

POPULATION DYNAMICS OF THE FISH  
*POECILIA GILLII* (POECILIIDAE) IN POOLS OF  
AN INTERMITTENT TROPICAL STREAM

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SUMMARY

(1) This study examines the population ecology of *Poecilia gillii* (Kner & Steindachner, 1863), a small algae- and detritus-feeding fish, inhabiting sixteen isolated, residual pools of a high-gradient, intermittent stream in Costa Rica following floods which severely reduced the number of fish in the stream.

(2) Immediately after the floods, population sizes averaged 20% and pool surface areas 130% of their pre-flood values, periphyton production was relatively low and dissolved oxygen was relatively high. Among pools, population densities were not correlated with their pre-flood values, and the population growth rates showed a weak negative correlation with density, a marginal positive correlation with periphyton production and no correlation with oxygen.

(3) Near the end of the 153-day post-flood study period, population sizes had risen to 50% of their pre-flood values, while pool areas had fallen to 73% of their pre-flood values. Periphyton production was relatively high and dissolved oxygen was very low. Among pools, population densities were correlated with their pre-flood values, and the population growth rate showed a strong negative correlation with population density and strong positive correlations with periphyton production and dissolved oxygen level.

(4) These results suggest that in highly seasonal tropical environments, temporal patterns of population abundance in high-gradient streams will be very different from those in floodplains, where the rainy season is a time of increase and the dry season a time of decline. Spatial variation in environmental characteristics which control periphyton, detritus and oxygen availability may produce characteristic population densities in different pools. An increase in the proportion of males and a decrease in their size after the floods suggest social inhibition of sexual maturation during the late dry season.

INTRODUCTION

In many tropical regions, rainfall shows extreme seasonal variations, dramatically altering the habitats of aquatic organisms. These changes play a prominent role in the movement patterns and distribution of fishes (Daget 1957; Holden 1963; Bonetto et al. 1969; Lowe-McConnell 1964, 1967; Welcomme 1979; Goulding 1980; Smith

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1981). During high water, fishes can move freely and select among a wide range of habitats, while low water restricts them to isolated pools or the main channels of larger rivers. Here, habitat quality deteriorates due to desiccation, decomposition of plant and animal remains, loss of refuges from predation, and reduced food availability (Ihering & Wright 1935; Lowe-McConnell 1964, 1975; Kushlan 1974; Welcomme 1979; Cordiviola & Pignalberi 1981). As fish in residual pools must tolerate whatever adverse conditions develop, variability among residual pools may contribute to the divergence of populations and community assemblages as the dry season progresses. However, the effect of seasonal and spatial variation on the population dynamics of tropical fishes has received surprisingly little attention from aquatic ecologists.

Here, we address the effects of spatial heterogeneity among residual dry season water bodies on their fish populations. We focus on *Poecilia gillii* (Kner & Steindachner 1863), a small fish inhabiting an intermittent tropical stream in the dry forest of north-west Costa Rica. We document the changes in population size and composition in relation to pool size, water quality and pre-flood population characteristics in a series of isolated residual pools following a period of flooding which severely reduced the populations. Related studies (Chapman 1990) examine the role of the floods in dispersal and population loss, and document in detail the seasonal and spatial patterns in water quality in the same system.

#### SPECIES AND STUDY SITE

In Costa Rica, *P. gillii* is found in swamps, small streams, fast flowing rivers and even estuaries, but is most common in quiet waters (Bussing 1987). It feeds primarily on detritus and periphyton (Bussing 1987; L.J. Chapman, pers. obs.), and is viviparous, producing young throughout the year if conditions are favourable.

The study site, Quebrada Jicote (described in detail in Chapman 1990), is a small, high-gradient, first-order tributary of the Rio Poza Salada, located within Santa Rosa National Park, Guanacaste Province, Costa Rica (10°50'N Latitude, 85°38'W Longitude). Several gobies in one pool were the only other fish species present. The climate of the region is highly seasonal. Rainfall in the park has averaged 1527 mm year<sup>-1</sup> (range 915–2240 mm year<sup>-1</sup>, D.H. Janzen, unpublished 1988), mostly falling between May and November. During the rainy season, the streams and rivers flow only during and after substantial rains, but form a series of isolated pools the rest of the time. During the dry season, only a few springs and pools retain water. These residual pools may be isolated for up to 90% of the year. By the late dry season, Q. Jicote consists of about twenty pools. The most upstream of these, the 'Source Pool', is also the largest (18 m diameter, 167 cm mean depth). Fed by a 16-m high waterfall during the rainy season, it represents the upstream limit of fish distribution.

The data for this study were collected between May 1987 and March 1988 with supplementary observations from earlier visits to the study site. This study period included two periods of stream flow. The first was a severe flood in early August followed by 10 days of flow. The second flood which occurred in early October following 51 days without flow was milder and accompanied by 12 days of flow. During both floods, many fish moved out of their dry season refuges. In the first flood, population loss per pool averaged 75% (range 12–99%) primarily due to fish becoming trapped in desiccating 'graveyard' pools. Variation in loss was correlated most strongly with pool size and streambed slope, with a weak effect of population

density. In the second flood, population loss was insignificant (Chapman 1990).

## METHODS

A detailed description of the measurement of environmental variables is provided by Chapman (1990). Briefly, the location of the pools within the streambed, their area and bathymetric characteristics were measured in the late dry season. Pool perimeters were remapped following the floods when they were close to their maximum size. Water levels were recorded throughout the study. Mid-afternoon dissolved oxygen concentration was monitored with oxygen meters at 4–6 week intervals in all study pools, using three to six readings from randomly selected locations in each pool. Relative net periphyton production among pools was estimated after the floods (November) and in the dry season (February), using algal growth on pieces of filter paper suspended 15 cm below the water surface in plastic cups ( $n = 3$  per pool) covered with fine mesh netting to exclude fish and larger invertebrates. After 7 days the pigment was extracted in 20 ml of absolute alcohol and estimated by light transmission to a simple photometer.

Population size, density and composition in sixteen pools (fourteen in Q. Jicote and two in R. Poza Salada) were examined before and after the two major floods and four times over a 153-day period following the second flood. (Three of these pools did not have fish before the period of stream flow.) A mark–recapture sampling regime was established in June 1987 prior to the first flood, to estimate the population size of fish  $\geq 25$  mm (total length, TL). Fish were captured using six baited minnow traps, set in grids randomly selected for each sample, with the mark sample on one day and the recaptures later the same day or 1–2 days later. Fish were measured to 0.5 mm (TL) and weighed to 0.05 g. Individuals greater than 30 mm were tagged with small individually coded external tags (Chapman & Bevan 1990), while fish 25–30 mm were marked with a colour/position code of tattoo ink injected into the muscle with a fine-gauge surgical needle (Riley 1966; Thresher & Gronell 1978) permitting identification of pool and marking date. Toward the end of the study, larger fish were also tattooed rather than tagged to minimize the number of tags left after the study. Fish smaller than 25 mm were measured but were too small to mark.

In male poeciliids, the anal fin metamorphoses to become an intromittent organ referred to as the gonopodium. Maturity of the males was estimated by field examination of the gonopodium (Grobstein 1940; Turner 1941) and verified by the laboratory examination of small collections of males (Chapman 1990). As  $<1\%$  of males with fully developed gonopodia were less than 25 mm, fish in this size-class were designated as juveniles, while those of 25–30 mm are referred to as ‘small’ males and those  $>30$  mm as ‘large’ males.

The population size of fish  $\geq 25$  mm was estimated assuming a closed population with no mortality or recruitment during the interval between mark and recapture (Krebs 1989). 95% C.L. were calculated using Poisson, normal approximation, or binomial confidence limits depending on the size of the population in relation to the samples taken (Krebs 1989). For the estimation of population structure, each random sample was considered independent, and the two catches were summed. The proportions of very large fish ( $\geq 45$  mm), of juveniles ( $<25$  mm), and of males were derived from samples containing more than nine fish ( $\geq 25$  mm). In calculating the proportion of

males that were small, only samples containing more than four males were used. Rate of population increase between pairs of samples was calculated as the slope of the logarithmic relationship between population size and the duration of the interval in days. Geometric means are presented for average population size and density, number of small males, pool area, and percentage change in these variables.

The Friedman test for repeated measures was used to test for variation in population characteristics among sampling dates (Winer 1971; Conover 1980). Pearson correlations were used to examine how the values of the population size, density, and area were related between sampling periods. Partial correlation analysis was used to determine the degree to which differences among pools in rate of population change were related to population density, relative periphyton production and dissolved oxygen.

## RESULTS

When the pools became isolated after the second flood, population sizes averaged 47.8 fish (range 2–1018 fish) and pool areas averaged 22.5 m<sup>2</sup> (5.5–227.1 m<sup>2</sup>), resulting in densities of 2.1 fish per m<sup>2</sup> (0.13–9.11 fish per m<sup>2</sup>) (Fig. 1). For pools inhabited before the floods, these values represent an average of 20.2% of the population size, 130.3% of the area and 15.2% of the density of the same pools before the floods. No pools that had been populated prior to the floods were uninhabited afterwards. However, pool 3-2 contained only two males and pool 3-4 three males and a single female, which subsequently disappeared. Three pools without fish prior to the floods were colonized but dried up before the end of the study (Fig. 1). These five pools were excluded from the analysis of population trends developed below. Over 153 days following the floods, population sizes increased to an average of 124.2 individuals per pool (range 20–3135) (Fig. 2) and pool area decreased to 15.8 m<sup>2</sup> (2.90–202.2 m<sup>2</sup>). These represent statistically significant increases ( $P < 0.03$ ) in population size averaging 68% (–17%–537%), significant decreases ( $P < 0.0001$ ) in pool size averaging 48% (4–90%) and significant increases ( $P < 0.0006$ ) in population density averaging 222% (0–6128%) (Fig. 2). By the end of the study, population sizes had reached 50% of their pre-flood values (11–254%) and densities had reached 68% of their pre-flood values (31–275%), while pool areas had declined to 73% of their pre-flood values (35–103%).

Population size was correlated with pool area both before ( $r = 0.62$ ,  $<0.05$ ) and after ( $r = 0.93$ ,  $<0.001$ ) the floods. However, pool density was not correlated with pool area at either time (before:  $r = 0.19$ ,  $P = 0.57$ ; after:  $r = 0.30$ ,  $P = 0.40$ ). After the floods, pool population sizes were correlated with their pre-flood values but population densities were not (Table 1). During the post-flood period, the correlation between population density and its pre-flood value gradually increased, becoming highly significant by the last sample. Population size remained correlated with its pre-flood values but did not show a systematic trend (Table 1). After the floods, net periphyton production was relatively low, but in the third sampling period was both higher and more variable. Dissolved oxygen showed the opposite trend, being higher (mean 5.4, range 1.7–8.1 mg l<sup>-1</sup>) right after the floods and lower (mean 1.8, range 0.1–4.8 mg l<sup>-1</sup>) in the third sampling period. Population density was not correlated with net periphyton production in the first ( $r = 0.04$ ,  $P = 0.91$ ) or second ( $r = -0.13$ ,  $P = 0.71$ ) post-flood samples, but it was weakly

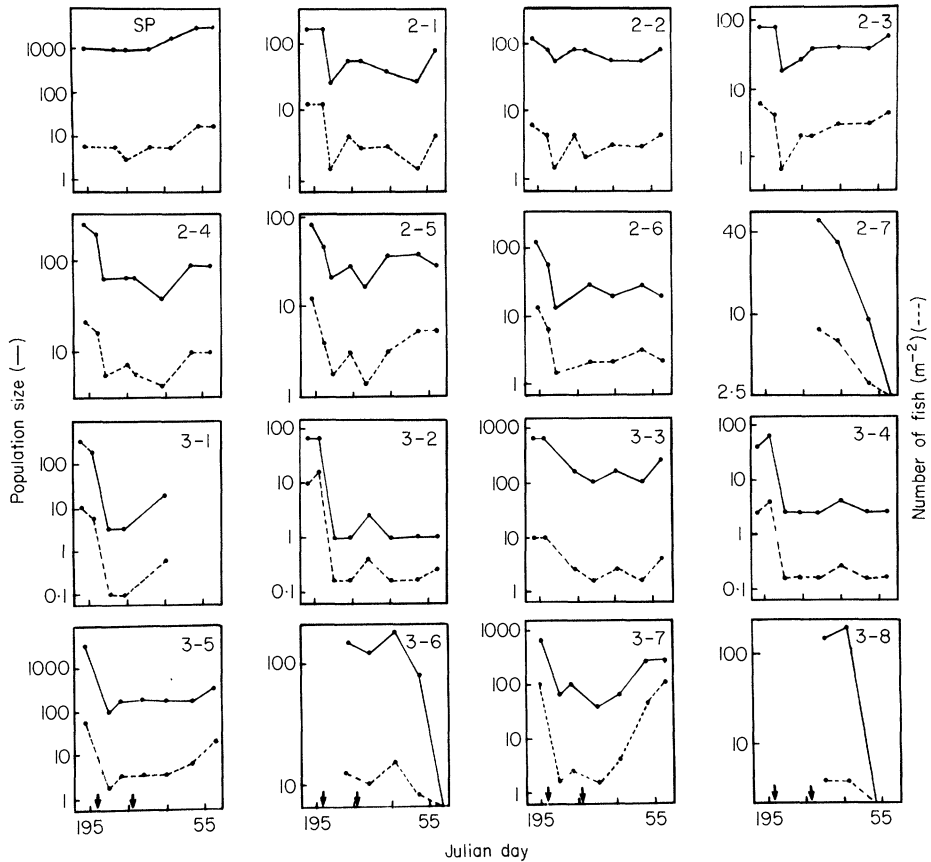


FIG. 1. Temporal changes in *P. gillii* populations in sixteen residual pools of Q. Jicote. The solid line represents population size (number of fish  $\geq 25$  mm, TL) and the dashed line population density (fish per  $m^2$ ). Pools 2-7, 3-6 and 3-8, colonized during seasonal flooding, dried up before the end of the study. Arrows indicate the time of the floods. Pool identification codes match Chapman (1990, Ch. 1, Fig. 1).

TABLE 1. Correlations between pre-flood and six post-flood values of the density and size of *P. gillii* populations in residual pools of Q. Jicote. Mean Julian day of each sampling period is indicated. All values are compared to day 203 (22 July)

Date	Density (fish per $m^2$ )		Population size	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Day 229 (17 Aug. 1987) (after first flood)	0.298	0.403	0.678	0.031
Day 262 (19 Sept.)	0.205	0.571	0.644	0.044
Day 296 (23 Oct.) (after second flood)	0.055	0.880	0.767	0.010
Day 344 (10 Dec.)	0.144	0.673	0.752	0.008
Day 33 (2 Feb. 1988)	0.557	0.094	0.762	0.010
Day 73 (14 Mar.)	0.785	0.007	0.826	0.003

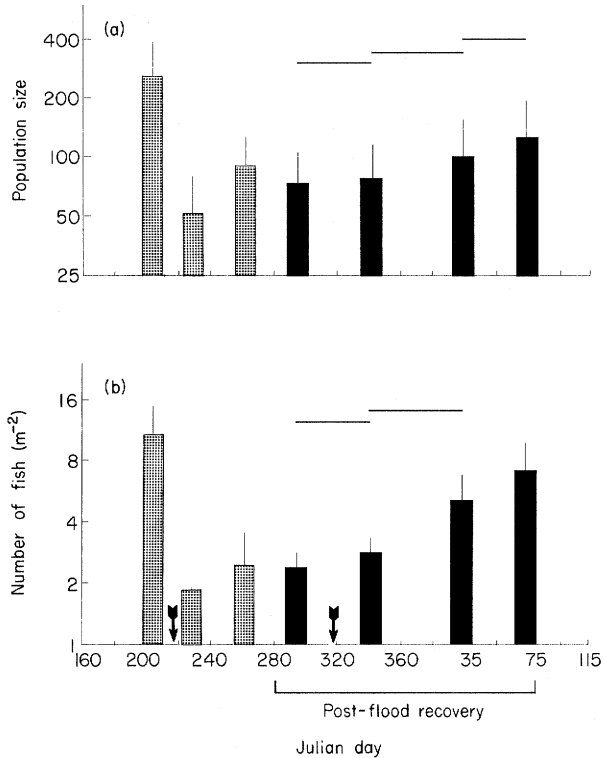


FIG. 2. Temporal changes in mean ( $\pm$  S.E.) size (a) and density (b) of *P. gillii* populations ( $\geq 25$  mm, TL) in separated pools before and after two periods of flooding (arrows). Post-flood sampling periods that are not significantly different from each other (Friedman test) are joined by lines above each histogram.

correlated by the third ( $r = 0.69$ ,  $P < 0.03$ ) and strongly by the fourth ( $r = 0.80$ ,  $P = 0.006$ ). Population density was not correlated with oxygen concentration in any post-flood sampling period ( $P > 0.05$ ).

The rate of population increase during the first inter-sample interval following the floods was negatively correlated to population density, weakly positively correlated to net periphyton production and not correlated to dissolved oxygen concentration, when the effects of the other variables were removed by partial correlation analysis (Table 2). In the last inter-sample interval, the rate of population increase was more strongly correlated to population density and net periphyton production, and dissolved oxygen also became significantly correlated (Table 2).

There were major temporal changes in overall size distributions and in proportion of males and juveniles in the pool populations (Fig. 3). The proportion of juveniles dropped from an average of 33% (6–58%) prior to the first flood to 18% (3–38%) after the first flood ( $t = 2.3$ ,  $P = 0.053$ ). Subsequently, individual pools experienced bursts of recruitment into this size-class following periods of low juvenile numbers (e.g. pool 2-1 from day 262 to day 296 and pool 3-7 from day 229 to day 262). However, the overall trend (Fig. 4a) was non-significant (Friedman test,  $\chi^2 = 2.5$ ,

TABLE 2. The relationship of rate of change in population size between sampling periods (dependent variable) and three independent variables: population density, relative net periphyton production, and dissolved oxygen concentration. Interval (1), immediately following the floods (Julian day 296–day 344, 1987), (2) 4 months after the second flood (Julian day 33–day 73, 1988)

Interval	Total $r^2$	<i>P</i> value	Factor	Partial correlation coefficient	<i>P</i> value
1	0.64	0.088	Density	-0.72	0.043
			Periphyton	0.68	0.062
			Oxygen	-0.035	0.930
2	0.80	0.016	Density	-0.89	0.0034
			Periphyton	0.87	0.0049
			Oxygen	0.80	0.018

$P = 0.47$ ), possibly due to a lack of synchrony among pools. Very large fish ( $\geq 45$  mm) comprised on average 14% (7–25%) of the population before the floods and 15% (6–30%) immediately afterwards, subsequently declining to only 5% (0–12%, Fig. 4b). Although the population size of very large fish showed a trend similar to the proportion, only the proportion was significant ( $\chi^2 = 5.5$ ,  $P = 0.14$ ;  $\chi^2 = 167$ ,  $P = 0.001$ , respectively).

Before the floods, few mature males were  $< 30$  mm (Fig. 3), and the majority of males which matured between captures were 30–40 mm. After the floods, most pools experienced a sudden recruitment of 25–30 mm males, though not all at the same time (e.g. pool 2-3 between day 296 and day 344 and pool 2-4 between day 344 and day 33 (Fig. 3). The proportion of males that were 25–30 mm therefore increased from 27% (0–71%) on day 296 to 52% (0–92%) on day 33 ( $\chi^2 = 11.5$ ,  $P < 0.01$ ) then declined to 30% (0–92%) by day 73 (Fig. 4c). The increased proportion of small males was not due simply to a loss of large males, as the number of small males increased more rapidly than the population as a whole ( $t = 3.15$ ,  $P < 0.02$ ). There was an average of 12.5 small males per pool (2–56) prior to the first flood and 27.5 per pool (0–536) by day 31. The actual sex ratio could not be determined because the non-destructive nature of the study prevented assessment of size at maturity for females and separation of immature males from females. However, the proportion of fish  $\geq 25$  mm externally recognizable as males rose with the recruitment of small males, increasing from 26% (14–45%) on day 296 to 47% (33–64%) on day 33, then declining to 38% (23–59%) on day 73 ( $\chi^2 = 15.6$ ,  $P < 0.002$ , Fig. 4d).

## DISCUSSION

### *Seasonal trends*

In Q. Jicote, both population size and density of *P. gillii* increased during the dry season. The average rate of increase was low immediately after the floods, but rose as the dry season progressed. This may reflect seasonal variation in food supply. The availability of algae and detritus was probably reduced after the floods when the

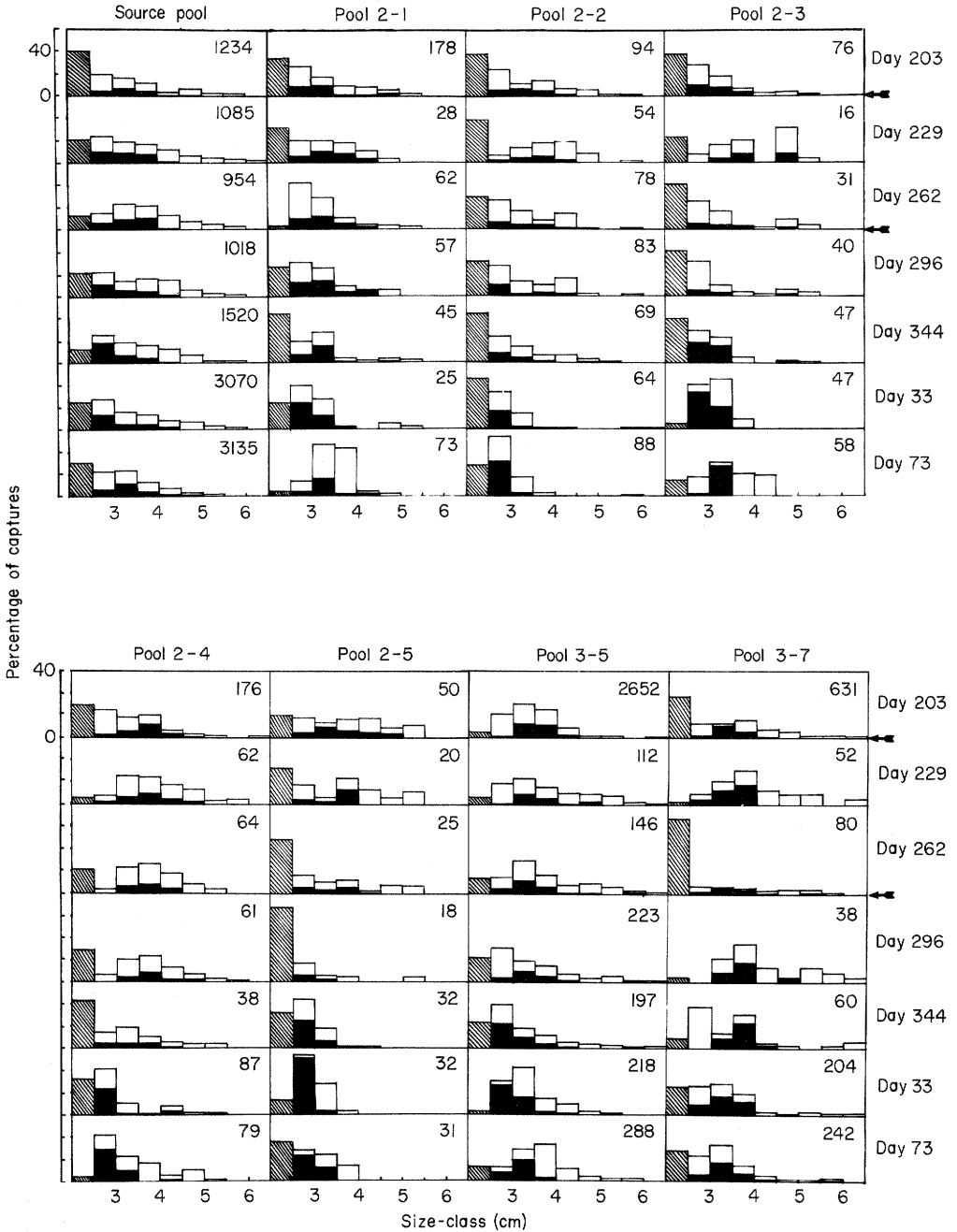


FIG. 3. Size distribution of *P. gillii* in eight of the pools with the largest populations in the Q. Jicote over seven sampling periods. Hatched sections of the bars represent juveniles, clear sections represent females and immature males, and dark sections represent mature males. Size-classes are 5 mm (TL) except the first size-class which represents all fish <25 mm. The right-hand column indicates mean Julian day of each sampling period, and arrows indicate the time of the floods. Estimated population sizes are indicated in the upper right-hand section of each histogram.



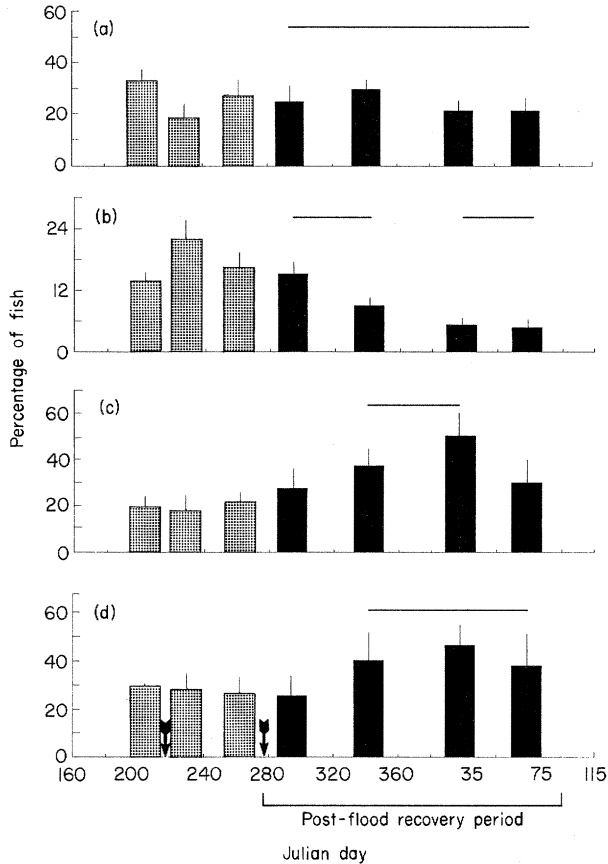


FIG. 4. Mean percentage ( $\pm$  S.E.) of (a) juveniles (fish <25 mm, TL), (b) very large individuals (fish  $\geq$ 45 mm, TL), and (d) externally recognizable males in *P. gillii* populations inhabiting isolated pools over the post-flood recovery period; (c) the percentage of males that were in the smallest size-class (25–30 mm, TL). Post-flood sampling periods that are not significantly different from each other are joined by lines above each histogram. In addition, in (c) the fourth post-flood sampling period does not differ significantly from the first or second.

streambed had been scoured, temporarily flooded areas became inaccessible and light levels were reduced by seasonal leaf flush. As the dry season progressed, pools continued to shrink, but net periphyton production increased and detrital food sources may have also increased as a consequence of seasonal leaf fall (Chapman 1990). In contrast, the rainy season in Q. Jicote was the time of population loss, due primarily to mortality in desiccating graveyard pools of fish which had moved into temporarily flooded areas.

This cycle of events differs fundamentally from the seasonal phenology of tropical floodplain rivers. In these systems flood waters may persist for several months during which many fishes disperse from dry season refuges and reproduce in the highly productive waters (Johnels 1954; Jackson 1961; Lowe-McConnell 1975, 1979; Welcomme 1979; Goulding 1980). These expanded populations must then resettle

into refuges as the flood waters recede. As in our study, death due to stranding of fish in temporary water bodies is a major source of mortality in the floodplain rivers (Johnels 1954; Bonetto *et al.* 1969; Lowe-McConnell 1964, 1967, 1975; Welcomme 1979). Nevertheless, the initial densities of fish in the permanent refuges are often very high, and both reproduction and feeding may be inhibited (Lowe-McConnell 1964, 1975; Welcomme 1979). These contrasting patterns of population growth and recruitment are likely to be related to the stream gradient. In high-gradient streams, floods are likely to be violent and of short duration. The only refuges are larger pools (Chapman 1990), and the floods therefore remove both fish and food sources and provide little time for populations to exploit the expanded area. In streams with a lower gradient, lateral areas provide a refuge from violent floods and longer-lasting, quiet, productive waters in which small fish can feed and grow.

#### *Variation among pools*

The large interpool variation in Q. Jicote provides evidence for the influence of environmental and population characteristics on the recovery from massive population loss. After the second flood, when average oxygen concentration was high, and net periphyton production and population density were relatively low, the rate of increase was related to periphyton and density. This suggests that even though population densities had been greatly reduced, algae and detritus were low enough that some populations experienced density dependence in food availability. However, the relatively weak relationships indicate other, unmeasured factors may have important influences on the differences in rate of increase among pools. Four months after the second flood, net periphyton production and population density were higher, and dissolved oxygen was lower. The results of the partial correlation analysis indicate an increased importance of food supply and population density as influences on the variation among pools. This, together with the convergence of densities on pre-flood values, suggests that the upper limit to population growth in the pools is influenced by environmentally determined levels of food availability. The pools may therefore fluctuate between post-flood population size determined by characteristics which permit the fish to resist flooding (Chapman 1990) and late dry season population sizes determined by their characteristic food supplies.

An additional significant influence on population growth rate late in the dry season was dissolved oxygen. Laboratory studies have shown that hypoxia reduces feeding and growth in poeciliid fishes when access to the surface is prevented (Weber & Kramer 1983). With surface access, poeciliids meet their oxygen demands in part through aquatic surface respiration, spending up to 90% of their time at the surface (Kramer & Mehegan 1981). This behaviour, which was performed by *P. gillii* in Q. Jicote, may have reduced food intake and hence growth and reproduction by decreasing the time available for foraging.

#### *Size and abundance of males*

Seasonal trends in the number and size of small males suggest that size at maturity is flexible in *P. gillii*, as in other poeciliid fishes (Krumholz 1963; Borowsky 1973,

1978, 1984, 1987a,b; Sohn 1977; Farr 1980; Borowsky & Diffley 1981; Hughes 1985; Vondracek, Wurtsbaugh & Cech 1988). In some species, dominant juveniles grow faster and mature earlier while subordinates delay maturation until they are large enough to become dominant (Borowsky 1973, 1978; Farr 1980). Adult males may also inhibit the maturation of small individuals through agonistic behaviour (Borowsky 1973, 1987b; Sohn 1977; Farr 1980). In Q. Jicote, catastrophic population loss during flooding and the proportionately higher loss of large males was followed by a marked input of small males. Either process could explain these results, as highly competitive conditions at the end of the dry season would be reduced by the increased space and decreased population size resulting from the floods, permitting juveniles to mature. Other studies have noted that small males are less frequent in poeciliid populations containing relatively high densities of large males (Borowsky 1978; Barus, Libosvarsky & Cruz 1980). Hughes (1985) found that early in the breeding season, juvenile male *Gambusia affinis* (Baird & Girard) matured rapidly at a small size, but later delayed maturation until a larger size was recorded. Removing a large number of males decreased the mean total length of maturing individuals.

In many poeciliid populations, females predominate. For example, Haskins *et al.* (1961) found that males comprised only 38% of a sample of *Poecilia reticulata* Peters from South America and 39% of a Trinidadian population. Barus *et al.* (1980) found that low density populations of *Limia vittata* (Guichenot) from flowing rivers in Cuba averaged 34% males, while in the highly fluctuating dry season pools, males comprised only 13%. Hughes (1985) found that adult males comprised an average of 36% of all adults in a population of *Gambusia affinis*. In Q. Jicote, the proportion of recognizable males was lowest before the floods when both population densities and average male size were high. After the floods, the proportion of recognizable males increased to 47%, higher than that recorded for most other poeciliid populations. In the final sampling period, densities were once again relatively high and the proportion of males had declined to 38%. This again suggests that delayed maturation of juvenile males in response to social competition is a factor producing female-biased sex ratios in *P. gillii* and other species.

In conclusion, seasonal flooding and stagnation in a high-gradient tropical stream result in cycles of population size and structure. These trends are expressed despite large spatial variation in pool characteristics which appear to limit the size and rate of growth of populations.

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## REFERENCES

- Barus, V., Libosvarsky, J. & de le Cruz, J. (1980). Observations on *Limia vittata* (Poeciliidae) from Kuba. *Folio Zoologica*, **19**, 267–287.
- Bonetto, A., Pignalberi, C., Cordiviola de Yuan, E. & Oliveros, O. (1969). Ciclos hidrológicos del Rio Parana y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundacion. *Physis, Buenos Aires*, **29**, 213–223.
- Borowsky, R.L. (1973). Social control of adult size in males of *Xiphophorus variatus*. *Nature*, **245**, 332–335.
- Borowsky, R.L. (1978). Social inhibition of maturation in natural populations of *Xiphophorus variatus* (Pisces: Poeciliidae). *Science*, **201**, 933–935.
- Borowsky, R.L. (1984). The evolutionary genetics of *Xiphophorus*. *Evolutionary Genetics of Fishes* (Ed. by B.J. Turner), pp. 235–310. Plenum Press, New York.
- Borowsky, R.L. (1987a). Genetic polymorphism in adult male size in *Xiphophorus variatus* (Atheriniformes: Poeciliidae). *Copeia*, **1987**, 782–787.
- Borowsky, R.L. (1987b). Agonistic behaviour and social inhibition of maturation in fishes of the genus *Xiphophorus* (Poeciliidae). *Copeia*, **1987**, 792–796.
- Borowsky, R.L. & Duffley, J. (1981). Synchronized maturation and breeding in natural populations of *Xiphophorus variatus* (Poeciliidae). *Environmental Biology of Fishes*, **6**, 49–58.
- Bussing, W.A. (1987). *Peces de las Aguas Continentales de Costa Rica*. Editorial de la Universidad de Costa Rica.
- Chapman, L.J. (1990). *Population ecology of the fish Poecilia gillii in an intermittent tropical stream: the effects of seasonal flooding*. Ph.D. thesis, McGill University, Montreal, Quebec, Canada.
- Chapman, L.J. & Bevan, D. (1990). Development and field evaluation of a mini-spaghetti tag for individual identification of small fishes. *American Fisheries Society Symposium*, **7**, 101–108.
- Conover, W.J. (1980). *Practical Nonparametric Statistics*. John Wiley and Sons, New York.
- Cordiviola de Yuan, E. & Pignalberi, C. (1981). *Fish populations in the Parana River 2. Santa Fe and Corrientes areas*. *Hydrobiologia*, **77**, 261–272.
- Daget, J. (1957). Données récentes sur la biologie des poissons dans le delta central du Niger. *Hydrobiologia*, **9**, 321–347.
- Farr, J.A. (1980). The effects of juvenile social interaction on growth rate, size and age at maturity, and adult social behaviour in *Girardinus metallicus* Poey (Pisces: Poeciliidae). *Zeitschrift für Tierpsychologie*, **52**, 247–268.
- Goulding, M. (1980). *The Fishes and the Forest*. University of California Press, California.
- Grobstein, C. (1940). Endocrine and developmental studies of gonopod differentiation in certain poeciliid fishes. I. The structure and development of the gonopod in *Platypoecilius maculatus*. *University of California Publications in Zoology*, **47**, 1–22.
- Haskins, C.P., Haskins, E.F., McLaughlin, J.J.A. & Hewitt, R.E. (1961). Polymorphism and population structure in *Lebistes reticulatus*, an ecological study. *Vertebrate Speciation* (Ed. by W.F. Blair), pp. 320–395. University of Texas Press, Austin.
- Holden, M.J. (1963). The populations of fish in dry season pools of the River Sokoto. *Colonial Office Fishery Publications*, **19**, 1–65.
- Hughes, A.L. (1985). Seasonal trends in body size of adult male mosquitofish, *Gambusia affinis*, with evidence for their social control. *Environmental Biology of Fishes*, **14**, 251–258.
- Ihering, R. von & Wright, S. (1935). Fisheries investigations in Northeast Brasil. *Transactions of the American Fisheries Society*, **65**, 267–271.
- Jackson, P.B.N. (1961). *Ichthyology: The Fish of the Middle Zambezi, Kariba Studies*. Manchester University Press.
- Johnels, A.G. (1954). Notes on fishes from the Gambia River. *Arkiv For Zoologi*, **6**, 327–411.
- Kramer, D.L. & Mehegan, J.P. (1981). Aquatic surface respiration, an adaptive response to hypoxia in the guppy, *Poecilia reticulata* (Pisces, Poeciliidae). *Environmental Biology of Fishes*, **6**, 299–313.
- Krebs, C. (1989). *Ecological Methodology*. Harper and Row, New York.
- Krumholz, L.A. (1963). Relationships between fertility, sex ratio, and exposure to predation in populations of mosquitofish *Gambusia manni* Hubbs at Bimini, Bahamas. *Internationale Revue der Gesamten Hydrobiologie*, **48**, 201–256.
- Kushlan, J.A. (1974). Effects of a natural fishkill on water quality, plankton, and fish production of a pond in the Big Cypress Swamp, Florida. *Transactions of the American Fisheries Society*, **103**, 235–243.
- Lowe-McConnell, R.H. (1964). The fishes of the Rupununi savanna district of British Guiana, South America. Pt. I. Ecological groupings of fish species and the affects of the seasonal cycles on the fish. *Zoological Journal of the Linnaean Society*, **45**, 103–144.
- Lowe-McConnell, R.H. (1967). Some factors affecting fish populations in Amazonian waters. *Atas do Simposio sobre a Biota Amazonica*, **7**, 177–186.

- Lowe-McConnell, R.H. (1975).** *Fish Communities in Tropical Freshwaters*. Longman, London.
- Lowe-McConnell, R.H. (1979).** Ecological aspects of seasonality in fishes of tropical waters. *Symposia of the Zoological Society of London*, **44**, 219–241.
- Riley, J.D. (1966).** Liquid latex marking technique for small fish. *Journal du Conseil International pour l'Exploration de la Mer*, **30**, 354–357.
- Smith, N.J.H. (1981).** *Man, Fishes, and the Amazon*. Columbia University Press, New York.
- Sohn, J.J. (1977).** The consequences of predation and competition upon demography of *Gambusia manni* (Pisces: Poeciliidae). *Copeia*, **1977**, 224–227.
- Thresher, R.E. & Gronell, A.M. (1978).** Subcutaneous tagging of small reef fishes. *Copeia*, **1978**, 352–353.
- Turner, C.L. (1941).** Morphogenesis of the gonopodium in *Gambusia affinis affinis*. *Journal of Morphology*, **69**, 161–185.
- Vondracek, B., Wurtsbaugh, W.A. & Cech, J.J. (1988).** Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. *Environmental Biology of Fishes*, **21**, 45–57.
- Weber, J.-M. & Kramer, D.L. (1983).** Effects of hypoxia and surface access on growth, mortality, and behavior of juvenile guppies, *Poecilia reticulata*. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1583–1588.
- Welcomme, R.L. (1979).** *Fisheries Ecology of Floodplain Rivers*. Longman, New York.
- Winer, B.J. (1971).** *Statistical Principles in Experimental Design*. McGraw-Hill Book Company, New York.

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