

Natural history, life history, and diet of *Priapella chamulae* Schartl, Meyer & Wilde 2006 (Teleostei: Poeciliidae)

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Abstract

We report on basic natural history, life history, and diet of *Priapella chamulae* (Poeciliidae) from Arroyo Tres, a small creek in Tabasco, southern México. The tertiary (adult) sex ratio was heavily female-skewed, female *P. chamulae* produced medium-sized offspring (~2.3 mg), one clutch at a time (i.e., showed no superfetation), and relied predominantly on yolk for embryo provisioning (Matrotrophy Index: 0.71). Furthermore, *P. chamulae* at Arroyo Tres had relatively short guts, were highly carnivorous, and preyed mainly on terrestrial arthropods (especially ants).

Zusammenfassung

Wir berichten über grundlegende Naturgeschichte, Nahrung und Lebenszyklusdaten von *Priapella chamulae* (Poeciliidae), die im Arroyo Tres, einem kleinen Bach in Tabasco in Süd Mexiko gefangen wurden. Das tertiäre (adulte) Geschlechterverhältnis war weibchenlastig, weibliche *P. chamulae* produzierten nur eine Brut zur Zeit (d.h., sie zeigten keine Superfetation), die Embryonen wurden während Ihrer Entwicklung überwiegend durch Dotter ernährt (Matrotrophieindex: 0.73) und die Nachkommen waren von mittlerer Größe (ca. 2.3 mg). Außerdem hatten *P. chamulae* im Arroyo Tres relativ kurze Därme, waren karnivor und erbeuteten bevorzugt terrestrische Arthropoden (insbesondere Ameisen).

Résumé

Nous abordons l'histoire naturelle de base, l'histoire de la vie et le régime alimentaire de *Priapella chamulae* (Poeciliidae) d'Arroyo Tres, un petit cours d'eau de Tabasco, Mexi-

que méridional. Le sex ratio tertiaire (adulte) était surtout constitué de femelles ; la femelle *P. chamulae* produisait une descendance de taille moyenne (~ 2.3 mg), une ponte à la fois (càd. ne montrant pas de superfétation) et consistant surtout en jaune d'oeuf pour l'alimentation des embryons (Matrotrophy index: 0,71). En outre, *P. chamulae* d'Arroyo Tres avait des intestins relativement courts, était essentiellement carnivore et prélevait surtout des arthropodes terrestres (principalement des fourmis).

Sommario

Riportiamo la storia naturale, il ciclo vitale e la dieta di *Priapella chamulae* (Poeciliidae) da Tres Arroyo, un piccolo torrente in Tabasco, nel sud del Messico. Il rapporto tra i sessi nella terza fase del ciclo vitale (adulto) era fortemente spostato verso la femmina, la femmina produceva prole di taglia media (~ 2.3 mg), una nidata alla volta (cioè senza alcuna produzione sovrapposta di embrioni), che si basava prevalentemente sul tuorlo per il nutrimento degli embrioni (Indice di matrotrofia: 0.71). Inoltre, *P. chamulae* a Tres Arroyo avevano un intestino relativamente breve, erano prettamente carnivori predando principalmente artropodi terrestri (soprattutto formiche).

INTRODUCTION

Life-history evolution has been an integral part of evolutionary research over the past few decades, and livebearing fishes (Poeciliidae) have proven to be excellent models for studying life history adaptations (e.g., Reznick & Miles 1989; Magurran

2005). Originally, the more than 200 species and 22-29 genera of poeciliids were endemic to the Americas, but due to human introductions they are now found worldwide (Lucinda 2003). Within the Poeciliidae, at least three characters evolved to give rise to the present diversity within the family: (1) internal fertilization using a transformed anal fin in males, the gonopodium, for sperm transfer, (2) livebearing, and (3) different degrees of maternal provisioning for the developing young (Constantz 1989; Reznick & Miles 1989). With the sole exception of *Tomeurus gracilis* Eigenmann, which is characterized by oviparous egg retention, internal fertilization and viviparity are found in all species of poeciliids (Rosen 1964). Furthermore, some poeciliids are able to accommodate several clutches simultaneously, so-called superfetation (e.g., Turner 1937; Thibault & Schulz 1978; Reznick & Miles 1989).

Priapella chamulae Schartl, Meyer & Wilde (2006), is a medium-sized livebearing fish inhabiting the waters of the Río Grijalva basin in Tabasco, México (Schartl et al. 2006). The genus *Priapella*

comprises at least six species (e.g., Miller 2005; Schartl et al. 2006; Meyer et al. 2011) and is considered the least derived (i.e., most basal) group within the tribe Gambusiini (Hrbek et al. 2007). The other genera in this tribe are *Scolichthys*, *Carlhubbsia*, *Xiphophorus*, *Heterandria*, *Belonesox*, *Heterophallus*, and *Gambusia* (Miller 2005; Hrbek et al. 2007). The natural history of the members of the genus *Priapella* and several other genera in this tribe remains largely unknown (see Miller 2005; Schartl et al. 2006; Meyer et al. 2011; Riesch et al. 2011a). However, to fully understand the evolution of reproductive strategies in livebearing fishes (e.g., Reznick & Miles 1989; Pires et al. 2011), it is of utmost importance to also collect data on smaller and lesser-known clades.

We report on basic natural history of *P. chamulae* as observed over the last five years while conducting fieldwork in Tabasco, southern México. We also report on life history and diet data derived from specimens collected in January 2010. Furthermore, we describe the fish species communities in the lotic environments they inhabit.

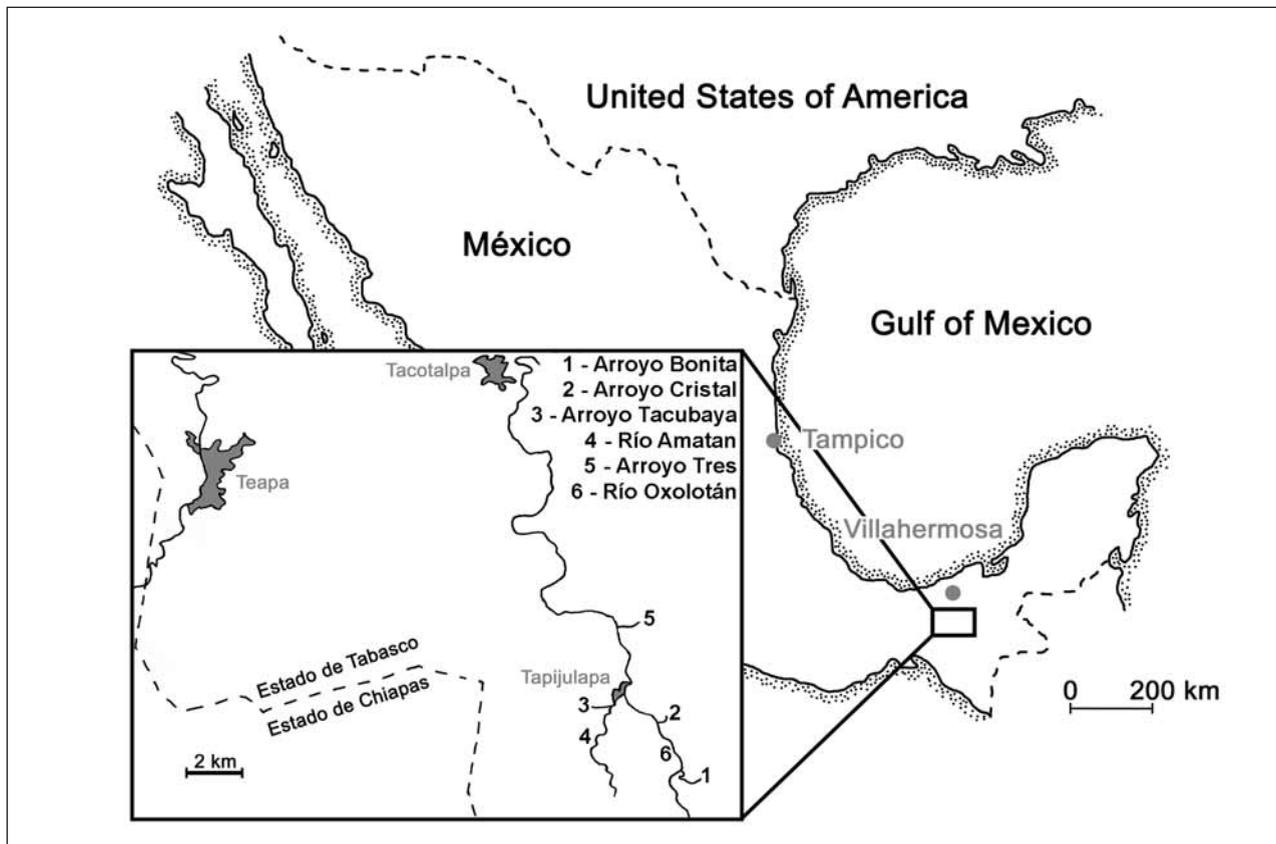


Fig. 1. Overview of the general study area in México with reference cities in gray (modified after Riesch et al. 2011a). Numbers indicate rivers and creeks; all *Priapella chamulae* analyzed in the present study were collected at Arroyo Tres (#5).

Table I. Raw values for male and mean±SD of female life history traits for reproductively active *Priapella chamulae* caught in Arroyo Tres (Tabasco, México) in January 2010. Values in parentheses provide minimum-maximum. GSI: gonadosomatic index; RA: reproductive allocation; MI: matrotrophy index.

	males	females
Sample size ^a	1/6	34/49
SL [mm]	28.4	30.30±4.20 (24-40)
Somatic dry mass [mg]	138	162.12±76.76 (72-386)
Fat content [%]	1.45	5.64±3.75 (0-14)
Fecundity	-	6.38±3.75 (2-16)
Estimated embryo dry mass at birth ^b [mg]	-	2.31
Embryo fat content [%]	-	16.92±3.91 (3-23)
GSI [%]	1.27	-
RA [%]	-	10.31±3.42 (4-23)
MI	-	0.71

^a the numerator corresponds to reproductively active males and females & the denominator equals the total number of collected and dissected males and females

^b estimated dry mass at birth is calculated using the slope and intercept from the regression between log-transformed embryonic dry mass and stage of development.

MATERIAL AND METHODS

Study population and sampling procedure: We conducted life-history dissections on a total of 55 *P. chamulae* (6 males and 49 females). All fish were collected in January 2010 in the Arroyo Tres (17°29'1.24"N, 92°46'34.57"W; Fig. 1), a small creek and tributary to the Río Oxolotán (part of the Río Grijalva drainage) near the village of Tapijulapa in Tabasco (Fig. 1). Collections were made using seine nets, and fish were field-preserved in 10% formaldehyde.

Life-history analysis: Following the protocol of Reznick & Endler (1982), all preserved fish were weighed and measured for standard length. Males were classified as mature based on the morphology of their modified anal fin (i.e. gonopodium; Fig. 2C). The anal fin in poeciliids undergoes a complex metamorphosis as fish attain maturity, and the endpoint of this metamorphosis provides a reliable index of sexual maturity, allowing us to determine the state of complete maturation based on external cues alone (e.g. Constantz 1989; Greven 2011; Langerhans 2011). We therefore consulted the illustration of the fully developed gonopodium of *P. chamulae* presented by Scharl et al. (2006). Unfortunately, almost all males that we collected turned out to be sexually immature (5 out of 6), and so their data had to be discarded for most life history analyses. However, male poeciliids are characterized by determinate growth and therefore

almost completely cease growth after reaching sexual maturity (Snelson 1989). Since all immature males were within days of reaching sexual maturity (i.e., only the terminal structures of the gonopodium were not yet fully developed; Turner 1941) we did use their standard length (SL) data for statistical comparisons with females, and included them in our gut length analysis (see below).

The reproductive tissue (i.e., testes for males and ovaries for females) and, if present, all developing offspring were removed. Offspring were counted and their stage of development determined (Haynes 1995; Reznick 1981). Somatic tissues, reproductive tissues, and embryos were then dried for 10 days at 40 °C and weighed again. To assess male, female, and embryo condition, somatic tissues and embryos were rinsed six times for at least six hours in petroleum ether to extract soluble non-structural fats (Heulett et al. 1995; Riesch et al. 2010a, b, 2011b) and were then dried again and reweighed.

We thus measured standard length [mm], dry mass [mg], lean mass [mg] (i.e., weight after fat extraction), and fat content [%] for males and females, gonadosomatic index [GSI, %] for males only, and fecundity [number of developing embryo], reproductive allocation [RA, %], embryo dry mass [mg], offspring lean weight [mg], and embryo fat content [%] for females only. GSI is calculated as testis dry mass [g] divided by the sum of

testis dry mass [mg] and somatic dry mass [mg]. RA, on the other hand, was calculated as the total dry mass of all developing embryos [mg] divided by the sum of the total dry mass of all developing embryos [mg] and somatic dry mass [mg].

Finally, we calculated the matrotrophy index [MI] as a measure to indirectly evaluate post-fertilization maternal provisioning (Marsh-Matthews 2011). The MI equals the estimated dry mass of the embryo at birth divided by the estimated dry mass

of the oocyte at fertilization and is derived from a linear regression of log-transformed embryo dry mass against stage of development (Marsh-Matthews 2011). Thus, if the eggs were fully provisioned by yolk prior to fertilization (lecithotrophy), we would expect the embryos to lose 30-40% of their dry mass during development ($MI \leq 0.75$; Marsh-Matthews 2011; Pires et al. 2011). On the other hand, in the case of continuous maternal provisioning even after fertilization (matrotrophy), one

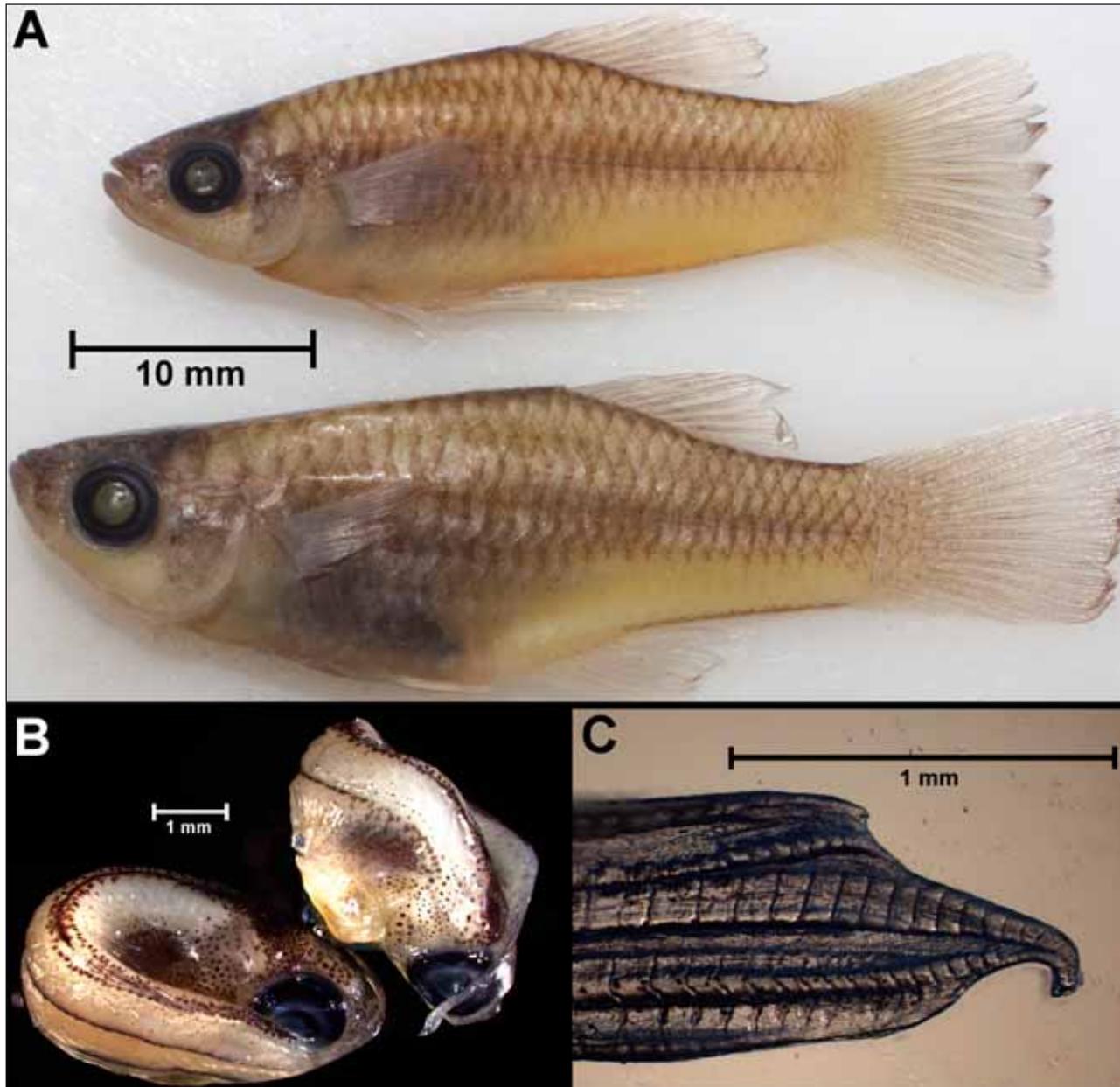


Fig. 2. *Priapella chamulae* SCHARF, MEYER & WILDE. (A) Male (top) and female (bottom); (B) ready-to-be-born embryos; (C) tip of the gonopodium of a male *P. chamulae*. B and C were stacked using Helicon Focus V. 4.2.7 (2010 Helicon Soft Ltd.).

Table II. Diet of *Priapella chamulae* as inferred by gut-content analysis.

Diet categories	Number of diet items	Individuals with diet item [%]*	Total diet [%]
Arachnida	4	7	2
Blattaria	1	1	< 1
Chironomidae larvae	5	7	2
Coleoptera adults	14	18	6
larvae	7	10	3
Diptera adults	27	21	11
Gastropoda	1	1	< 1
Hemiptera	1	1	< 1
Hymenoptera adult ants	59	54	25
adult wasps	12	16	5
Lepidoptera larvae	2	3	< 1
Oligochaeta	1	1	< 1
Orthoptera	6	10	1
Unidentified insects adults	88	65	37
larvae	6	10	3
Plant material seeds	2	3	< 1
rootlets	—	18	—

* percentages may not sum to 100 due to rounding

would expect the embryos to lose less mass (MI between 0.75 and 1.00) or even to gain mass during development (MI \geq 1.00; Marsh-Matthews 2011; Pires et al. 2011).

Gut content analysis: We inferred the diet of *P. chamulae* by dissecting the guts of all preserved fish and identifying the contents. We identified gut contents to Order in most cases. If this was not possible, we identified items to the lowest possible taxonomic level. We counted the number of gut contents within each diet category – except for woody plant material – and calculated the percentage of guts containing each diet category, and the proportion of each diet category relative to the total diet, and in total for all individuals.

Additionally, before dissecting out gut contents we measured gut length [mm] with digital calipers. We used these gut length measures to calculate relative gut length (gut length/standard length) and tested for sexual dimorphism in relative gut length with a Mann-Whitney *U*-test.

RESULTS

General natural history: Over the last five years and while sampling other poeciliid fishes, we found *P. chamulae* at a variety of habitats in Tabasco, ranging from small creeks [Arroyo Tres, Arroyo Bonita (17°25'37.42"N, 92°45'6.98"W), Arroyo Cristal

(17°27'2.13"N, 92°45'49.40"W), and Arroyo Tacubaya (17°27'12.78"N, 92°47'4.16"W)] to large rivers [Río Amatán (17°27'33.26"N, 92°46'42.53"W)] all near the village of Tapijulapa (Fig. 1). Surprisingly, we have so far never caught *P. chamulae* in the Río Oxolotán, but this is probably an artifact of our sampling efforts, as all other positive locations suggest that *P. chamulae* also inhabits that river (Fig. 1). Teleost species communities at these habitats are quite complex (Tobler et al. 2006; Riesch et al. 2009) and at Arroyo Tres *P. chamulae* share the habitat with *Poecilia mexicana* Steindachner, *Xiphophorus hellerii* Heckel, *Heterophallus milleri* Radda, *Heterandria bimaculata* Heckel (all Poeciliidae), *Astyanax aeneus* Günther (Characidae), *Thorichthys helleri* Steindachner, and *Vieja bifasciata* Steindachner (both Cichlidae) (see also Tobler et al. 2006). In some of the other habitats, species communities are even more complex (e.g., Riesch et al. 2011a). More generally, *P. chamulae* appears to prefer the slightly faster flowing parts (e.g., riffles) of these habitats, as we rarely catch significant numbers in the stagnant pools that are usually dominated by *P. mexicana* and *A. aeneus*.

Life-history analysis: General life history data are compiled in Table I. *Priapella chamulae* at Arroyo Tres was characterized by sexual size dimorphism, with males being smaller than females (female

SL = 30.30±4.21 mm; male SL = 26.02±2.93 mm; *t*-test: $t_{38} = 2.379$, $P = 0.022$; Fig. 2A). The tertiary (adult) sex ratio was female-biased and approximately 1:8.2 (males:females; Table I). The majority of dissected females (69.3%) were reproductively active, but only one out of the six collected males was sexually mature (16.7%). Embryo weight decreased with developmental stage ($R^2 = 0.292$, $P < 0.001$) in a fashion corresponding to a predominantly lecithotrophic provisioning strategy (MI = 0.71; Fig. 2B, Fig. 3). We did not find any evidence for superfetation in *P. chamulae*, as all developing embryos of the same clutch were always of approximately the same developmental stage.

Gut content analysis: Only one individual had an empty gut (except for some incidental woody plant material). *Priapella chamulae* at Arroyo Tres are almost exclusively carnivorous (Table II); on average, individual *P. chamulae* had 4.6±2.5 (mean±SD, range: 0-10) diet items in their guts, and the vast majority of their diet was made up by terrestrial arthropods (~98%), with ants being the single most common identifiable diet item (Table II). Males and females did not differ in their rela-

tive gut length (females: median = 21.08%, IQR = 9.22%; males: median = 23.75%, IQR = 11.55%; Mann-Whitney *U*-test: $U = 166.00$, $P = 0.545$).

DISCUSSION

Our observations confirm previous accounts that described *P. chamulae* to prefer the medium to fast flowing parts of small creeks (Miller 2005; Schartl et al. 2006). Like many other life history traits, offspring size and fecundity are usually related to female body size (Reznick & Miles 1989). It is therefore slightly surprising that this medium-sized poeciliid produces only relatively few, average-sized offspring, which translates into low values for RA. For example, similar sized *Poecilia mexicana* from comparable creeks around Tapijulapa produce two to three times more offspring, which are also larger (Riesch et al. 2010b). However, RA-values of *P. chamulae* are surprisingly similar to those of *P. mexicana* (given the pronounced differences in fecundity and offspring size), while more closely related poeciliids like *H. milleri* or *Gambusia sexradiata* Hubbs (that are also considerably smaller in body size) from nearby habitats invest almost twice as much per

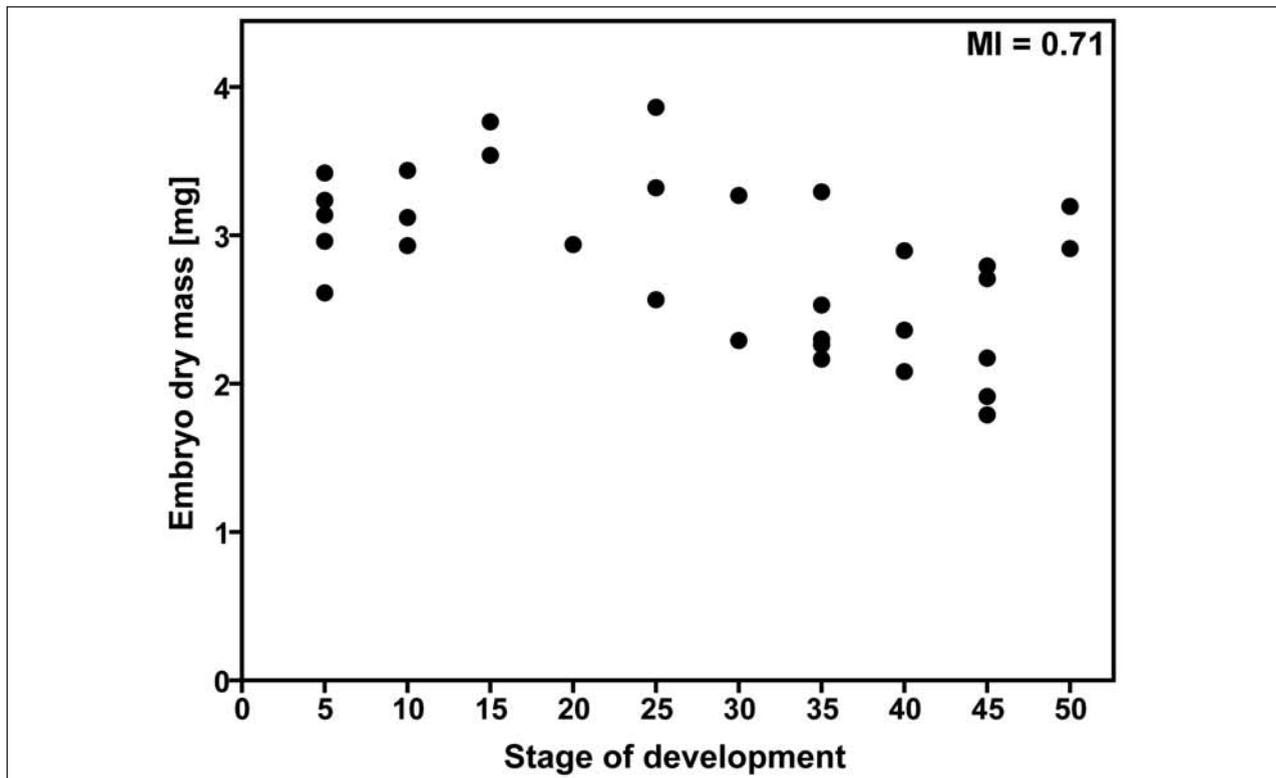


Fig. 3. Scatter plot of mean embryo dry mass vs. stage of development. Stages are determined on a progressive scale with the earliest (5) being the neurula stage and the oldest (50) being equivalent to embryos that are ready-to-be-born (Riesch et al. 2011c; after Reznick 1981; Haynes 1995).

clutch (i.e., RA around 20 %; Riesch et al. 2010a, 2011a). Nonetheless, several life history traits of *P. chamulae* are similar to those of other members of the tribe Gambusiini (e.g., no superfetation and lecithotrophy; but see Pires et al. 2011 for citations on rare occurrences of superfetation in Gambusiini). Likewise, offspring fat content matches that found in other Gambusiini from the same drainage (i.e., *G. sexradiata* and *G. eurystoma* Miller, Riesch et al. 2010a; *H. milleri*, Riesch et al. 2011a).

Furthermore, the sexual size dimorphism we report on here is typical for most poeciliids (Pires et al. 2011). Most natural populations of poeciliids are characterized by a female-skewed sex ratio (Snelson 1989; Magurran 2005) and *P. chamulae* from Arroyo Tres were no exception. Since secondary sex ratios (i.e., sex ratio at birth) are typically 1:1 in poeciliids, higher male mortality is usually thought to be the reason for a female-biased sex ratio at maturity (Snelson 1989).

Our results clearly demonstrate that *P. chamulae* at Arroyo Tres are carnivorous. While there is at least one other purely carnivorous species in the tribe Gambusiini (i.e., *Belonesox belizanus* Kner; Miller 2005), the diet of *P. chamulae* more closely resembles that described for *Heterandria bimaculata*, *Gambusia affinis* (Baird & Girard), *G. holbrooki* Girard, *G. sexradiata*, and other *Gambusia* spp. that are known to prey heavily on insects and other invertebrates (Miller 2005; Trujillo-Jiménez & Beto 2007). Other close relatives, swordtails and platyfish of the genus *Xiphophorus*, however, are known to be mostly omnivorous with an emphasis on herbivory (e.g., Maddern et al. 2011). In agreement with this apparent carnivorous dietary specialization, *P. chamulae* had relatively small gut-to-SL ratios. This clearly sets them apart from other more herbivorous/omnivorous species like *Poecilia latipinna* (Lesueur) and all-female *Poecilia formosa* (Girard) that have considerably longer gut-to-SL ratios (Scharnweber et al. 2011a, b). However, based on the predominance of terrestrial arthropods in the diet it is likely that *P. chamulae* is an opportunistic feeder that, rather than actively hunting for its prey, mainly waits for arthropods to fall or land on the water surface.

This study represents the first diet and life history characterization of a poeciliid fish from the little investigated genus *Priapella*. While the present study already provides us with relevant insights into their general biology, it is important to keep in mind that the diet data and life history data we report on here were derived from specimens collected from a single

point in space and time. Previous studies have clearly shown that diet and life histories vary considerably between habitats and seasons in livebearing fishes (e.g., Reznick & Endler 1982; Meffe & Snelson 1989; Reznick & Miles 1989; Johnson & Bagley 2011; Riesch et al. 2010a-c, 2011; Scharnweber et al. 2011b). However, water chemistry and the teleost community at Arroyo Tres are representative for a range of similar environments in this part of southern México (Tobler et al. 2006, 2008; Riesch et al. 2009). We are therefore fairly confident that the life history data presented in the current study are largely representative of *P. chamulae* life-history strategies in the other creek environments inhabited by this species (i.e., Arroyos Bonita, Cristal, and Tacubaya). Nonetheless, *P. chamulae* from larger rivers, such as the Ríos Amatan and Oxolotán, may differ in life histories (and potentially also diets) from those reported here, and more extensive studies (i.e., comparisons of *P. chamulae* from different sample sites, or of laboratory-reared specimens with field-caught fish) are clearly warranted to help characterize the full dietary niche width and breadth of life-history strategies exhibited by this species.

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