil.

Conclusion

We conclude that the population densities recorded for the troglobitic species of *Potamolithus* can be considerable. In relation to reproduction, both troglobitic species of *Potamolithus* were non-seasonal. In the epigean species, an apparent seasonality was registered but no reproductive pattern was detected.

Acknowledgements

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