

## **Seasonality of reproduction by livebearing fishes in tropical rainforest streams**

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**Abstract.** Reproductive ecology, population structure, and diets of three common livebearing poeciliid fishes (*Alfaro cultratus*, *Phallichthys amates*, *Poecilia gilli*) from rainforest streams in Costa Rica were investigated over ten continuous months. The region experiences little annual temperature variation, and although monthly rainfall is continuous each year, two brief dry seasons typically occur. Monthly changes in indices of ovarian condition, percentages of females with developing embryos, and population size structure revealed that reproductive output by females of all three species varied seasonally. Based on testicular condition, males were reproductively active year-round, however the mean gonadal index for males of two algivorous species showed low levels of seasonal cycling that largely coincided with female variation in reproductive effort. All three species had seasonal differences in the female size-brood size relationship, whereby larger females tended to carry more embryos during the wet season. Several important adult and neonate food resources are more available in the flooded forest during the wet season, which is also the period when conspecifics and predators are at their lowest per-area densities. Three hypotheses are discussed: (1) brood size in relation to conspecific density-mating frequency, (2) reproductive allocation in response to variation in adult food resources, and (3) selection for greater reproductive effort during conditions optimal for juvenile growth and survival. Data for *Alfaro* were consistent with the latter two hypotheses. In *Phallichthys* and *Poecilia*, diets were poorer during wet seasons, indicating that reproductive effort does not coincide with availability of adult food resources, and that selection probably favors greater reproductive effort during periods optimal for juvenile growth and survival.

**Key words:** Costa Rica – Poeciliid fishes    Reproductive seasonality

Most populations show some degree of seasonality in reproduction, particularly in temporally variable environments at intermediate or high altitudes or latitudes. In tropical regions characterized by strong wet-dry seasonality, reproduction is also often markedly seasonal (Janzen 1967, 1979; Lowe-McConnell 1979; Winemiller 1989). Organisms in temporally variable habitats may allocate annual reproductive effort in either of two manners: (1) production of large clutches during a brief and presumably optimal period, or (2) production of multiple clutches, each consisting of a few offspring over short intervals during a more extended favorable period. Among freshwater fishes, large species living at higher latitudes tend to be associated with the former strategy (Mahon 1984; Wootton 1984; Winemiller and Rose 1992), whereas small species from either tropical or temperate regions may exhibit either strategy (Hubbs and Strawn 1957; Kramer 1978; Constantz 1979; Hubbs 1982, Heins and Rabito 1986; Burt et al. 1987; Winemiller 1989; Winemiller and Rose 1992). In environments characterized by relatively small annual variation, organisms may have extended and relatively asynchronous or continuous reproduction. An inverse trend has been noted for the relationship between latitude and spawning season duration and multiple clutching among species of both marine (Johannes 1978) and freshwater fishes (Hubbs 1985; Gotelli and Pyron 1991; Winemiller and Rose 1992).

Fishes of the neotropical family Poeciliidae are almost exclusively ovoviviparous and viviparous (Thibault and Schultz 1978; Constantz 1989). The family shows large interspecific variation in life-history characteristics such as egg size, brood size, interbrood interval, and age at maturity (Reznick and Miles 1989). In addition, several poeciliid species have large within-species variation in life-history traits (Hester 1964; Constantz 1979; Reznick 1982; Stearns 1983; Burns 1985; Snelson 1984, 1985; Trexler 1985; Andersson 1986; Travis et al. 1989; Meffe 1990). Because poeciliids are relatively small and unconstrained by special spawning or larval rearing habitats by virtue of internal gestation, continuous annual reproduc-

tion should be a viable strategy for poeciliids in habitats characterized by low environmental seasonality. Species of the genus *Gambusia* have extended summer spawning seasons in temperate North America (Hughes 1985; Meffe 1985; Botsford et al. 1987; Reznick and Braun 1987; Yan 1987). Even within the temperate zone where annual reproduction remains markedly seasonal, *Gambusia* reproductive periods tend to be of longer duration in more constant spring-fed habitats (Meffe 1985; Yan 1987). In Florida, two seasonal peaks in reproduction, early and late summer, were documented for *Poecilia latipinna*, and no reproduction occurred between November and March (Snelson 1984). Only a few studies have monitored reproduction by natural poeciliid populations in tropical settings. Near the Tropic of Cancer in Mexico, three sympatric species of *Poecilia* (2 sexual species and 1 triploid unisexual species) mate year round but have different periods of peak reproductive output (Balsano et al. 1981). Because males do not discriminate well between unisexual females and bisexual conspecifics, it was hypothesized that asynchrony in reproductive effort might facilitate interspecific coexistence. In Central America, Turner (1938) observed continuous reproduction in *Brachyrhaphis episcopi*. Morris and Ryan (1992) documented continuous reproduction by three *Xiphorus* species in Central Mexican streams. Their preliminary data indicated that females of equivalent size may produce fewer offspring during the summer-fall rainy season when mountain streams are turbid from flooding. Winemiller (1989) collected gravid female guppies, *Poecilia reticulata*, throughout the year in seasonal wet-dry habitats in Venezuela. In Trinidad, Reznick (1989) documented lower reproductive effort by guppies from two wet season samples in comparison with fish from two dry season samples.

This study reports findings from a ten month investigation of poeciliid population ecology in a Central American tropical rainforest. Data obtained from three locally abundant poeciliids demonstrate large intraspecific variation in adult body size and seasonal patterns of gonadal condition, brood size, and population size structure. Available evidence indicates that reproductive effort in these species is greater during wet periods and corresponds with changes in aquatic habitat dimensions, fish densities, the availability of juvenile food resources, and for at least one species, the availability of adult food resources.

## Materials and methods

### A. Study region

Fish populations were investigated in two streams located within Tortuguero National Park in the Caribbean coastal lowlands of Costa Rica's Limon province between 10° 20' and 10° 35' lat. N. The region averages about 5.0 m of rainfall per year with two principal rainy seasons from July to August and November to January (Fig. 1). Generally, no month receives less than 50 mm precipitation, and temperature shows little seasonal variation around annual means ranging between 23–26° C (Hirth 1963). During exceptional years, rainfall may exceed 7.0 m at Tortuguero.

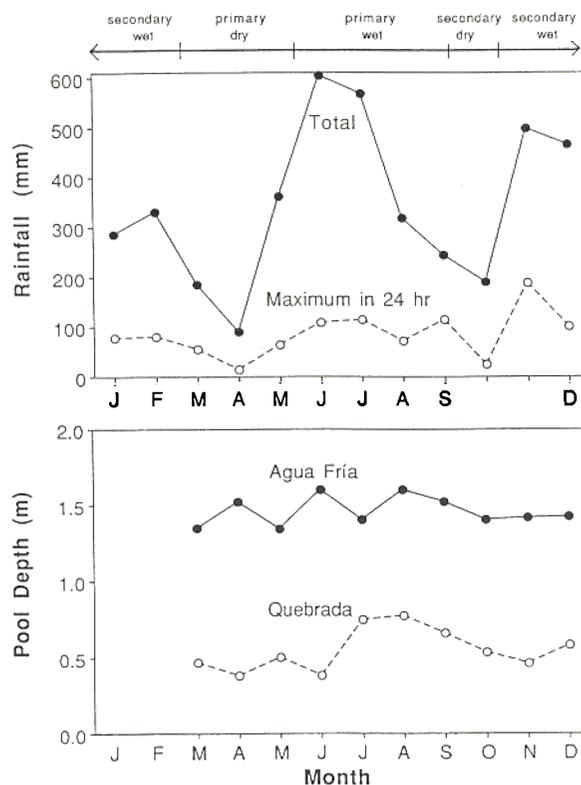


Fig. 1. Monthly rainfall totals and maximum rainfall during a 24 h period for each month recorded at Tortuguero during 1985 (top), and maximum pool depths recorded during each month of the study at two sites (bottom)

During 1985, two wet and two dry seasons were recognized (Fig. 1). Although actual dates may vary by as much as a month and a half, this bimodal rainfall distribution is typically observed each year. Wet seasons occurred from late May until mid-September (referred to here as the "primary wet season") and from early November through March (secondary wet season). Dry seasons occurred from March until early May (primary dry season), and during October (secondary dry season).

Most of the western area of the park is covered by pristine, lowland tropical rainforest, but at least four other vegetative zones are recognized within the reserve: cativo swamp forest, low marsh woodland, herbaceous marshland, and halophytic coastal vegetation. Many of the low marsh woodlands are dominated by the palm *Raphia taedigera*. Apart from the hills of the Lomas de Sierpe in the park's western sector, most of the region is coastal plain lying only several meters above sea level. Sediments of the plain are of alluvial origin, formed by a coalescence of river deltas. A distinctive network of narrow lagoons lies parallel to the coast (for additional descriptions of regional aquatic habitats see Winemiller and Leslie 1992).

### B. Sampling and field measurements

Fishes were sampled each month from two streams in Tortuguero National Park between February and December, 1985. A description of methods used for assessment of habitat characteristics at sampling locations appears in Winemiller and Leslie (1992). The larger habitat, Caño Agua Fria Viejo (AF), is a sluggish braid of the Rio Tortuguero. Some pools of AF exceed 3.0 m depth, but most stream reaches range between 0.5 and 2.0 m. AF exhibits little or no water current during dry periods, and salinity measurements in Caño Agua Fria Viejo never reached 0.1 ppt during the 1985 study period. The substrate of AF consists of sand and patches of

coarse detritus, the latter being most common near the stream margins under floating sedges and associated aquatic plants. Dense mats of floating aquatic plants (*Eichhornia*, *Hydrocotyl*, *Salvinia*, *Azolla*) sometimes cover the entire surface of stream segments during dry periods and are removed by faster currents during wetter periods. During extended wet periods, large areas of the forest bordering AF become flooded with standing water and are colonized by several fish species, including poeciliids.

The other site, Quebrada (QB), is a small creek at the park's northern boundary on the barrier island that separates the sea and the coastal lagoon, Laguna Tortuguero. Because QB has a negligible gradient and drains directly into the lagoon, its lower reaches are under tidal influence during much of the year. Salinity fluctuations were small (<1.0 ppt) in the stream reach adjacent to the lagoon, and salinity measurements from the upper reaches of QB and nearby forest pools never exceeded 0.1 ppt during 1985. The substrate at QB was essentially the same as AF. Water current velocity was relatively slow (0–0.20 ms<sup>-1</sup>) on a year-round basis. Like AF, the forest adjacent to QB is covered with shallow standing water during the wettest months.

Fishes were collected using dipnets (1.0; 3.2 mm mesh) and seines (6.2 × 1.9 m, 4.7 mm mesh; 2.5 × 1.9 m, 3.2 mm mesh) at both sites. A castnet (1.9 m dia., 12 mm mesh) was also used to capture some of the larger *Poecilia gilli* and other large species from the deeper pools (> 1.5 m) at AF. Monthly field sampling did not target any particular fish species or size class; rather, the principal goal was attainment of a large random sample of all species that approximated the natural relative proportions of species at each site. Each monthly sampling effort lasted from 0.5 to 1 day (QB) or from 3 to 5 days (AF), and each day's effort was continued until an hour of collecting produced no additional rare species for the sample (further details given in Winemiller 1990). The capture methods were effective for adult and larger immature size classes of all poeciliid species, but the smallest immature size classes were underrepresented. Fishes were preserved in 10% formalin and later transferred to 45% isopropanol. Voucher specimens and records of sample sites and dates are on file at the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas.

### C. Measurements, indices, diet analysis

All poeciliids were measured for standard length (SL) using vernier calipers. For each monthly sample and each of the two study sites, 20–30 individual specimens were selected for dissection and examination of gonads and stomach contents. The selection of specimens for dissection subsamples was based on size, and sought to represent the approximate size distribution in the larger sample. Whenever fewer than 30 specimens were collected during a particular month at a site, all of the specimens were dissected.

The condition of male and female gonads was coded based on the relative size, texture (smooth, fine grainy, coarse granular), and color (clear, translucent opaque) criteria of Winemiller (1989), in which fully immature and completely regressed gonads are recorded as 1.0 and ripe gonads are coded as 4.0 (for males- large testes with a milky or creamy white appearance; for females- large ovaries with large vitellogenic oocytes). Most gonads at stages 1.5 through 3.5 appeared to be in the processes of maturation; however regressing gonads and post-parturition ovaries would fall within this range as well. Briefly, the index is computed as follows for females: (size[1-small; 2-medium small; 3-medium; 4-medium large; 5-large]) + (color/texture[1-clear or translucent yellow; 2-opaque yellow with visible oocytes; 3-opaque yellow with large mature oocytes])/2. Gonad size criteria for males were the same as those for females, and testis color/texture criteria were 1-clear or translucent, 2-opaque white, 3-smooth milky white. Gonads of females containing embryos at any developmental stage were recorded as condition 5.0. The gonad index scale contains 7 possible values for males and 8 possible values for females. Males that possessed incompletely formed gonopodia (anal fin modified to serve as an intromittent

organ) were recorded as transitional/maturing. Females without dark pigmentation (gravid spot) near the base of the anal fin were recorded as immature, whereas females with gravid spots and stage-1 ovaries were considered mature body size class with immature ovaries. Many of the females in the latter group were probably in a transitional stage of maturation. Relative amounts of visceral fat deposits in males, females, and immatures were estimated following Winemiller's (1989) scale which ranges from 1.0 for no observable fat deposits within the coelomic cavity to 4.0 for a coelom filled with fat deposits that produce a visible bulge in the belly region (scale incremental units = 0.5, resulting in 7 possible values).

Diameters of the largest oocytes from stage 4.0 ovaries were measured through the long axis using a dissecting microscope fitted with an ocular micrometer. The stage of embryonic development was classified according to the following criteria: (1) recently fertilized, or embryo appears as a thin opaque white streak; (2) uneyed embryo; (3) early eyed embryo; (4) intermediate eyed embryo; and (5) late eyed embryo = embryos approximately one week or less away from parturition. This index compares with the index developed by Reznick (1981) for *Gambusia* in the following manner: 1 = Reznick 0 and R 10, 2 = early portion of R 20, 3 = later portion of R 20 plus R 30, 4 = R 40, and 5 = R 50. The number of embryos in each ovary and, when present, the occurrence of multiple embryonic stages within an ovary were recorded. Number of developing embryos was used as the estimate of brood size.

Stomach contents were analyzed following the methods in Winemiller (1990). Most animal food items were identified to order, and plant and detritus categories were grouped according to broader taxonomic and functional categories (e.g., spores, small seeds, vegetative detritus, diatoms, filamentous algae). For *Alfaro*, contents from the anterior half of the gut were identified, sorted, and quantified volumetrically by water immersion. For detritivore/algivores, *Phallichthys* and *Poecilia*, a small sample of the contents from the anteriormost gut was removed and placed on a wet mount slide and examined under a light microscope. Percentages of identified items were visually estimated and the total volume of each consumed item was calculated based on the measured volume of the entire gut and contents (only for the region containing food). Diets are compared as percent volumes of items consumed.

### D. Data analysis

Seasonal variation in species relative abundances in the two local fish assemblages was estimated from monthly field samples. Standard length distributions of mature individuals (females with gravid spots, males with fully formed gonopodia), distributions of relative gonad condition for mature size classes, the percentage of mature females with embryos, and the numbers of juveniles in samples (juveniles = SLs < the minimum SL for confirmed mature individuals) were examined in relation to temporal variation. Because some monthly samples contained fewer than 30 individuals of a given species/sex and the two streams exhibited similar temporal changes in habitat conditions (e.g., habitat and food availability in response to rainfall), life-history analyses were performed on combined AF and QB monthly samples in order to increase sample sizes for comparisons. The distributions of body lengths during the wet (March–May, Oct.) and dry (June–Sept., Nov.–Dec.) seasons did not differ significantly between the two streams in four out of six comparisons (i.e., 3 species × 2 seasons; ANOVA,  $P > 0.05$ ). In addition, the distributions of gonadal indices were compared between sites by species, sex, and season (yielding 12 comparisons), and none of the 12 gonadal comparisons were significantly different (Kolmogorov-Smirnov test,  $P > 0.05$ ).

Relationships between body length and brood size were explored using linear regression (least squares method based on ln-transformed data) and relationships among body length, gonadal condition, and visceral fat deposits were examined with Spearman's correlation coefficient ( $r_s$ ). For each species, the minimum length at

maturity, maximum body length, brood size, mature oocyte diameter, relationship between female size and fecundity, and seasonal diet shifts were determined. The effect of season on brood size was examined by comparing slopes and intercepts of the female body size-brood size regressions for each season. Relative consumption of different food categories during different seasons was compared using Chi Square (class entries are the volumetric proportions).

## Results

### A. Species relative abundances

Excluding consideration of the lower stream reach adjacent to the lagoon, a total of 21 species was collected from the small creek, QB. Only three poeciliid species *Alfaro cultratus*, *Phallichthys amates*, and *Poecilia gilli*, were continuously present during the entire 10 month sampling period. Total numbers of individuals collected from QB during the study were 630 (*Alfaro*), 533 (*Phallichthys*), and 322 (*Poecilia*). Approximate numerical relative abundances based on the entire fish community and 10 month sample period were 0.19 for *Alfaro cultratus*, 0.16 for *Phallichthys amates*, and 0.11 for *Poecilia gilli*. Sample relative abundances of *Alfaro* change little with season (0.18 wet, 0.21 dry), whereas relative abundances changed approximately two-fold in *Phallichthys* (0.11 wet, 0.21 dry) and *Poecilia* (0.15 wet, 0.07 dry) at QB. During the wet seasons, all three poeciliids were commonly captured from both stream channel and flooded forest pools.

Of the 57 fish species collected at AF, five were poeciliids (*Alfaro*, *Belonesox belizanus*, *Phallichthys*, *Poecilia*, *Brachyrhaphis parismina*). Total numbers of individuals collected from AF during the study were 165 (*Alfaro*), 142 (*Belonesox*), 51 (*Brachyrhaphis*), 451 (*Phallichthys*), and 313 (*Poecilia*). The numerical relative abundances (estimated over 10 mo) were 0.12 for *Phallichthys*, 0.105 for *Poecilia*, 0.02 for *Alfaro*, 0.02 for *Belonesox*, and 0.005 for *Brachyrhaphis*. *Belonesox* and *Brachyrhaphis* samples were too small for analysis of reproductive seasonality. The relative abundances of the three common poeciliids changed little with season (*Phallichthys*- 0.10 wet, 0.13 dry; *Poecilia*- 0.10 wet, 0.11 dry; *Alfaro*- 0.01 wet, 0.03 dry). AF poeciliids also dispersed into the forested floodplain during the wet seasons, however some individuals remained in the main stream channel where they were frequently observed and captured.

### B. Temporal pattern of reproductive indice and population structure

The three common species display a considerable range of values between minimum and maximum adult sizes of each sex (Table 1, Fig. 2), and the range was greater in females than males. Size frequency distributions were unimodal for both mature males and females of all three species (Fig. 2). There were no statistically significant relationships between body length and gonadal index for males of any of the species ( $r_s$  ranging from 0.02 to 0.26, df range = 44–70,  $P > 0.05$ ). Females had statis-

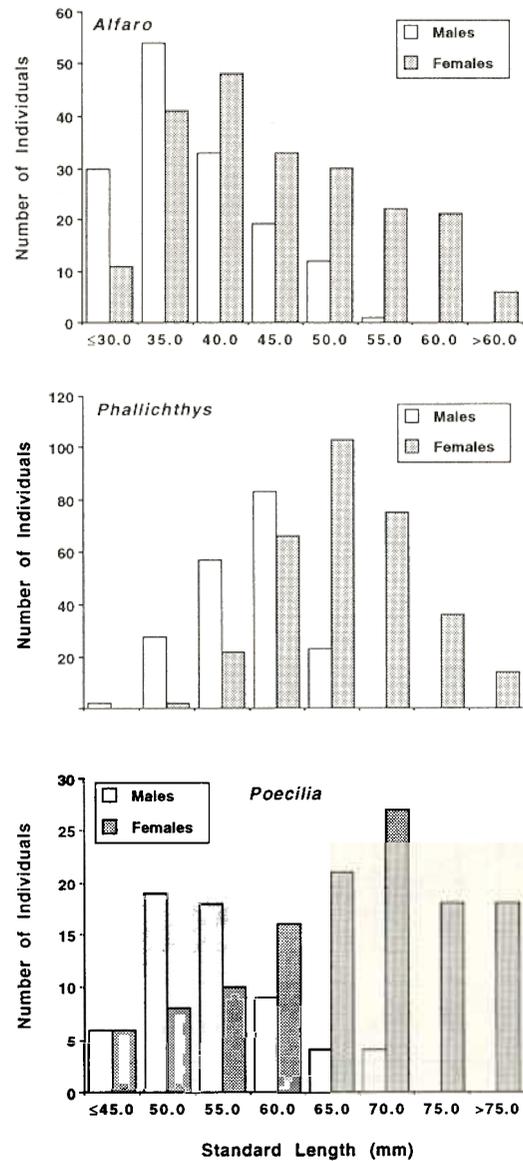
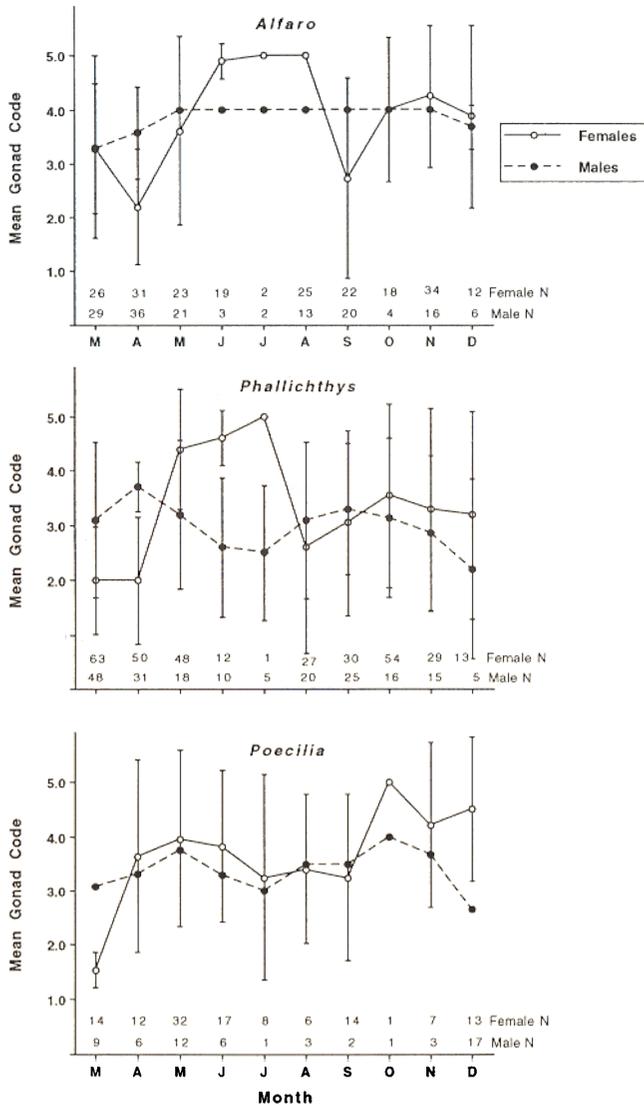


Fig. 2. Frequency distributions of size intervals of mature male and female *Alfaro cultratus*, *Phallichthys amates*, and *Poecilia gilli* (species data combined for all months and both streams)

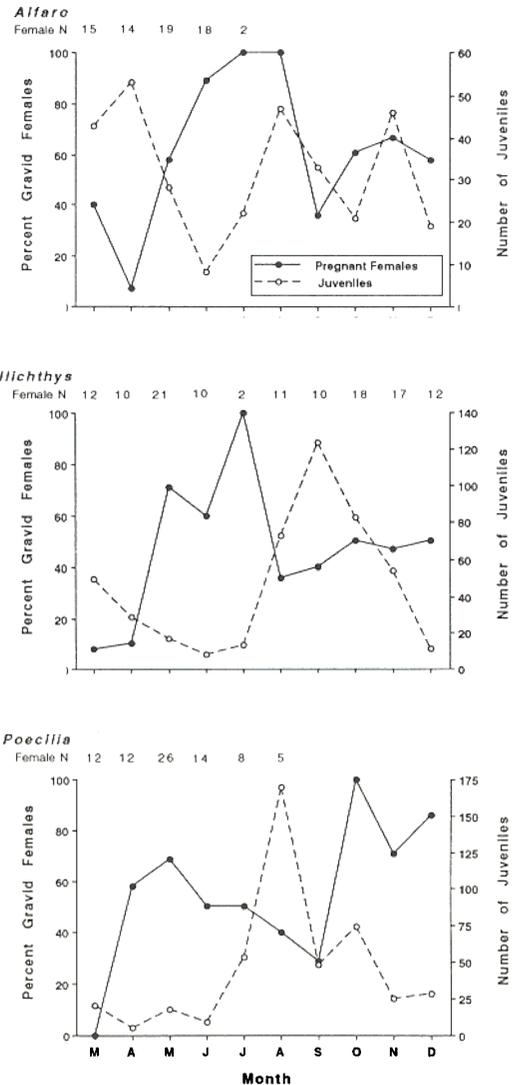
Table 1. Life history data recorded for three common poeciliids at Tortuguero, Costa Rica. All units are in mm standard length (SL); ranges are for smallest to largest SLs recorded for mature individuals;  $N_{\text{Adults}}$  is the total number of mature individuals examined

	Smallest mature	Largest immature	Largest mature	Range <sub>sm-lg</sub>	$N_{\text{Adults}}$
<i>Alfaro</i>					
Males	24.7	31.8	50.3	25.6	150
Females	27.8	37.4	65.5	37.7	212
<i>Phallichthys</i>					
Males	19.6	32.8	38.0	18.4	193
Females	21.6	35.9	55.0	33.4	328
<i>Poecilia</i>					
Males	39.8	52.0	71.9	32.1	
Females	37.3	57.6	93.2	55.9	



**Fig. 3.** Mean gonadal index values (with standard deviation bars) for monthly samples of mature male and female *Alfaro cultratus*, *Phallichthys amates*, and *Poecilia gilli*. Values for males may range between 1 (no evidence of gonadal recrudescence) and 4 (maximum gonadal development) for males and between 1 (no recrudescence) and 5 (pregnant) for females (species data combined for all months and both streams)

tically significant but low correlations for body length with gonadal index (*Alfaro*  $r_s=0.25$ ,  $df=130$ ,  $P<0.05$ ; *Phallichthys*  $r_s=0.43$ ,  $df=124$ ,  $P<0.0001$ ; *Poecilia*  $r_s=0.49$ ,  $df=105$ ,  $P<0.0001$ ). The dissected material yielded enough data to plot means and standard deviations of gonad condition for each sex/species over ten continuous months (Fig. 3). Male *Alfaro* showed little evidence of seasonality in the condition of testes, whereas females exhibited two peaks and two brief periods of depression (April, September) in the mean condition of ovaries (Fig. 3). The pattern observed in the percentage of adult female *Alfaro* containing embryos mirrors the mean gonad index (Fig. 4). A reduction in the relative occurrence of juveniles followed the April reduction in ovarian and embryonic indices by approximately two months (Fig. 4), and a second reduction in the relative



**Fig. 4.** Percentages of pregnant females and the number of juveniles in monthly samples of three live-bearing poeciliid fishes (species data grouped across streams). Juveniles are defined as individuals <SL of the smallest mature male of the species (values appear in Table 1)

occurrence of juveniles coincided with the second reduction in ovarian and embryonic indices.

Both *Phallichthys* and *Poecilia* exhibited seasonal patterns of female ovarian and embryonic indices similar to those observed in *Alfaro*. Compared with *Alfaro*, the beginning of the first peak occurred a month earlier (May) in *Phallichthys* and two months earlier (April) in *Poecilia*, whereas the temporal pattern for the second peak was nearly identical in the three species (Fig. 3). Unlike *Alfaro* males, *Phallichthys* and *Poecilia* males had seasonal patterns of mean testicular condition, although the amplitude of the seasonal cycle was much smaller than the female amplitude (Fig. 3). Most of these adult males had medium to large, smooth-white testes (mean index values 3–4) and were probably reproductively active year round. The low-amplitude cycle of the mean

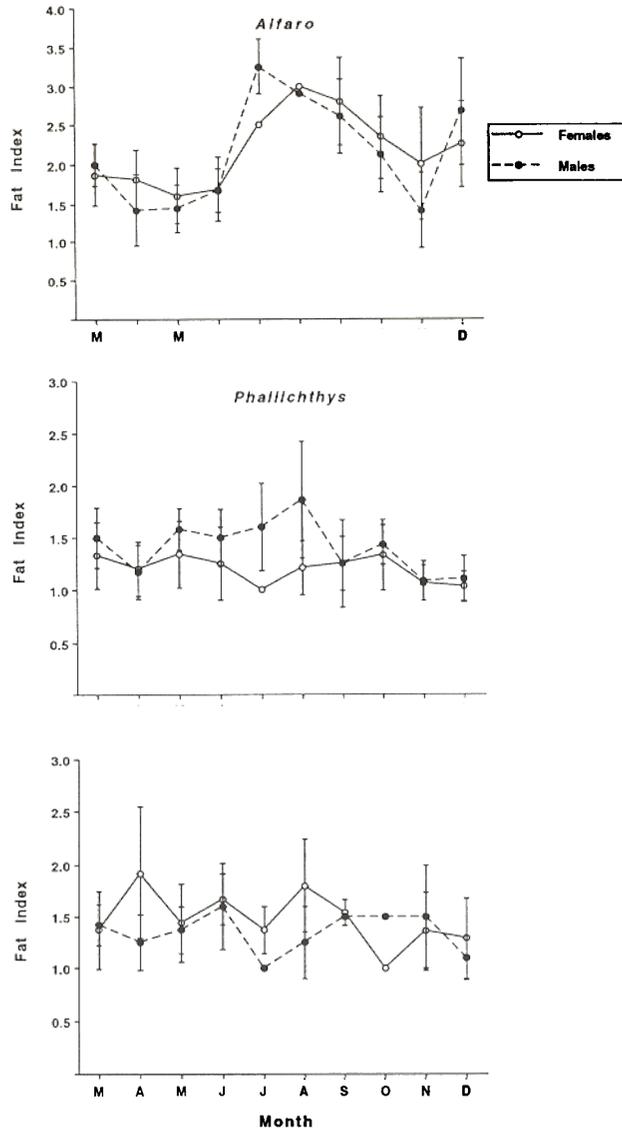


Fig. 5. Monthly variation in the mean visceral fat index in male and female poeciliids. (bars equal one standard deviation, sample sizes are the same as in Fig. 3)

testicular index of male *Phallichthys* was advanced by about one month relative to the female cycle. In the case of *Poecilia*, the relatively small variation in the mean testicular index closely matched the temporal pattern displayed by female reproductive indices. The temporal trends in the percentages of immatures shown by *Phallichthys* and *Poecilia* were qualitatively similar to that shown by *Alfaro*; except that the juvenile peak that began in June lasted much longer into the primary wet season for *Phallichthys* and *Poecilia*, and the second juvenile depression began later, during October or November–December compared with August–September in *Alfaro* (Fig. 4).

The visceral fat index was only weakly associated with body length in male *Poecilia* ( $r_s = 0.34$ ,  $df = 44$ ,  $P < 0.05$ ) and in females of two species (*Alfaro*  $r_s = 0.23$ ,  $df = 130$ ,  $P < 0.025$ ; *Poecilia*  $r_s = 0.30$ ,  $df = 105$ ,  $P < 0.05$ ). The mean fat index varied in a cyclic pattern in both sexes of

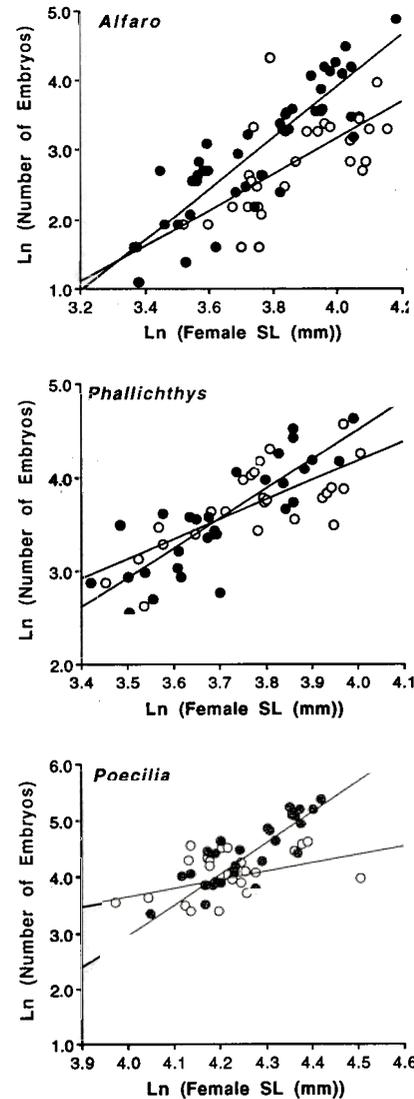
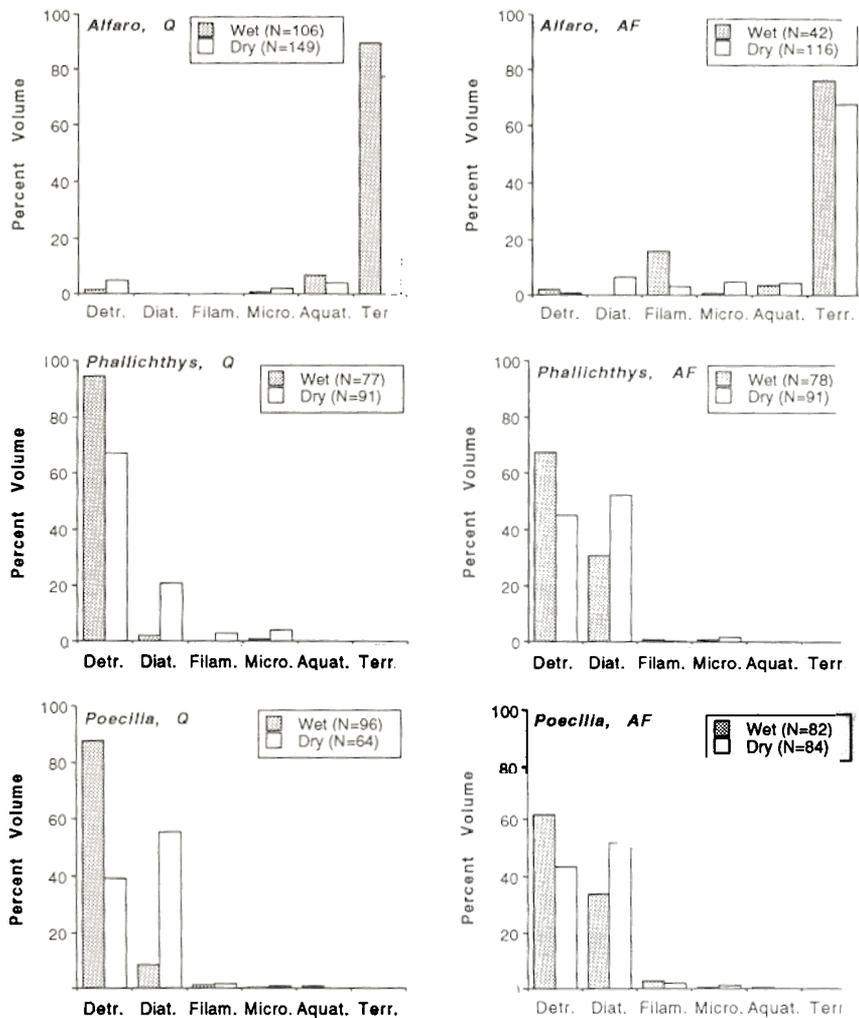


Fig. 6. Relationships between female body length and the number of embryos for three poeciliids. Filled circles correspond to wet season samples, open circles are from dry season samples. Correlations between  $\ln(\text{standard length})$  and  $\ln(\text{number of embryos})$  were as follows: *Alfaro*, wet,  $r^2 = 0.77$ ,  $F_{1,42} = 137.49$ ,  $P < 0.0001$ ; *Alfaro*, dry,  $r^2 = 0.44$ ,  $F_{1,27} = 20.50$ ,  $P < 0.0001$ ; *Phallichthys*, wet,  $r^2 = 0.71$ ,  $F_{1,27} = 65.40$ ,  $P < 0.0001$ ; *Phallichthys*, dry,  $r^2 = 0.56$ ,  $F_{1,24} = 28.81$ ,  $P < 0.0001$ ; *Poecilia*, wet,  $r^2 = 0.55$ ,  $F_{1,26} = 31.45$ ,  $P < 0.0001$ ; *Poecilia*, dry,  $r^2 = 0.10$ ,  $F_{1,24} = 2.58$ ,  $P = 0.12$  (see Results for comparisons of regression slopes and intercepts)

*Alfaro* (Fig. 5), each with a large peak during July–September (primary wet season) and the beginnings of another increase in fat deposits during December (secondary wet season). The fat index for both sexes of *Phallichthys* and *Poecilia* varied relatively little on a temporal basis and produced no discernible seasonal pattern (Fig. 5). Male *Phallichthys* had relatively more visceral fat than females during the primary wet season.

Samples were female-dominated when adult sex ratio ( $N_{\text{males}}/N_{\text{females}}$ ) was calculated on an annual basis (*Alfaro*-0.71; *Phallichthys*-0.59; *Poecilia*-0.48). Adult sex ratios based on monthly samples were all either nearly even or



**Fig. 7.** Volumetric percentages of aggregate diet items consumed by three poeciliids at Quebrada (Q) and Agua Fria (AF) during the wet and dry seasons (*Detr.* = detritus, *Diat.* = diatoms, *Filam.* = filamentous algae, *Micro.* = microcrustacea, *Aquat.* = aquatic insects, *Terr.* = terrestrial arthropods. Sample sizes for each season appear in legend boxes

female-biased (ratio  $\leq 1.0$ ), except for two instances in which sample sizes were very small ( $n < 10$ ).

### C Season-length-fecundity relationships

All three species had positive slopes in the relationship between female size and number of embryos (Fig. 6). Slopes were significantly greater for females collected during the wet season compared with the dry season (*Alfaro*,  $t = 3.44$ ,  $df = 53$ ,  $p < 0.01$ ; *Phallichthys*,  $t = 9.51$ ,  $df = 53$ ,  $p < 0.0001$ ; *Poecilia*,  $t = 4.86$ ,  $df = 52$ ,  $p < 0.0001$ ). Because regression slopes were different, ANCOVA for the effect of season on brood size (with SL as the covariate) was not performed. Figure 6 clearly illustrates a marked tendency for the largest females to produce larger broods during the wet seasons. Table 2 presents the average brood size for each species by season broken down by three different body length criteria. Average brood sizes were much larger during the wet seasons, and the differences between seasons were greater when comparisons were based on larger female size classes (Table 2).

Based on intraovarian embryos, clutch sizes ranged from 3 to 130 (*Alfaro*,  $x = 24$ ), 13 to 103 (*Phallichthys*,

**Table 2.** Seasonal comparisons of the average number of developing embryos in ovaries of female poeciliids broken down by different minimum body length criteria (sample sizes in parentheses)

Season	<i>Alfaro</i>		
	All females	Females > 45 mm	Females > 55 mm
Dry	18.9 (29)	26.0 (16)	26.9 (9)
Wet	27.2 (44)	44.3 (21)	66.7 (6)
Season	<i>Phallichthys</i>		
	All females	Females > 40 mm	Females > 45 mm
Dry	42.0 (26)	50.3 (19)	55.1 (9)
Wet	43.7 (29)	57.4 (15)	67.3 (10)
Season	<i>Poecilia</i>		
	All females	Females > 65 mm	Females > 75 mm
Dry	57.8 (26)	71.8 (18)	81.7 (4)
Wet	91.7 (28)	103.0 (22)	152.4 (9)

$x=43$ ), and 7 to 210 (*Poecilia*,  $x=75$ ). The mean standard lengths of females containing embryos were 45.6 mm (*Alfaro*), 42.5 mm (*Phallichthys*), and 69.7 mm (*Poecilia*). Maximum diameters of mature oocytes were 3.75 mm (*Alfaro*), 2.10 mm (*Phallichthys*), and 3.00 mm (*Poecilia*), and oocyte diameter was unrelated to female size in each case ( $P>0.05$ ).

#### D. Seasonal diet shifts

Volumetric analysis of stomach contents revealed three feeding guilds among the five poeciliid species captured at the two study sites: algivore/detritivores (*Phallichthys*, *Poecilia*), terrestrial arthropod feeders (*Alfaro*, *Brachyrhaphis*), and a piscivore (*Belonesox*). *Phallichthys* and *Poecilia* each consumed significantly greater fractions of detritus during the wet seasons and greater fractions of diatoms during the dry seasons at both the QB (*Phallichthys*  $X^2=20.14$ ,  $df=1$ ,  $P<0.0001$ ; *Poecilia*  $X^2=53.89$ ,  $df=1$ ,  $P<0.0001$ ) and AF (*Phallichthys*  $X^2=10.58$ ,  $df=1$ ,  $P<0.0025$ ; *Poecilia*  $X^2=7.20$ ,  $df=1$ ,  $P<0.01$ ) study sites (Fig. 7). *Alfaro* consumed mostly small terrestrial insects, especially ants, throughout the year. However during wet seasons, greater diet fractions consisted of ants and other terrestrial insects, particularly at site QB (Fig. 7; site QB,  $X^2=5.09$ ,  $df=1$ ,  $P<0.05$ ; site AF,  $X^2=1.59$ ,  $df=1$ ,  $P=0.21$ ).

## Discussion

### A. Rainfall distribution, resource availability, and reproductive phenology

The mesic tropical environment of the Tortuguero region supports relatively stable aquatic habitats compared with other tropical regions, such as savannas (Lowe-McConnell 1964; Winemiller 1989; Chapman and Kramer 1991) and large floodplain ecosystems (Lowe-McConnell 1979; Welcomme 1979). The park's dense rainforests may partially buffer aquatic habitats from seasonal changes in the intensity of insolation and stream discharge rates due to subsurface flow and precipitation runoff. Yet these aquatic environments are not constant, and the heavy rainfall during June–August and November–December resulted in a variety of environmental changes in both streams during 1985. At each site, increased stream discharge resulted in higher midchannel current velocities, scouring of sandy substrates, downstream transport of coarse detritus and aquatic macrophytes, and extensive flooding of the forest adjacent to the stream channels (Winemiller 1990).

From the perspective of poeciliid fishes inhabiting these streams, sheet flooding of the forest should have the greatest influence on ecological interactions. Among the species examined here, a major portion of each local population inhabited the flooded forest during the wet seasons. For example, the terrestrial arthropod-feeder, *Alfaro cultratus*, was usually captured near the edge of shallow pools during dry seasons and from both shallow pools and flooded forest during wet seasons. The availability of shallow aquatic habitat increased many-fold

during the rainy season floods at both study sites. Even though the total numbers of individual fishes could actually increase during the wet seasons (via higher reproductive effort in females), densities on a per-area basis are greatly reduced within the expanded floodplain habitat.

The available evidence for the three poeciliids supports a hypothesis of year-round reproduction by these populations. However, there was also good evidence that the condition of female gonads and proportions of gravid females of the three species peaked just prior to or during the early phase of the two wet seasons at Tortuguero (Figs. 3, 4). Males exhibited relatively little seasonal variation in mean testicular condition, although *Phallichthys* and *Poecilia* showed low amplitude cycles that were either in phase with, or slightly ahead of, those exhibited by conspecific females (Fig. 3). In all three species, the average clutch size was larger during the wet season, primarily because the largest females tended to produce much larger than average broods (Fig. 6, Table 2). During the wet season, environmental conditions in the flooded forest are better for the growth and survival of juveniles (see discussion below), and production of the largest clutches by the largest females largely coincides with this period. This synchronization of reproductive effort with optimal habitat conditions could result from several different potential mechanisms, including: (1) greater incidence of fertilizations due to more frequent encounters with males during the low water period of high fish densities just prior to the beginning of the rainy season, (2) greater availability of energy-rich adult food resources leading to greater reproductive output during the wet season, and (3) synchronization of reproductive effort with optimal conditions for juvenile growth and survival involving physiological response to subtle physicochemical environmental cues.

*Mating frequency-fecundity hypothesis.* Males should encounter females with greater frequency during the peak dry season and with less frequency during the wet seasons when the population is dispersed within the flooded forest. During wet seasons, adult poeciliids were almost always collected as isolated individuals and were never collected or observed as dense aggregations within the flooded forest. In contrast, groups of approximately 10–50 conspecifics were frequently pursued with nets from open water into vegetation during the dry season (observed for all three species). All three species store sperm in their ovaries, so that broods are produced for several months in the absence of contact with males. More frequent matings may produce larger broods. In at least one poeciliid (*Xiphophorus maculatus*), fertilizations from stored sperm produced significantly smaller broods than those from multiple recent inseminations (Borowsky and Kallman 1976). In many insect species, greater mating frequency yields higher fecundity (reviewed in Ridley 1988).

Annual adult sex ratios were heavily female biased in the three poeciliids, and this raises the possibility that adult males may suffer higher levels of predation than females, especially during low water periods (but see also Kallman 1984 for evidence of female biased secondary

sex ratios in (*Xiphophorus maculatus*). Conspicuous coloration and courtship have been shown to increase predation mortality in male guppies and other poeciliids (Farr 1975; Endler 1980, 1982). Additionally, male poeciliids tend to be significantly smaller than female conspecifics, and predation is frequently size-dependent in aquatic communities with smaller organisms suffering higher mortality rates (Miller et al. 1988). At Tortuguero, adult males might be less common than females, because they suffer higher mortality during dry periods when fishes are confined to stream channels at relatively high densities per unit area. This would be consistent with Reznick's (1989) comparative study of Trinidad guppies, in which he noted a greater effect of predation on male traits in dry season samples.

Although additional information is required to falsify the mating frequency-fecundity hypothesis, it seems somewhat unlikely based on the consistent seasonal pattern of cycling in mean ovarian condition observed in all three species. If the frequency of recent inseminations explains brood size variation, then the mean ovarian index (revealing the relative stage of gonadal recrudescence) should not produce a consistent seasonal pattern. Only in the case in which many mature females were virgins might the mean gonadal index reflect mating frequency, because virgins would attain developmental ovarian stage 4 (ripe) while mated females would progress to stage 5 (gravid).

*Nutrition-fecundity hypothesis.* If resources are more limited in crowded stream channels during dry periods, then slower rates of gonadal recrudescence and smaller broods could result from lower nutritional intake. Constantz (1979) reported that *Poeciliopsis occidentalis* from desert springs allocated relatively less energy to reproduction during periods when food was less available. Female guppies grow faster and have larger clutches when provided with more food in the laboratory (Hester 1964; Reznick 1983). Reznick and Braun (1987) showed that male fat reserves in *Gambusia affinis* were lowest during the late summer when food was less available, but that female fat reserves increased and reproductive effort decreased during the same period. They hypothesized that fat reserves allow females to store energy and shift the timing of reproductive effort to optimize fitness under changing environmental conditions in the temperate zone. Fat deposits in the two algivorous/detritivorous Tortuguero poeciliids varied only to a small extent in either sex on a monthly basis. Monthly variation in mean fat deposits in both sexes of the insectivorous *Alfaro* produced a cyclic pattern that was shifted from one to two months behind the seasonal cycle of precipitation and female reproductive effort. During the wet seasons, frequent heavy rains wash ants and other terrestrial invertebrates into the water, so that *Alfaro* very likely have greater rates of encounter with small terrestrial invertebrates trapped at the water's surface. During the wet seasons at site QB, ants comprised 72% of *Alfaro*'s diet (by volume) with only 2% detritus and chitin fragments (at site AF wet season, 77% terrestrial arthropods, 5% detritus and chitin). In contrast, the dry season diet of

*Alfaro* in the channel of QB consisted of 54% ants and 11% detritus and chitin (site AF dry season, 68% terrestrial arthropods, 5% detritus). Detritus and chitin fragments were probably consumed either incidentally with other food items or were sampled while searching for more nutritious food items.

Diets of *Phallichthys* and *Poecilia* were actually dominated by more nutritious food items during dry seasons compared with the wet seasons when reproductive allocation was greatest. During dry seasons, algae, especially diatoms, were the major diet component of both species, and each switched to feeding on greater fractions of detritus during high water (Fig. 7). Guppies from piedmont streams in western Venezuela show very similar diet shifts in relation to season (dry season diet = 39% algae by volume, 41% detritus; wet season diet = 13% algae, 46% detritus; total N = 146; and see Winemiller 1990 for more description of the Caño Volcán ecosystem). Living algal cells have greater nutritional content than detritus. For example, algivorous loricariid catfishes in Panama grew much faster on an algae diet and lost weight on a diet comprised of silt (Power 1984). Standing stocks of algae were visibly greater in stream channels during the dry season at Tortuguero, and the community-wide pattern of consumption reinforced this view (Winemiller 1990). Much of the dry-season algal biomass was diatoms attached to the surfaces of aquatic macrophytes and coating the surface of stable sand banks in shallow water. Wet season rains increase stream current velocities, and much of the macrophyte biomass and associated periphyton and microfauna (collectively referred to as "aufwuchs") is transported to the coastal lagoon and ultimately to the sea. Periphyton remaining in wet season channels is largely restricted to the margins where currents are slow, plus areas of swift current where submerged *Eichhornia* are rooted in the substrate beneath a layer of shifting sand (the latter refers to AF).

The seasonal pattern of diet shift in the algivorous/detritivorous species ran counter to the hypothesis that reproductive allocation is synchronized with the availability of adult food resources. Unlike the insectivorous *Alfaro*, visceral fat bodies in these species did not seem to be heavily utilized for nutrient storage (Fig. 5). Because poeciliids are livebearers, there could be a time lag of several weeks between the sequestering of acquired nutrients into oocytes, fertilization, and parturition. In these species, nutrients gained during dry season foraging could be allocated to reproductive tissues very quickly, resulting in little visceral fat accumulation. Brood sizes might be augmented during the initial phase of the ensuing wet season, but this effect could not endure for more than 4–6 weeks (the gestation time). In contrast to the current study, Reznick (1989) found that female guppies from two wet season samples in Trinidad had significantly lower reproductive output than females from dry season collections. He concluded that food resources are less available for guppies during the wet season because high stream discharge leaves a layer of silt that may interfere with algae-scraping by guppies. He also noted that sizes at maturity and parturition were greater for wet season guppies, and this ran counter to expectations of a food

limitation hypothesis based on earlier laboratory findings. Foraging dynamics similar to those inferred for Trinidad populations were documented in guppies inhabiting a Venezuelan piedmont stream. The primary difference between the Tortuguero streams and the examples from Trinidad and Venezuela is the greater topographical relief in watersheds of the latter. In moderate and high gradient streams in the tropics, the dry season produces a relatively stable aquatic environment for algivorous poeciliids. In low gradient streams, like sites AF and QB, heavy rains cause large-scale and persistent lateral flooding rather than the brief spates experienced by high gradient streams. Whereas attached algae are more available during the dry season in both kinds of stream systems, alternative food resources, such as soil humus and its associated microfauna, are readily available in flooded forests along low gradient streams.

If food limitation were a factor driving higher wet season reproductive effort, then seasonal changes in the density of competitors, both conspecific and heterospecific, might reinforce a pattern of reduced reproductive effort during periods of lower food availability. The density of conspecifics was shown to influence the fecundity of female topminnows, *Poeciliopsis occidentalis*, in the field (Schoenherr 1977) and female guppies in the laboratory (Dahlgren 1979). Warren (1973) found that guppies housed at low densities achieved significantly lower fecundities when water from high density populations was introduced into their aquarium. However, it seems doubtful that poeciliid densities at Tortuguero could have been high enough to produce either an intraspecific competitive bottleneck or a chemical inhibition effect (maximum densities were estimated between 1.7 and 2.0 gm<sup>-2</sup> for the three species).

*Synchrony of reproductive effort with optimal conditions for juvenile growth and survival.* With regard to physiological response to environmental cues, longer photoperiod was shown to increase the production of yolked eggs and embryos and increase gonadal indices of male *Poeciliopsis gracilis* at ~14° N in El Salvador (Burns 1985). Photoperiod varies only slightly at Tortuguero (~8° N) but potentially could provide a cue for predicting future ecological conditions (Schwassman 1978). If the Tortuguero poeciliids possess physiological mechanisms for adjusting reproductive output in response to perceived environmental cues, this would imply either that the physiological responses are adaptive in the current environmental setting, or that they are neutral or maladaptive and derived from the ancestral condition and may have been adaptive in a historical setting.

Regardless of the proximate mechanism that may yield greater reproductive effort during the wet season, this strategy should be adaptive with respect to juvenile predation mortality. Desiccation of the forest floor during dry periods results in higher absolute densities of fishes, both piscivores and their prey. For example, the largest common piscivore at QB, *Rhamdia guatemalensis* (Pimelodidae), was very dense during September–November (mean biomass approximately 33.5 gm<sup>-2</sup>). At this time, most of these catfish were young-of-the-year

individuals that entered the creek coincident with the drying of the forest floor, and many had empty stomachs and were extremely thin. The other large piscivore at QB, *Gobiomorus dormitor* (Eleotridae), was captured from the stream channel, but not from the flooded forest. At both study sites, several potential predators of poeciliid neonates were taken at their highest densities within the stream channel during the dry season, and include: *Astyanax fasciatus* (Characidae), *Belonesox belizanus* (Poeciliidae), *Cichlasoma dovii* (Cichlidae), *Cichlasoma loisellei*, and *Eleotris amblyopsis* (Eleotridae) (see Winemiller 1990 for additional information on fish assemblages). Clearly, the threat of predation on small immature poeciliids was much greater within the confines of the dry-season creek channel in relation to the expanded wet season environment in the flooded forest.

Neonate and juvenile food resources should be more abundant and growth should be faster in the vast area of the flooded forest compared with the confines of dry-season stream channels. Clearly, the availability of microfauna that form important parts of juvenile diets of all three species is greatest in the flooded forest. Estimates of prey availability based on volumetric consumption by the entire fish community indicated that detritus, associated microfauna (protozoa, rotifers, microcrustacea) and tiny arthropods at the water-air interface (Collembola, Insecta) were relatively more abundant during the wet season at both Tortuguero sites (Winemiller 1990 and unpublished data). Alternative mechanisms for seasonal reproductive effort in rainforest poeciliids could be tested with field studies that use enclosures to control the access of males to conspecific females, the access of females to different habitats and food resources, and the densities of predatory fishes in different microhabitats.

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