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RESEARCH ARTICLE

Phenology of *Promestosoma boggianii* (Diplopoda: Polydesmida: Paradoxosomatidae) in a Neotropical floodplain

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ABSTRACT. Studies that address biodiversity and its supporting mechanisms in different ecosystems are fundamental to understanding the relationships between species and the prevailing environmental conditions within each habitat type. This study presents information on the phenology of *Promestosoma boggianii* (Silvestri, 1898) and its association with seasonal flood and dry events in a floodplain of Mato Grosso's northern Pantanal region, Brazil. Sampling was carried out in three areas located between the Bento Gomes and Cuiabá rivers, on the Porto Cercado Road, Poconé-MT. Each sample area was composed of two treatments: (I) floodable habitats and (NI) non-floodable habitats. Three quadrats (10 x 10 m) were established within each treatment, with sampling carried out using pitfall traps and mini-Winkler extractors during the dry season, rising water, high water and receding water phases for the duration of two hydrological cycles within the Pantanal (2010/2011 and 2011/2012). A total of 295 *P. boggianii* individuals were sampled at different stages of development (except stages I and II), distributed between the rising water (209 ind., 70.8%), dry (76 ind., 25.8%) and receding water (10 ind., 3.4%) seasons. No specimens were sampled during the high water season. The higher abundances recorded between the dry and rising water seasons, primarily at early stages of development, indicate that *P. boggianii* is characterized as a univoltine species in these habitats. The data demonstrate that individuals of *P. boggianii* were more abundant in floodable habitats. In addition, the results show that the life cycle of this diplopod is sinchronized to the seasonal nature of this floodable environment, as a strategy to survive the extreme conditions of terrestrial and aquatic phases Brazil's northern Pantanal region.

KEY WORDS. Biodiversity, conservation, Myriapoda, wetlands.

INTRODUCTION

Diplopoda constitute an important part of soil and detritus macrofauna in most terrestrial biomes, particularly in tropical and subtropical regions (Adis 2002a, Battirola et al. 2011, Minelli and Golovatch 2013), due to their biomass, abundance and diversity, both in natural and altered environments (Tapia-Coral et al. 1999), where they act in the reduction and fragmentation of detritus and the formation of organic soil (Hoffman et al. 2002). It is estimated that there are up to 80,000 species of these myriapods worldwide, constituting one of the largest classes of terrestrial arthropods, of which only about 12% have been described (Golovatch et al. 1995, Adis and Harvey 2000, Hoffman et al. 2002, Sierwald and Bond 2007).

Among the diplopods, the order Polydesmida, which includes *Promestosoma boggianii* (Silvestri, 1898) (Paradoxosomatidae), is represented by 5,156 described species, 1,437 genera and 30 families, and is considered the largest order of Diplopoda in terms of specific and generic diversity (Enghoff et al. 1993, Hoffman et al. 2002, Shelley 2003, Sierwald and Bond 2007). The size of adult polydesmidans varies between 2 to 130 mm. Individuals from diverse families possess a large variety of colors and shapes, and mostly inhabit the soil surface and detritus, with few strictly arboreal or cavernicolous species (Hoffman et al. 2002). Most have a short life cycle that is completed within one year (Hoffman et al. 2002). Adults of most species construct nests for the protection of eggs, primarily against variations in humidity and temperature (e.g. Pinheiro et al. 2009, Youngsteadt 2009).

In many of the tropical polydesmidan species, each body segment may be ornamented with upright or prominent spines, often with adhered detritus (Hoffman et al. 2002). Based on the number of these body segments it is possible to determine the post-embryonic development stage of the species (Blower 1985). This is considered an important characteristic as there is little to no variation in the development patterns of these taxa (Enghoff et al. 1993), thus allowing aspects of their phenology to be evaluated (David et al. 2003, Pinheiro et al. 2009, Youngsteadt 2009, David and Coulis 2015).

Phenology is the study of the temporal aspects of recurrent natural phenomena and their relation to weather and climate (Lincoln et al. 1983), including distribution of developmental phases throughout the life cycle of a species. These studies allow us to understand the development and reproduction of most terrestrial arthropods, as the cycle is closely adjusted to seasonal changes, with development and reproduction limited to specific periods of the year (David et al. 2003). Diplopoda are generally very sensitive to environmental changes and, in areas prone to seasonal flooding, develop specific survival strategies to tolerate oscillations in the seasonal hydrological regime (Adis 1986, Adis and Ribeiro 1989, Adis 1997, Adis et al. 2001, Battirola et al. 2009, Wantzen et al. 2016).

In the Brazilian Pantanal specific strategies and adaptations to the seasonal hydrological cycle were identified in *Plusioporus salvadorii* Silvestri, 1895 (Spirostreptidae), a terrestrial species that migrates to tree trunks during floods, where it remains until the end of the flood (Adis et al. 2001). *Poratia salvator* Golovatch & Sierwald, 2000 (Pyrgodesmidae) synchronizes its life cycle and phenology to the region's flood cycles (Pinheiro et al. 2009, 2011, Wantzen et al. 2016). Polyxenida also show a pattern of distribution between the soil and crowns of trees in the same region, influenced by the seasonal variation of environmental conditions, especially periodic flooding (Battirola et al. 2009).

Promestosoma boggianii is the sole species of its own genus, which seems to be restricted to the Pantanal region at least within Brazil and Paraguay (Silvestri 1898, Golovatch et al. 2005, Battirola et al. 2009, Nguyen and Sierwald 2013). However, little is known about its distribution, biology and ecology. Considering the importance in understanding the adaptations and phenology of the species, especially in wetlands such as the Pantanal of Mato Grosso, Brazil, this study analyzes aspects of *P. boggianii*'s phenology and its association with the seasonal flood and terrestrial phase events typical of the region, determining its seasonal distribution and periods of reproduction.

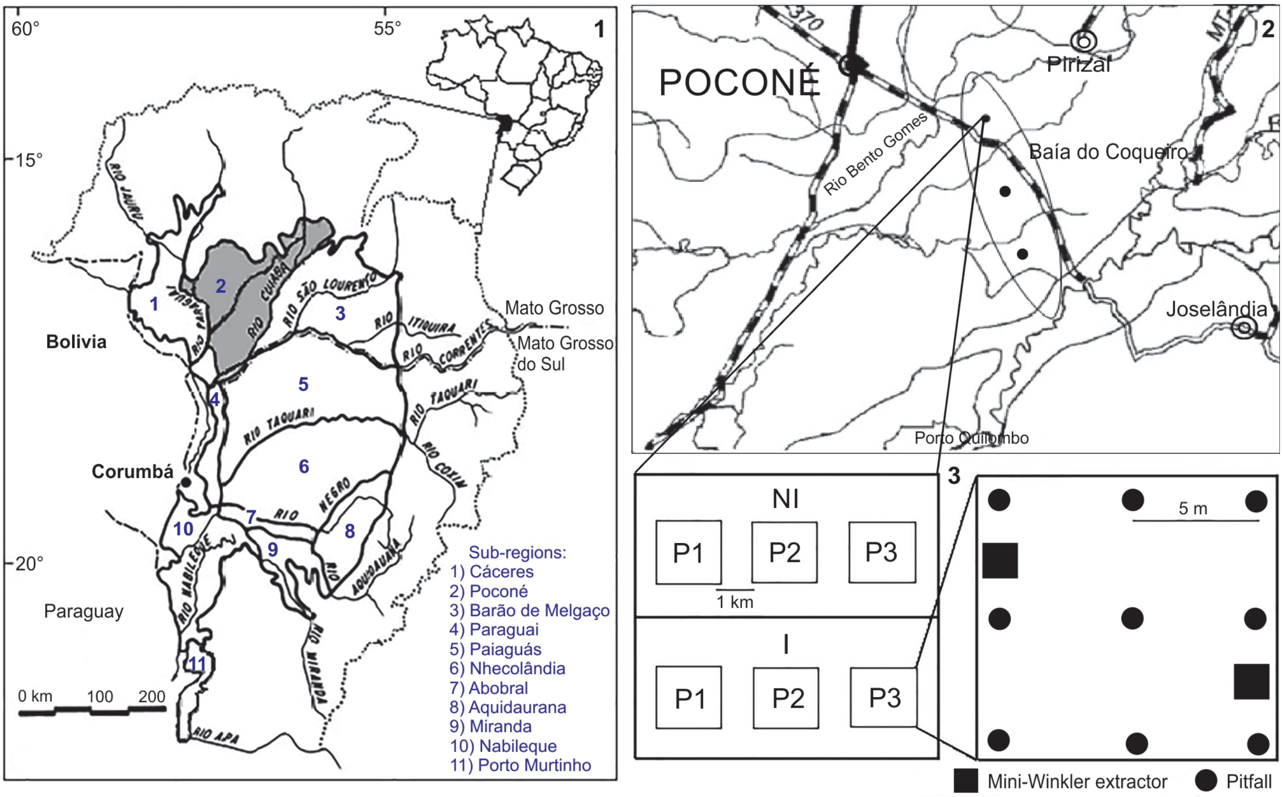
MATERIAL AND METHODS

Sampling was carried out in areas located along the Porto Cercado road, a floodplain area between the Bento Gomes and Cuiabá rivers, at the Advanced Pantanal Research Base (Base Avançada de Pesquisas do Pantanal – BAPP) of the Federal University of Mato Grosso (Universidade Federal de Mato Grosso – UFMT) at SESC Pantanal, Poconé, Mato Grosso, Brazil (16°20'56"S, 56°29'69"W and 16°29'82"S, 56°23'95"W) (Figs 1–3). The local climate is tropical savannah, characterized by dry winters and rainy summers, with a mean monthly daily temperature between 22 and 32 °C (Hasenack et al. 2003). It is described as type AW under the Köppen classification system. Annual rainfall varies between 1,000 and 1,500 mm, with rainfall below 10 mm during dry seasons. Sampling occurred throughout the four seasonal periods typical of the region (dry season, rising water, high water and receding water) during two annual cycles (2010/2011 and 2011/2012), characterized according to Heckman (1998).

Three sampling areas were established within the region (A1, A2, A3) which were considered as independent replicates (N = 3). The three areas were distributed along three altitudinal and inundation gradients. The A1 area represented a higher elevation with low flood amplitude (mean amplitude = 0.1 m), situated closer to the Bento Gomes river; A2 was located in a median section of the gradient, with intermediate elevation and flood amplitude (mean amplitude = 0.25 m); and A3 was located near the Cuiabá River, constituting the lowest area of the gradient and therefore susceptible to a greater flood amplitude (mean amplitude = 0.5 m) (Figs 1–3).

All sample areas were composed of two specific treatments: floodable habitats (I) and non-floodable habitats (NI). Three quadrats (10 x 10 m) were established within each habitat, considered sample points (P1, P2 and P3). At each sampling point, nine pitfall traps were distributed five meters apart. Twenty-seven pitfall traps per habitat were used, 54 per area, totaling 162 traps sampled in the terrestrial, rising water and receding water seasonal periods (Figs 1–3). Sampling in floodable habitats (I) during the high water period was not considered possible due to the depth of floodwaters, therefore only non-floodable habitats (NI) were sampled during the high water period, totaling 27 pitfall traps per habitat area and 81 traps in the high water period.

Mini-Winkler extractors (Bestelmeyer et al. 2000) were used to sample 2 m^2 areas of leaf-litter and surface soil complementary to all floodable (I) and non-floodable (NI) habitats. Six samples of leaf-litter and surface soil per habitat were collected, 12 m^2 per area, 36 m^2 in each seasonal period of dry, rising water and receding water. Due to the inability of sampling in floodable habitats (I) during the high water phase as a result of floodwater depth, only non-flooded habitats (NI) were sampled, totaling 6 m^2 of leaf-litter and surface soil per habitat and area, and 18 m^2 of leaf-litter during the high water period.



Figures 1–3. (1) The Pantanal and its 11 sub-regions, with emphasis on the Pantanal of Poconé, Mato Grosso, Brazil. (2) Study area with the location of the three sample units (A1, A2 and A3), along the Porto Cercado Road, between the Bento Gomes and Cuiabá rivers, within the floodplain of the Poconé Pantanal, Mato Grosso. (3) Illustration indicating the floodable (I) and non-floodable (NI) habitats, with the three quadrats (P1, P2, P3) and layouts for the pitfall traps and mini-Winkler extractors. (Source: Silva et al. 2000, Meurer 2015, modified).

Pitfall traps consisted of a 20 cm long polyethylene vial with a 5–6 cm diameter opening containing 250 ml of 4% formalin solution with plastic protective covers (20 × 20 cm) (Adis 2002b). All traps were buried at ground level to intercept moving arthropods and remained functioning in the field for seven days. Pitfall samples were taken to the laboratory where sample material was withdrawn from the formalin solution, sorted and stored in vials containing 70% ethanol. Samples from the mini-Winkler extractors were taken to the laboratory, where they remained suspended for 72 hours in an air-conditioned environment for desiccation before subsequently ‘dropping’ into collection flasks containing 70% ethanol. Samples from both the pitfall traps and mini-Winkler extractors were consolidated for analysis.

Individuals of *P. boggianii* were quantified, sexed and the number of body segments evaluated to determine the stage of development. All material was deposited in the Acervo Biológico da Amazônia Meridional – ABAM, at the Instituto de Ciências Naturais, Humanas e Sociais, Universidade Federal de Mato Grosso, Sinop-MT University campus.

Each study area possesses different vegetation formations based on their respective locations along the inundation gradient. The A1 area is characterized by non-floodable cordilheira (hilly/mountainous formations with dense arboreal savanna) (Silva et al. 2000, Nunes-da-Cunha et al. 2007, Fantin-Cruz et al. 2010), while fields of murundus (mounds of land constructed by termites which project above the floodline) predominate the sampling points within the floodplain areas of A1. There is also established cerrado (savanna) woodland vegetation present in areas not susceptible to inundation (Oliveira-Filho 1992, Nunes-da-Cunha et al. 2007, De Morais et al. 2013).

The A2 area consists of monodominant *Callisthene fasciculata* (Spr.) Mart. (Vochysiaceae) (carvoal) forest with soil sparsely covered by grass and herbaceous vegetation, and dense banks of *Bromelia balansae* Mez. and *Ananas ananassoides* (Baker) L.B. SM. (Bromeliaceae) (Nunes-da-Cunha et al. 2007). The sampling points within the floodable areas (field limpo) consist primarily of the grasses *Axonopus purpusii* (Mez.) Chase and *Reimarochloa brasilienses* (Spreng.) (Poaceae), which are recognized for their high palatability and nutritional value to livestock (Santos et al. 2012, Nunes-da-Cunha and Junk 2015).

At the non-floodable sampling points of the A3 area we observed densities of *Attalea phalerata* Mart. (Arecaceae) (acurizal) (Santos et al. 2003, Nunes-da-Cunha et al. 2007), and mixed formations of evergreen flooded forests (landizal and cerradão) at the floodable habitat sampling points (Silva et al. 2000, Nunes-da-Cunha et al. 2007, Fantin-Cruz et al. 2010).

Descriptive analysis was used to evaluate the abundance distribution of *P. boggianii* development stages across the seasonal periods, with the two annual hydrological cycles used as a single data block. The differences in *P. boggianii* abundance between sample areas (A1, A2, A3), floodable (I) and non-floodable (NI) habitats, were assessed using a Generalized Linear Model (GLM) with a Negative Binomial distribution (based on the Aikake and Bayesian evaluation criteria). In all analyses the adopted significance level was 0.05, calculated using the R 3.3.2 (R Development Core Team 2016) and VEGAN software packages (Oksanen et al. 2016).

RESULTS

A total of 295 *P. boggianii* individuals were sampled, the majority of which were captured with pitfall traps (188 ind., 63.7%), and the remaining captured with mini-Winkler extractors (107 ind., 36.3%). Female specimens (214 ind., 72.5%) predominated over males (81 ind., 27.5%). Samples taken during the rising water phase (209 ind., 70.8%) were more abundant than those taken during the dry (76 ind., 25.8%) and receding water (10 ind., 3.4%) phases. No individuals were captured during the high water phase (Fig. 4). Abundance distribution varied significantly between the three sample areas (GLM, $Z = 5.94$, $p < 0.001$), with the A2 area the most abundant (226 ind., 76.6%), followed by A3 (65 ind., 22%) and Al (4 ind., 1.4%). There was no significant variation in abundance of individuals (GLM, $Z = 1.16$, $p = 0.2$) between floodable (182 ind., 61.7%) and non-floodable (113 ind., 38.3%) habitats.

Different post-embryonic stages of *P. boggianii* were captured throughout the study, with the exception of individuals from development stages I and II. Variations were observed in the abundance of individuals at different stages within each seasonal period (Fig. 4). During the dry season, 65 individuals (85.5%) were adults. Immature specimens were largely represented by individuals in stages VII (9 ind., 11.8%) and VI (2 ind., 2.6%). Following the dry season, adult individuals continued to predominate the rising water phase (116 ind., 55.5%), followed by stage V (50 ind., 23.9%), IV (25 ind., 12.0%), III (16 ind., 7.7%) and VI (2 ind., 1.0%) individuals. Following the rising water phase, no *P. boggianii* individuals were captured during high water, while in the receding water phase after the inundation period, few specimens were sampled, with one adult (1 ind., 10.0%), and a total of 9 juveniles at stages VI (5 ind., 50.0%) and VII (4 ind., 40.0%). The higher abundances recorded between the terrestrial and rising water periods, markedly for early stages of development (from stage 3), indicates that *P. boggianii* is characterized as a univoltine species in these habitats.

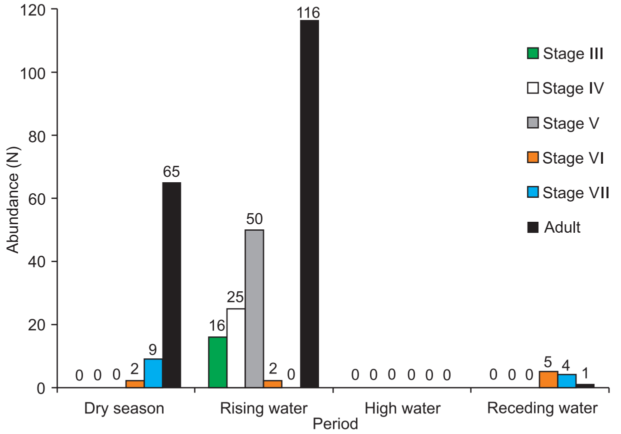


Figure 4. Distribution of *Promestosoma boggianii* according to stages of development (juvenile stages III, IV, V, VI, VII and adult) throughout the seasonal periods (dry season, rising water, high water and receding water) in a floodplain of Mato Grosso's northern Pantanal region, Brazil.

Despite the variation between distinct vegetation formations of the three sampled areas (A1, A2 and A3), we observed that the occurrence of *P. boggianii* predominated at sites characterized as limpo fields (grasslands with small shrubs, 147 ind., 49.8%), followed by areas of carvoal (79 ind., 26.8%) and acurizal (33 ind., 11.2%). The cerradão (23 ind., 7.8%), landizal (9 ind., 3.1%), murundu fields (3 ind., 1.0%) and cordilheira vegetative formations (1 ind., 0.3%) showed lower occurrences of this species.

DISCUSSION

Within the Pantanal's northern floodplain region, the polydesmidan *P. boggianii* presents a heterogeneous pattern of distribution throughout the different seasonal periods, both in relation to abundance and developmental stage. These results infer that this species employs univoltine behavior within this region, with peak reproductive activity occurring during the dry and rising water seasons, evidenced by the high number of individuals in early juvenile (from stage III) and adult stages, as sampled in the periods preceding the region's seasonal flood.

The higher occurrence of *P. boggianii* during the dry (25.8%) and rising water (70.8%) phases within this region reveals univoltine characteristics of this species, and shows that environmental conditions during these periods of transition between the dry and rainy season are considered more propitious to the development of soil fauna (e.g. Battirola et al. 2010, Marques et al. 2011, Aranda 2013). At the onset of sampling in 2010, the terrestrial phase was atypical in the region, with a higher rainfall index than that of previous years at 6.72 mm, guaranteeing greater soil moisture, which could explain the higher occurrence of individuals sampled during the rising water phase.

Battirola et al. (2009) assessed the temporal distribution of diplopods in a monodominant *Vochysia divergens* Pohl. (Vochysiaceae) forest within the same region of the Pantanal, and similar to the results observed in this study, found considerable increases in abundance of *P. boggianii* and other diplopod species at the beginning of the rainy season, which comprises the end of the dry phase and the beginning of the rising water phase. These results confirm diplopod preference for more humid environments or for periods of the year with higher humidity (Hoffman et al. 2002, Battirola et al. 2009, Pinheiro et al. 2009, 2011), as these conditions favor the reproduction, development and survival of immature individuals which are known to be fragile and susceptible to desiccation (Enghoff et al. 1993, David and Vannier 2001, Pinheiro et al. 2009).

The high water phase can be seen as the least favorable period in the development of organisms which inhabit the soil due to the intense stress caused by sustained inundation (Adis 1997). This is shown for *P. boggianii* in this study, as no individuals were sampled within this period during two annual cycles. Seasonal flooding is responsible for high mortality rates of edaphic organisms, considering the rapid increase in water levels caused by rain and overflowing rivers, as well as the short amount of time available for escape (Adis 1997, Adis and Junk 2002). Diplopods in particular suffer from the impacts of rapid flooding due to their small body size, fragile exoskeletons in juvenile forms, and low mobility (e.g. Enghoff et al. 1993, David and Vannier 2001, Pinheiro et al. 2009). The few individuals sampled during the receding water phase were most likely remnants of the previous year's generation that were able to survive the inundation in non-flooded habitats.

The intensity and duration of seasonal flooding influences the phenology and behavior of species that inhabit the floodable areas, affecting many species to develop specific survival strategies as adaptations to the seasonal environmental conditions (Adis and Ribeiro 1989, Junk et al. 1989, Adis 1992, 1997, Adis et al. 2001, Hoffmam et al. 2002). The alternation between terrestrial and aquatic phases caused by floods is a determining factor in the area's ecological processes, influencing and selecting biota (Junk et al. 1989, 2006, Machado et al. 2012), with the flood pulse and variation in humidity being fundamental factors in the maintenance of the region's diversity (Silva et al. 2000, Rebellato and Nunes-Da-Cunha 2005).

Battirola et al. (2009) categorized *P. boggianii* as a species which migrates horizontally following the flood line, based on the specie's high activity rate upon the soil at the beginning of the rainy season. It is reasonable to infer that *P. boggianii* synchronizes its life cycle and phenology to the environmental conditions, as observed for other taxa in this region such as *Poratia salvator* and Polyxenida (Battirola et al. 2009, Pinheiro et al. 2009, 2011, Wantzen et al. 2016). In addition to the synchronization of the life cycle with flood oscillations, there are other known survival strategies for diplopods occurring within these environments, such as vertical migration recorded for *Plusioporus salvadorii* Silvestri, 1895 in the Pantanal of Mato Grosso (Adis et al. 2001), as well as *Epinannolene exilio* (Brölemann, 1904) (Pseudonannolenidae) and *Poratia insularis* (Kraus, 1960) (Pyrgodesmidae) (Golovatch et al. 1997, Bergholz et al. 2004) in central Amazonia. In some other diplopods such as *Myrmecodesmus adisi* (Hoffman, 1985) (Pyrgodesmidae), the juvenile stages show certain morphological adaptations to flooding (plastron respiration) to survive submerged for periods of several months (Adis 1986, Golovatch 1999, Adis et al. 2003).

In addition to morphological, physiological and phenological adaptations, diplopods can also show different occurrences between the habitats and microhabitats present within a region. The highest occurrence of this species was found in floodable habitats, as opposed to non-floodable habitats, and in the A2 (226 ind., 76.6%) and A3 (65 ind., 22%) areas in relation to area A1 (4 ind., 1.4%). Considering the location of the sample areas along the inundation gradient, floodable habitats and the higher flood amplitude of areas A2 and A3 influenced the distribution of *P. boggianii*, as these areas maintained humid environments for a sustained period of time throughout the year, contributing to the persistence of these individuals. In addition, *P. boggianii*'s adjustment of reproduction to appropriate conditions ensures the survival of offspring during extreme dry periods and flooding, as has been observed for other invertebrate species within the same region (Adis et al. 2001, Battirola et al. 2009, Marques et al. 2014, Wantzen et al. 2016).

In response to the seasonal factors and flood amplitude of the northern Pantanal region, *P. boggianii* seems to have successfully adapted to the environmental conditions through synchronization of its life cycle to the seasonal oscillations of the hydrological regime, moving to non-floodable habitats during periods of inundation and returning to floodable habitats after flood waters have retreated. The abundance distributions recorded between the dry and rising water periods, primarily for early stages of development, indicates that *P. boggianii* is characterized as a univoltine species in these habitats.

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