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Dietary niche overlap in sympatric asexual and sexual livebearing fishes *Poecilia* spp.

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The present study investigated the spatiotemporal patterns in trophic resource use in a system of a gynogenetic poeciliid fish, the Amazon molly *Poecilia formosa*, and its sexual congeners the sailfin molly *Poecilia latipinna* and the Atlantic molly *Poecilia mexicana* using gut contents analysis. No statistically significant differences in trophic resource use were found between sexual and gynogenetic species, but gut contents varied significantly across sites and over time. In addition, variation in trophic morphology (*i.e.* gut length) was significant across sites but not species, and laboratory experiments indicated that gut length is phenotypically plastic. Overall, trophic differentiation between coexisting asexual and sexual *Poecilia* appears to be minimal, and it is unlikely that niche differentiation contributes to a stable coexistence of the two reproductive forms.

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Key words: gut content analysis; gynogenesis; *Poecilia formosa*; trophic niche segregation.

INTRODUCTION

A major question in evolutionary ecology considers the maintenance of sexual reproduction (Kondrashov, 1993; Redfield, 1994; West *et al.*, 1999). In theory, sexual reproduction is associated with considerable costs (Bell, 1982). For example, sexual organisms have to produce males that cannot produce offspring themselves, which effectively results in a two-fold reduction of the intrinsic population growth rate at a balanced sex ratio (Maynard Smith, 1978). Furthermore, sexual organisms face the cost of recombination as only half of their genes are passed to the next generation, and successful genotypes can be eliminated in every reproductive cycle due to meiosis (Williams, 1975). Consequently, asexual organisms avoiding these costs should have an advantage and be able to invade and rapidly displace populations of sexual organisms (Maynard Smith, 1978; Bell, 1982; Lively & Lloyd, 1990; Barton

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& Charlesworth, 1998). There is, however, a striking mismatch between theory and reality, as most metazoans have two sexes and engage in genetic recombination in each reproductive cycle.

In the Animal Kingdom, there are several examples of closely related sexual and asexual taxa coexisting in similar habitats (Dawley, 1989), including molluscs (Lively, 1987), insects (Kearney & Moussalli, 2003), fishes (Vrijenhoek *et al.*, 1978), amphibians (Semlitsch *et al.*, 1997) and reptiles (Paulissen *et al.*, 1988). Naturally, for both reproductive strategies to co-occur, sexual individuals must have some advantages that outweigh the two-fold genetic fitness benefit of asexual reproduction. To solve the paradox of stable coexistence, numerous theoretical models have been proposed to explain mechanisms balancing the short-term benefits of asexuality with possible disadvantages (*e.g.* Red Queen hypothesis; Van Valen, 1973; Hamilton, 1980; Salathé *et al.*, 2008; Tobler & Schlupp, 2008). Also, coexistence of closely related sexual and asexual organisms has interesting ecological implications. The Competitive Exclusion Principle predicts coexistence between species as a function of resource exploitation and interspecific competition (Gause, 1934; Hardin, 1960). Competition may lead to ecological character displacement, imposing disruptive selection on resource use and associated phenotypic traits (Losos, 2000; Schluter, 2001). There are multiple examples for niche segregation promoted by competition. For example, spadefoot toads *Spea multiplicata* and *Spea bombifrons* have undergone ecological character displacement in the tadpole trophic phenotype (Pfennig & Murphy, 2000; Rice *et al.*, 2009). When coexisting in the same pond, *S. multiplicata* produces almost entirely omnivorous tadpoles and *S. bombifrons* produces carnivorous tadpoles, whereas in allopatry both species produce similar, intermediate frequencies of the two trophic phenotypes. Similarly, populations of pumpkinseed sunfish *Lepomis gibbosus* (L. 1785) produce both molluscivorous and planktivorous morphotypes due to intraspecific competition (Robinson *et al.*, 1993). Accordingly, coexistence of clonal and sexual lineages should be facilitated if there is some degree of ecological differentiation between asexual and sexual organisms (Vrijenhoek *et al.*, 1978; Vrijenhoek, 1979; Case & Taper, 1986; Wetherington *et al.*, 1989; Vrijenhoek & Pfeiler, 1997). Divergent patterns of trophic resource use have been documented for asexual and sexual lizards (Paulissen *et al.*, 1988) and for asexual fishes and their sexual relatives (Schenck & Vrijenhoek, 1989; Gray & Weeks, 2001).

The present study investigated the potential niche differentiation in a system of closely related, coexisting live-bearing fishes that includes the Amazon molly *Poecilia formosa* (Girard 1859). This species is an all-female (unisexual) fish that originated from a single hybridization event between two sexual species, the sailfin molly *Poecilia latipinna* (Lesueur 1821) and the Atlantic molly *Poecilia mexicana* Steindachner 1863 *c.* 100 000 years ago (Schartl *et al.*, 1995; Loewe & Lamatsch, 2008; Stöck *et al.*, 2010). *Poecilia formosa* reproduces *via* gynogenesis; although inheritance is strictly clonal, females require sperm of related host species to trigger the onset of embryonic development (Hubbs & Hubbs, 1932; Schlupp, 2005). To obtain sperm, gynogenetic females mate with heterospecific males; in the case of *P. formosa*, host males are usually from either of the parental species (Schlupp *et al.*, 1998). The sperm dependency of *P. formosa* has an important ecological consequence: the asexual organisms always have to coexist with their sexual relatives (sperm donors) in the same habitats (Niemeitz *et al.*, 2002), and they have even been reported to form mixed-species shoals in natural habitats (Schlupp & Ryan, 1996).

Accordingly, *P. formosa* co-occurs with *P. latipinna* in Texas and coastal areas of north-eastern Mexico and with *P. mexicana* in inland waters from the Río San Juan southward to the mouth of the Río Tuxpan in Mexico (Darnell & Abramoff, 1968; Miller, 1983; Schlupp *et al.*, 2002). Within a limited range in Mexico, Tamesí mollies *Poecilia latipunctata* Meek 1904 serve as a third host species (Niemeitz *et al.*, 2002).

Several studies have been conducted to investigate the mechanisms underlying stable coexistence of the two reproductive modes in this system, but so far, no single mechanism was found to be able to cause a full reduction of the two-fold advantage of asexual fishes. Behavioural studies suggest that male mate choice may at least partly regulate coexistence (Schlupp, 2009). Males of both host species prefer to mate with conspecifics and transfer more sperm to them, so that asexual females could be sperm limited in nature (Schlupp & Plath, 2005; Riesch *et al.*, 2008; Robinson *et al.*, 2008). Tests of the Red Queen hypothesis found no evidence for differential parasitization of asexual and sexual reproductive forms (Tobler *et al.*, 2005; Tobler & Schlupp, 2008). Asexual and sexual fishes, however, seem to differ in susceptibility to environmental stress, as *P. formosa* suffer from higher offspring mortality under food stress (Tobler & Schlupp, 2010) and higher adult mortality at cold temperatures (Fischer & Schlupp, 2009). Heubel (2004) studied the population ecology of this system and explained spatial and temporal variation of the abundance of *P. formosa* but did not explicitly test for niche segregation.

So far, ecological interactions as a potential mechanism for stable coexistence of sexual and asexual *Poecilia* spp. are poorly understood. Here, the trophic ecology was compared between coexisting asexual and sexual fishes by investigating their gut contents. Specifically, the following questions were addressed: (1) What is the diet of *P. formosa* and its sexual sperm donors and is there evidence for trophic niche segregation in this system? Studies of resource use in other *Poecilia* (Darnell, 1962; Winemiller, 1993; Kramer & Bryant, 1995a; Tobler, 2008) and *Poeciliopsis* species (Schenck & Vrijenhoek, 1989; Weeks *et al.*, 1992; Gray & Weeks, 2001) revealed that they primarily feed on detritus and algae; hence, patterns of resource use similar to asexual and sexual *Poeciliopsis* spp. were expected (Gray & Weeks, 2001). (2) Do *Poecilia* spp. with different reproductive modes have the same niche width? Due to recombination, sexual populations are expected to express more variable phenotypes, which could precipitate into wider ecological niches. (3) Do asexual and sexual fishes differ in aspects of their trophic morphology? Because morphological traits frequently reflect dietary characteristics in fishes (Winemiller *et al.*, 1995; Horstkotte & Strecker, 2005; Tobler, 2008), gut length in asexual and sexual fishes were compared. It was also tested whether variation in intestinal length is phenotypically plastic, using a laboratory feeding experiment.

MATERIALS AND METHODS

FISH COLLECTIONS

In this study, four different populations of *P. formosa* were investigated; three populations coexisting with *P. latipinna* were sampled in Texas, U.S.A., and one population coexisting with *P. mexicana* in Tamaulipas, Mexico (see Table I for collection sites). Collections took place between January and August 2009, and all sites were visited twice with at least

TABLE I. Field sites sampled for this study

Study site	Sampling dates	River basin	Latitude N	Longitude W
Sites with <i>Poecilia latipinna</i>				
Lincoln Park	18/05/2009 and 14/07/2009	Rio Grande (Bravo)	25-900	97-479
Central Texas	25/06/2009 and 10/08/2009	Guadalupe River	29-857	97-868
Weslaco	18/05/2009 and 14/07/2009	Rio Grande (Bravo)	26-121	97-962
Site with <i>Poecilia mexicana</i>				
Río Mante	03/03/2009 and 18/06/2009	Río Guayalejo	22-705	99-001

2 months in between (spring and summer). Fishes were caught using a seine (length 4 m; mesh width 4 mm). Immediately after capture, fishes were euthanized using MS222 (tricaine methanesulphonate) and then fixed in a 10% formalin solution for subsequent analyses in the laboratory. To eliminate potential confounding effects of niche differentiation between males and females of the sexual species, only females were investigated.

GUT CONTENTS ANALYSIS

Methods for gut contents analysis were adapted from the studies by Hyslop (1980), Winemiller (1990) and Tobler (2008). Whenever available, 15 individuals of each species per study site and collection date were analysed. When a collection contained >15 individuals, a subset of specimens was chosen to reflect the size distribution of the sample. Specimens were measured for standard length (L_S) to the nearest millimetre and weighed to the closest 0.01 g (blotted wet mass). Specimens were dissected, and the length of the entire gut, which is tubular and without a discrete stomach in *Poecilia*, was measured. For identification of gut contents, the first quarter of the intestine was examined under a dissecting microscope to sort out large dietary items. To enhance resolution, items unidentifiable under the dissecting microscope were placed on a glass slide for wet-mount examination under a compound microscope. Five different areas on the slide were sampled at random, and the volumetric proportion of each dietary item in each area was estimated visually. The following diet categories were recognized for this study (Winemiller, 1990): fine detritus, diatoms, desmids and unicellular green algae, filamentous algae, parts of vascular plants, Protozoa, Rotatoria, plant parts and sand. All items with an overall occurrence of <5% (including Protozoa, Rotatoria, plant parts and filamentous algae) were merged into a group of rare items for data analysis.

STATISTICAL ANALYSES

For the analyses of resource use, specimens with empty intestines were excluded. Proportions of dietary items were arcsine (square-root) -transformed to normalize distributions, subjected to principal component analyses (PCA) based on a covariance matrix, and principal components (PC) with an Eigenvalue >1 (two PCs accounting for 60.18% of variance; see Table II for axis loadings) were used as dependent variables in a multivariate analysis of covariance (MANCOVA). To compare the gut contents between reproductive modes, *P. mexicana* and *P. latipinna* were categorized as 'sexual' and *P. formosa* as 'asexual'. Independent variables in the MANCOVA model were reproductive mode (sexual or asexual), time (spring or summer), host species (*P. latipinna* or *P. mexicana*), study site (nested within host species), as well as L_S (covariate) and the interactions of the independent variables. The F ratios were approximated using Wilks' lambda and effect sizes using partial eta squared

TABLE II. Component matrix of the PCA on the proportion of food items ingested by sexual and asexual *Poecilia* spp.

	Percent variation explained	Fine detritus	Sand	Diatoms	Desmids/ green algae	Rare items
PC 1	36.072	-0.827	-0.043	0.771	0.719	-0.078
PC 2	24.103	0.040	-0.605	-0.264	0.378	0.790

Axis loadings for the first two principal components (PCs) are shown (including the per cent variation explained by each PC).

(η_p^2). The assumptions of normal distribution and homogeneities of variances and covariances were met for all analyses.

The dietary niche width of each individual was calculated using the inverse of Simpson's (1949) diversity measure $\beta = (\sum p_i^2)^{-1}$, where p is the proportional utilization of each dietary item i (Pianka, 1973, 1986). Niche width values were subjected to ANCOVA using reproductive mode, time, host species, study site (nested within host species) and their interactions as factors and L_S as a covariate.

Gut length was compared among reproductive forms as a morphological indicator for potential niche segregation. Here, individuals with empty guts were included in the analysis. Gut length was analysed using ANCOVA with a model similar to the one described above. Kramer & Bryant (1995a, b), however, suggested using individuals' body mass rather than size as a covariate in comparisons of gut length; thus, a mass-based covariate ($10 \text{ mass}^{0.33'}$) adapted from the Zihler index (Zihler, 1982) was included.

As differences in gut length among populations varying in trophic resource use were documented in a previous study (Tobler, 2008), it prompted the question of whether variation in intestinal tract lengths reflects phenotypic plasticity (Winemiller & Adite, 1997; Piet, 1998; Hugueny & Pouilly, 1999). An experiment was conducted to test whether gut length changes in sexual and asexual organisms in response to dietary changes. To do so, *P. formosa* and *P. latipinna* were collected from the central Texan site. Fishes were returned to the laboratory alive, kept in $120 \times 30 \times 40$ cm tanks at densities of 30–50 fish per tank and were fed twice a day with nutritious, artificial fish food (Hikari tropical algae wafers; www.hikari.info/tropical). After 4 weeks, fishes were sacrificed and their gut length measured. To compare the length of their intestines to those of fish collected at the same site 4 weeks earlier, ANCOVA was performed using gut length as dependent variable, environment (laboratory or wild), reproductive mode and the interactions as independent variables and body mass as a covariate. Since interactions were not significant (ANCOVA, d.f. $\leq 1,120$; $P \geq 0.05$), only main effects were analysed.

RESULTS

In total, 267 individuals were examined; 141 of them were asexual. An empty gut was only found in a single *P. latipinna* female at Weslaco. The most abundant food item in the gut of all species and from all sites was detritus (Table III). As typical for deposit feeders, the second most abundant item was sand. A comparison of gut contents between *P. formosa* and coexisting sexual species revealed no significant differences (Table IV). Most importantly, the multivariate analysis indicated site- and species-specific changes in gut content composition over time (significant time \times study site and time \times host species interactions in Table IV; see also Fig. 1).

TABLE III. Volumetric proportion of dietary items averaged across individuals of different *Poecilia* species for each site (including the sample size, *n*; values are means \pm s.d.)

	Sexual species		<i>Poecilia formosa</i>	
	Spring	Summer	Spring	Summer
<i>(a) Lincoln Park (P. latipinna)</i>				
<i>n</i>	15	15	15	15
Niche width	0.83 \pm 0.01	0.90 \pm 0.00	0.81 \pm 0.02	0.88 \pm 0.01
Fine detritus	0.56 \pm 0.10	0.36 \pm 0.09	0.61 \pm 0.13	0.38 \pm 0.13
Sand	0.10 \pm 0.04	0.12 \pm 0.06	0.09 \pm 0.07	0.16 \pm 0.14
Diatoms	0.03 \pm 0.03	0.21 \pm 0.04	0.05 \pm 0.04	0.23 \pm 0.09
Desmids/green algae	0.24 \pm 0.12	0.26 \pm 0.06	0.21 \pm 0.08	0.20 \pm 0.06
Rare items	0.07 \pm 0.04	0.04 \pm 0.03	0.05 \pm 0.05	0.03 \pm 0.02
<i>(b) Central Texas (P. latipinna)</i>				
<i>n</i>	16	19	30	20
Niche width	0.79 \pm 0.01	0.75 \pm 0.02	0.77 \pm 0.02	0.76 \pm 0.01
Fine detritus	0.66 \pm 0.06	0.71 \pm 0.11	0.68 \pm 0.14	0.70 \pm 0.09
Sand	0.07 \pm 0.06	0.11 \pm 0.05	0.12 \pm 0.08	0.11 \pm 0.04
Diatoms	0.06 \pm 0.05	0.05 \pm 0.03	0.03 \pm 0.03	0.05 \pm 0.03
Desmids/green algae	0.09 \pm 0.05	0.11 \pm 0.04	0.11 \pm 0.06	0.13 \pm 0.04
Rare items	0.12 \pm 0.06	0.02 \pm 0.01	0.06 \pm 0.05	0.02 \pm 0.01
<i>(c) Welsaco (P. latipinna)</i>				
<i>n</i>	15	16	15	16
Niche width	0.84 \pm 0.01	0.84 \pm 0.01	0.85 \pm 0.01	0.84 \pm 0.01
Fine detritus	0.56 \pm 0.09	0.52 \pm 0.18	0.46 \pm 0.15	0.51 \pm 0.20
Sand	0.02 \pm 0.02	0.19 \pm 0.07	0.02 \pm 0.02	0.19 \pm 0.08
Diatoms	0.20 \pm 0.05	0.14 \pm 0.07	0.29 \pm 0.13	0.11 \pm 0.06
Desmids/green algae	0.21 \pm 0.08	0.08 \pm 0.04	0.21 \pm 0.12	0.06 \pm 0.04
Rare items	0.01 \pm 0.01	0.01 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01
<i>(d) Río Mante (P. mexicana)</i>				
<i>n</i>	15	15	15	15
Niche width	0.76 \pm 0.02	0.84 \pm 0.01	0.77 \pm 0.02	0.81 \pm 0.01
Fine detritus	0.70 \pm 0.12	0.58 \pm 0.09	0.67 \pm 0.14	0.63 \pm 0.08
Sand	0.15 \pm 0.06	0.13 \pm 0.02	0.13 \pm 0.07	0.14 \pm 0.04
Diatoms	0.09 \pm 0.05	0.13 \pm 0.04	0.14 \pm 0.09	0.09 \pm 0.03
Desmids/green algae	0.06 \pm 0.04	0.10 \pm 0.03	0.04 \pm 0.03	0.08 \pm 0.03
Rare items	0.00 \pm 0.00	0.07 \pm 0.05	0.02 \pm 0.03	0.06 \pm 0.05

Contrary to prediction, dietary niche width did not differ between asexual and sexual *Poecilia* but varied across sites. Furthermore, L_S was a significant predictor of niche width in all analyses, with larger fishes having narrower niches than smaller individuals (Table IV).

As expected, gut length was positively correlated with body mass, but no consistent difference in gut length was found between the two reproductive modes. Gut length differences between asexual and sexual females varied, albeit not significantly, idiosyncratically among sites (Fig. 2).

Finally, the laboratory feeding experiment indicated that fishes collected in the wild differed strongly in gut length from individuals maintained in the laboratory for 4 weeks (ANCOVA, d.f. = 1,123; $P < 0.001$). After feeding nutritious food to the fishes in the laboratory, gut length declined in both species (Fig. 3). The ANCOVA

TABLE IV. Results of multivariate analysis of covariance (MANCOVA) and ANCOVA examining temporal variation in gut contents, niche widths and gut lengths of sexual and asexual *Poecilia* spp.

Effect	<i>F</i>	d.f.	<i>P</i>	η_p^2
<i>(a)</i> Gut contents				
L_S	12.507	2,247	<0.001	0.092
Reproductive mode	1.485	2,247	>0.05	0.012
Host species	8.871	2,247	<0.001	0.067
Study site (host species)	8.252	4,494	<0.001	0.063
Time	2.151	2,247	>0.05	0.017
$L_S \times$ reproductive mode	1.481	2,247	>0.05	0.012
$L_S \times$ host species	6.008	2,247	<0.01	0.046
$L_S \times$ study site (host species)	2.587	4,494	<0.05	0.021
$L_S \times$ time	1.263	2,247	>0.05	0.010
Reproductive mode \times host species	0.183	2,247	>0.05	0.001
Reproductive mode \times study site (host species)	0.206	4,494	>0.05	0.002
Reproductive mode \times time	0.145	2,247	>0.05	0.001
Host species \times time	72.934	2,247	<0.001	0.371
Study site (host species) \times time	20.172	4,494	<0.001	0.140
<i>(b)</i> Niche width				
L_S	17.226	1,245	<0.001	0.066
Reproductive mode	1.343	1,245	>0.05	0.005
Host species	1.332	1,245	>0.05	0.005
Study site (host species)	4.911	2,245	<0.01	0.039
Time	2.407	1,245	>0.05	0.010
$L_S \times$ reproductive mode	1.584	1,245	>0.05	0.006
$L_S \times$ host species	3.316	1,245	>0.05	0.013
$L_S \times$ study site (host species)	1.311	2,245	>0.05	0.011
$L_S \times$ time	0.826	1,245	>0.05	0.003
Reproductive mode \times host species	0.692	1,245	>0.05	0.003
Reproductive mode \times study site (host species)	0.166	2,245	>0.05	0.001
Reproductive mode \times time	0.833	1,245	>0.05	0.003
Host species \times time	9.331	1,245	<0.01	0.037
Study site (host species) \times time	5.343	2,245	<0.01	0.042
<i>(c)</i> Gut length				
$10 \text{ mass}^{0.33'}$	372.327	1,249	<0.001	0.599
Reproductive mode	0.363	1,249	>0.05	0.001
Host species	1.436	1,249	>0.05	0.006
Study site (host species)	0.175	2,249	>0.05	0.001
Time	1.774	1,249	>0.05	0.007
$10 \text{ mass}^{0.33'} \times$ reproductive mode	0.366	1,249	>0.05	0.001
$10 \text{ mass}^{0.33'} \times$ host species	8.671	1,249	<0.01	0.034
$10 \text{ mass}^{0.33'} \times$ study site (host species)	1.015	2,249	>0.05	0.008
$10 \text{ mass}^{0.33'} \times$ time	4.059	1,249	<0.05	0.016
Reproductive mode \times host species	7.102	1,249	<0.01	0.028
Reproductive mode \times study site (host species)	0.330	2,249	>0.05	0.003
Reproductive mode \times time	2.548	1,249	>0.05	0.010
Host species \times time	4.201	1,249	<0.05	0.017
Study site (host species) \times time	4.337	2,249	<0.05	0.034

L_S , standard length.

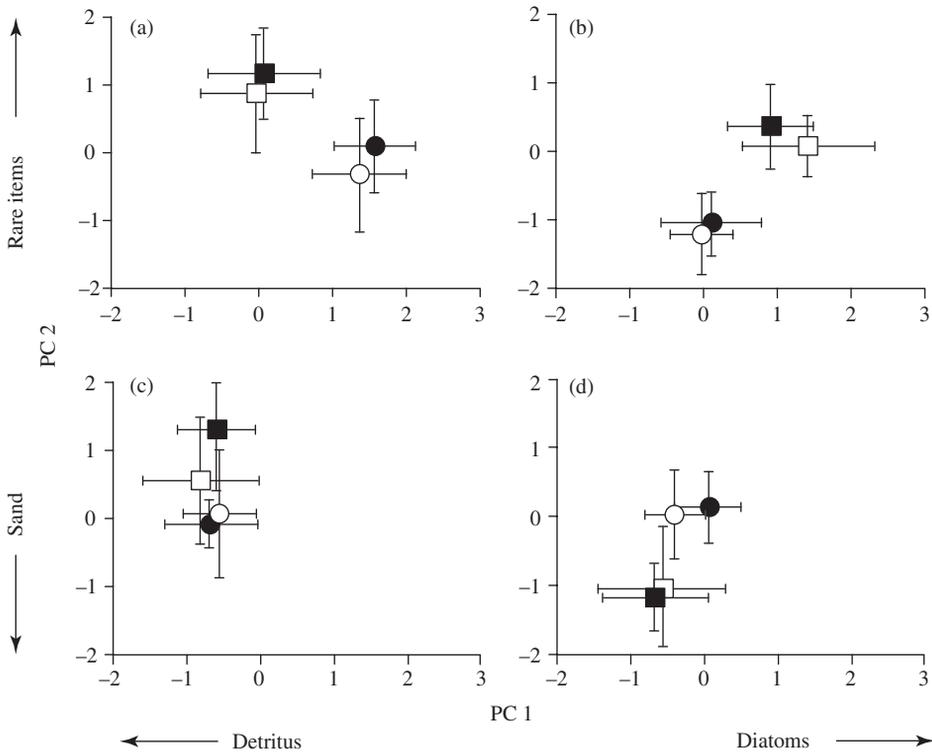


FIG. 1. Discriminant function plots for the PCA scores 1 and 2 for (a) Lincoln Park, (b) Weslaco, (c) Central Texas and (d) Río Mante (see Table I). The mean \pm s.d. discriminant function scores for the two times of sampling are shown (■, □ spring; ●, ○ summer) for sexual (*Poecilia latipinna* or *Poecilia mexicana*; ■, ●) and asexual (*Poecilia formosa*; □, ○) fishes.

indicated no significant difference between reproductive modes in the reduction of gut length in laboratory-housed fishes (ANCOVA, d.f. = 1,123; $P > 0.05$).

DISCUSSION

Considering the immediate cost of sexual reproduction, stable coexistence of closely related sexual and asexual species, as observed in the *P. formosa* system (Schlupp, 2005; Lampert & Scharl, 2008), remains a conundrum. Trophic niche segregation, a potential mechanism helping to mediate stable coexistence of different reproductive forms, does not appear to explain the coexistence of *P. formosa* with their sexual sperm donors. Fishes of all species from all field sites ingested large amounts of detritus, sand and algae. These results are consistent with previous dietary studies on closely related poeciliids (Darnell, 1962; Winemiller, 1993; Kramer & Bryant, 1995a; Tobler, 2008). Most variation in diet composition was explained by differences across collection sites, and there were no statistically significant differences between reproductive modes. Hence, gut content composition appears to be affected primarily by resource availability at specific locations.

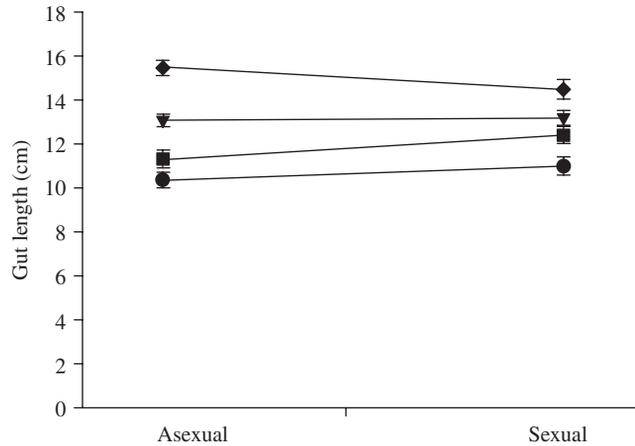


FIG. 2. Gut length of asexual *Poecilia formosa* and sexual (*Poecilia latipinna* or *Poecilia mexicana*) females at each study site: Lincoln Park (●), Central Texas (▼), Weslaco (■) and Río Mante (◆) (see Table I). Values are estimated as marginal means \pm s.e.

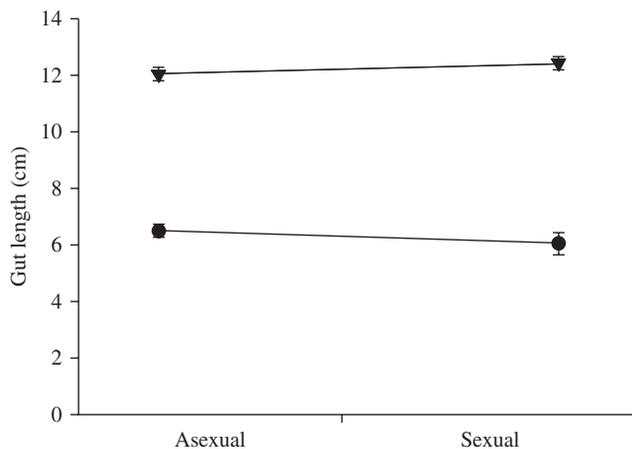


FIG. 3. Comparison of gut length of *Poecilia formosa* and *Poecilia latipinna* females, collected in their natural habitat (wild, ▼) and raised in the laboratory for 4 weeks (laboratory, ●). Values are estimated marginal means \pm s.e.

NON-EXISTENT TROPHIC NICHE SEGREGATION

If closely related species are nearly indistinguishable ecologically, then one population should stochastically drift to extinction (Hubbell, 2001) or suffer competitive exclusion if another species evolves dominance in the shared niche (Hardin, 1960). This outcome is based, however, on the assumption that resources are limited (Martin & Genner, 2009). Detritus tends to be abundant in most aquatic ecosystems (Moyle & Light, 1996); thus, there may be little opportunity for niche differentiation among detritivores [but see Bowen (1983) for exceptions in fish communities of South American river systems].

Evidence for trophic niche segregation was detected in a system of asexual and sexual *Poeciliopsis* species, a genus of poeciliids that also consume mostly detritus (Gray & Weeks, 2001). In *Poeciliopsis*, however, competition for food may be more intense because they inhabit ecosystems with large hydrological variability. Flash floods in desert streams occupied by *Poeciliopsis* scour the stream bed and reduce availability of organic sediments (Schenck & Vrijenhoek, 1986). All study sites investigated in this study represent comparatively stable habitats so competition for the ubiquitous resource detritus is probably very low.

SOURCES OF VARIATION IN RESOURCE USE

Diet composition and niche width varied most strongly across sampling sites, and significant differences were found between the site in Mexico (where the host species is *P. mexicana*) and the southern U.S.A. (host species is *P. latipinna*). This spatial pattern is probably related to general geographic differences in environmental conditions, namely, physiography, substratum composition and regional species pools. Whereas sites with *P. latipinna* (with possible exception of central Texas) were lowland waters with low flow, muddy substrata and elevated salinities, the site with *P. mexicana* was an inland river with rocky bottom and continuously flowing water. Also, temporal variation in gut content composition was observed in interaction with host species and study site nested within host species. Differences in gut contents may thus be directly related to variation in resource availability over time and across sites. Similar patterns of temporal variation in resource use were also reported in poeciliids from lowland aquatic food webs in Costa Rica and may be caused primarily by seasonal variation in resource availability (Winemiller, 1990).

In addition, intraspecific variation in diet and niche width was detected in relation to size. Generally, smaller (younger) individuals of all three species fed on different items than larger individuals, indicating an ontogenetic shift in resource use, a pattern commonly observed in fishes (Garcia-Berthou, 1999; Persson & Bronmark, 2002; Genner *et al.*, 2003; Rezsü & Specziar, 2006; Amundsen *et al.*, 2008). Smaller individuals also had broader niches; hence, larger (and older) fishes seem to be more trophically specialized. It remains to be determined whether size-specific microhabitat use accounts for dietary differences among *Poecilia* species in the manner reported for western mosquitofish *Gambusia affinis* (Baird & Girard 1853), in which young fish preferred densely vegetated shallow areas of the water body and older fish occupied open water (Miura *et al.*, 1979).

GUT LENGTH AND RESOURCE USE

The long gut of *Poecilia* spp. reported in this study is indicative of a herbivorous/detrivorous diet (Kramer & Bryant, 1995a, b). Variation in gut length across sites can reflect differences in resource use, *e.g.* in a previous study on the trophic ecology of several populations of *P. mexicana*, individuals from sulphidic and cave habitats, where less plant material is ingested, had shorter intestines (Tobler, 2008). In the present study, however, no significant effect of study site on gut length was detected. Although differences in gut content composition across sites were found, ingested items are most likely too similar in digestibility to affect gut length variation. The present study, however, found significant support for the idea that gut

length is highly plastic in response to diet. Both *P. formosa* and *P. latipinna* exhibited pronounced changes in this trait within a matter of weeks after switching to an artificial, protein-rich diet. Similar phenotypic changes have been documented in other fishes when switching from protein-rich to protein-poor diets (German & Horn, 2006; Ke *et al.*, 2008).

In conclusion, dietary segregation between sexual and asexual *Poecilia* species is weak, albeit variable over time. In another study, no difference in feeding behaviour between the two reproductive modes was detectable (Scharnweber *et al.*, 2011). *Poecilia formosa* was not inferior in acquiring resources, and competitive abilities did not differ between the two reproductive modes. Consequently, trophic differentiation between asexual and sexual *Poecilia* might play a minor role in the stable coexistence of this gynogenetic complex, and other factors, such as microhabitat preferences and daily shifts in activity between sexual and asexual fishes, should be examined.

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