Environmental Biology of Fishes **42**: 313–321, 1995.

Patchiness in the abundance of metacercariae parasitizing *Poecilia gillii* (Poeciliidae) isolated in pools of an intermittent tropical stream

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Received 9.9.1992 Accepted 6.7.1994

Key words: Environmental heterogeneity, Costa Rica, Dry season pools, Seasonal flooding, Black spot, Fish parasites

Synopsis

Prevalence and intensity of a clinostomatid in the fish *Poecilia gilliii* were measured in six dry season pools of a small intermittent Costa Rican stream, and the prevalence of two diplostomulid parasites ('diplostomulum' and 'neascus') were monitored in 14 residual pools of a second intermittent stream of the same drainage. There were significant among-pool differences in the prevalence of the three parasites. There was no evidence to suggest that clinostomatid or 'diplostomulum' prevalence was influenced by the position of pools within the downstream gradient; however, 'neascus' prevalence tended to decrease with distance downstream. Host length accounted for some of the variation in parasite prevalence among pools for both diplostomulids. Prevalence and intensity of a clinostomid in the body cavity varied with host gender and body size. There was a positive relationship between body size and clinostomatid parasitization in female hosts. Most males examined were less than 50 mm (total length). For fish less than 50 mm, males were more parasitized than females. Prevalence of the two diplostomulids was not related to the relative net periphyton production or the dissolved oxygen concentration of the pools. However, a positive correlation between the density of *P. gillii* and 'diplostomulum' prevalence was found across the fourteen pools, and 'neascus' prevalence was positively related to pool area.

Introduction

There has been considerable interest in the factors accounting for variation in the abundance of parasites in different host populations (Dogiel 1961, Price 1990, Kennedy 1985, 1990). The way variance in parasitism is partitioned across environments and hosts should determine the scale and dynamics of host-parasite interactions. Of particular significance is the degree to which life history and ecological factors such as host size, density, or feeding habits contribute to differing levels of parasitism (Dogiel 1961, Anderson 1982, Price 1990, Chandler 1993). Intermittent streams are particularly useful systems for examining questions pertaining to the heterogeneity of host-parasite interactions in natural populations. In the dry season, aquatic organisms inhabiting intermittent streams can be trapped for several months in isolated pools. During this time the characteristics of the pools can diverge, and heterogeneity in these characteristics may contribute to small scale variation in host-parasite dynamics.

In this study, we document the patchiness of parasite infections in a small freshwater fish, *Poecilia gillii* Kner & Steindachner 1863, from pools in two intermittent tropical streams. Potential life history and ecological correlates of the parasite prevalence are examined. During the dry season, both streams consist of small disconnected pools which vary in size, water quality, and densities of *P. gillii* (Chapman & Kramer 1991a, b, Chapman et al. 1991), and thus they represent a novel set of habitat patches with isolated host populations. We first describe the prevalence and intensity of a clinostomatid infection (Digenea: Platyhelminthes) in *P. gillii* from dry season pools in one small stream and consider relationships between host life history traits and parasite infections. We subsequently examine the prevalence of two other species of metacercariae (Digenea) in pools of a second stream in the same drainage and quantitatively describe relationships between ecological variables and parasite infestations. We consider four variables: pool population density, relative net periphyton production (a food source for *P. gillii*), dissolved oxygen concentration, and pool surface area. High densities of *P. gillii*, low periphyton production, and low dissolved oxygen concentration are related to low pool population growth rates in the late dry season in Quebrada Jicote (Chapman et al. 1991). If these three factors reflect the suitability of pools for fish, one would expect that variation in the prevalence of parasites among pools might be accounted for by variation in these three parameters. We considered the effects of pool area on prevalence, given that the smallest pools might not be suitable for the final hosts of the parasites, which, for all three digeneans, are piscivorous birds.

Methods

Study site

The ecology and behavior of *P. gillii* were studied for 20 months over 3 years in two small intermittent streams in Santa Rosa National Park, Costa Rica (10°50′ N, 85°38′ W). The first stream, Quebrada Costa Rica, is surrounded by low canopy forest and grassland with high light exposure. The upper section is on a relatively low gradient, and is separated by a 25 m waterfall from its downstream sector which feeds directly into the Rio Poza Salada. Parasite data were collected late in the dry season of 1985 between March and May from *P. gillii* populations in the five dry season pools (4 m^2 to 91 m^2 in area) that remained within a 300 m upper section of Quebrada Costa Rica and one pool at the base of the waterfall leading into the Rio Poza Salada. The second study site, Quebrada Jicote, is a high-gradient stream which flows into the Rio Poza Salada about 700 m below the Quebrada Costa Rica pools. The study site included a 0.5 km section of the Quebrada Jicote and a short section of the Rio Poza Salada. During the dry season this stream consists of about 20 small, disconnected pools. The most upstream permanent pool, which we refer to as the Source Pool, is the largest (18 m in diameter), and is fed by a 16 m high waterfall which prevents fish from moving upstream. Below this pool the stream falls over a distance of 0.5 km to its junction with the Rio Poza Salada. The streambed was divided into three sectors: (1) the Source Pool and 200 m of downstream area with no other permanent pools, (2) a series of approximately 12 permanent pools (2 m^2 to 21 m^2 in area) on a medium gradient, and (3) 40 m of dry streambed followed by six major pools (6 m^2 to 60 m^2 in area) on a relatively steep gradient in Quebrada Jicote and two pools in the Rio Poza Salada that were located approximately 50 and 550 m downstream from its junction with Quebrada Jicote. Parasite data were collected from the beginning to the middle of the dry season, December 1987 to March 1988. Fish were examined from 12 pools in Quebrada Jicote (the Source Pool, seven pools from Sector 2, 4 pools from Sector 3), and the two pools in the Rio Poza Salada. In both

Quebrada Costa Rica and Quebrada Jicote, water levels in pools declined as the dry season progressed, sometimes reducing *P. gillii* populations dramatically or eliminating them completely (Chapman & Kramer 1991a, Chapman et al. 1991). A more complete description of the two sites is found in Chapman & Kramer (1991a,b), and Chapman & Chapman (1993).

Fish-parasite collections and environmental monitoring

Fish from the six pools in Quebrada Costa Rica were sampled using baited minnow traps. A sample of males (mean total length = 42.8 ± 4.8 mm, SD) and females (mean total length = 46.6 ± 8.5 mm, SD) was selected. An attempt was made to sample approximately equal proportions of males and females, although the proportion of males among the adults of the population is generally lower than the proportion of females in these pools. The fish were placed on ice, preserved in 10% formalin, and stored in 70% alcohol. The total length and weight of each fish were recorded, and specimens were sexed by examination of the anal fin and gonads (Turner 1941). Prevalence and intensity of infection (number of parasites per host) were determined from dissections. Parasites found in the body cavity were identified as metacercariae of a species of clinostomatid (Clinostomatoidea: Digenea; D. Brooks personal communication). Further identification of the parasite was not possible. The life cycle of a related clinostomatid that infects fishes in North America can be summarized as follows: fish, which serve as the second intermediate host, are eaten by a piscivorous bird (e.g., heron), where the metacercariae develop into adults after a few days (Olsen 1974). The parasites then shed eggs for a period of about 14 days, before being lost. The free-swimming miracidia emerge from the eggs and penetrate a suitable snail host. When fully developed, the cercariae emerge to find a suitable fish host where they develop into metacercariae (Olsen 1974).

The study of Quebrada Jicote was used to quantitatively describe relationships between ecological variables, *P. gillii* population density, and parasite infestations. Random sampling of oxygen, temperature, and fish capture sites was conducted by dividing each pool into 1 m^2 quadrats using two to four lines of rope marked at 1 meter intervals and suspended above the pools. Every 4–6 weeks, three to six dissolved O_2 concentration and temperature readings were taken with an O_2 meter in each pool at randomly selected sites. In this study, we relate surface values collected between 13:00 and 15:30 hours to parasite infestation. No macrophytes grew in these pools. Relative net periphyton production was estimated for each pool using the procedures outlined by Chapman & Kramer (1991b). For more detailed accounts of environmental sampling procedures, see Chapman & Kramer (1991a, b).

Fish population size was estimated for each pool every 4–6 weeks. Baited minnow traps were set in randomly selected grids with recaptures later the same day or one to two days later. 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 color/position code of tattoo ink injected into the muscle with a fine-gauge surgical needle (Riley 1966, Thresher & Gronell 1978). Toward the end of the study, larger fish were also tattooed rather than tagged to minimize the number of tags left after the study. A capture-mark-recapture estimate for a closed population without mortality or recruitment (Krebs 1989) was applied to determine population size for fish ≥ 25 mm in each pool.

The study of *P. gillii* population dynamics using the capture-mark-recapture technique precluded the collection of individuals for dissection. However, two digenean parasites were visible externally on fish collected from Quebrada Jicote. These were dissected out from several fish, and both were found to be diplostomulids (Strigeidea: Digenea). Although the specific status of these parasites was impossible to determine (D. Brooks personal communication), one of the parasites infected the eye, and belongs to a group of parasites commonly referred to as 'diplostomulum'. The life cycle of a related species of 'diplostomulum' that parasitizes the lenses and vitreous humor of some temperate freshwater fishes is as follows: on making contact with

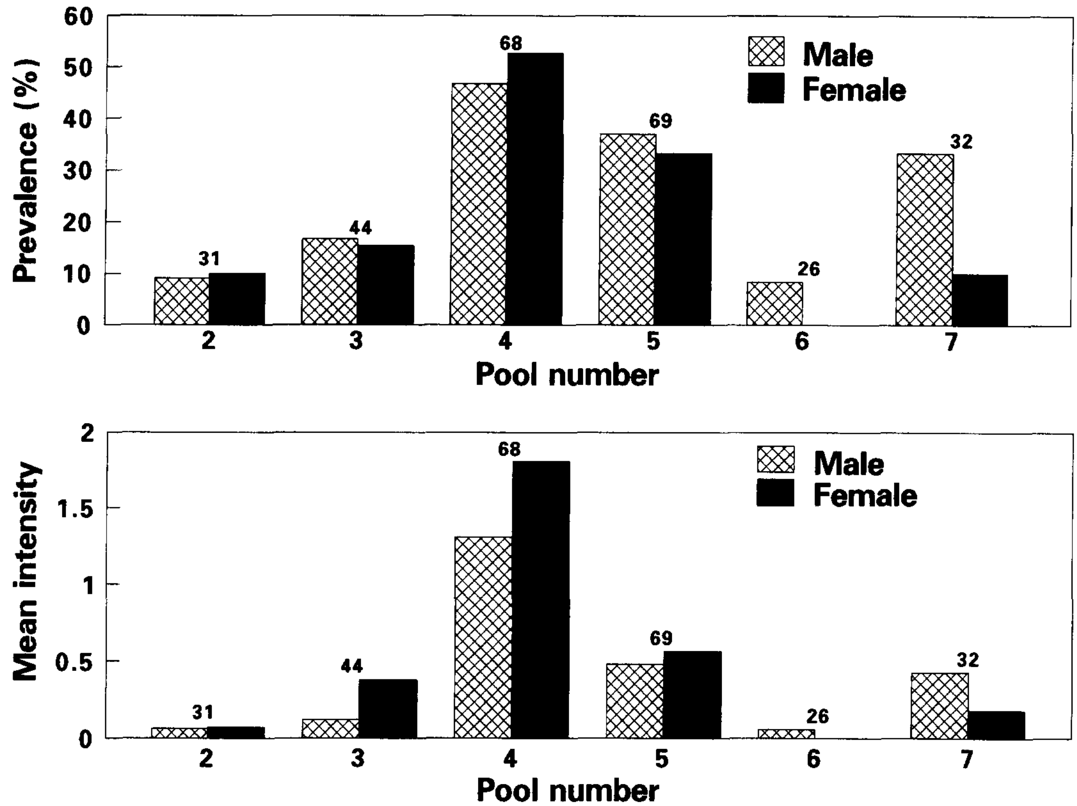

Fig. 1. Prevalence (a) and mean intensity of infection (b) of clinostomatid metacercariae found in *Poecilia gillii* in six Quabrada Costa Rica pools, separated by host gender. The sample sizes for each pool appear above each respective pool value. Pool numbers are as in Chapman & Chapman (1993).

the fish, the cercariae penetrate the skin and migrate to the eye where they remain until the host dies or is eaten by a piscivorous bird: development into an adult occurs in the bird's intestine (Ginetsinskaya 1961). The adult parasites shed their eggs which pass out into the water. The hatching miracidia must then penetrate as gastropod, the next host, before becoming infective to fish. The metacercariae develop within the fish to the stage where they can infect the final avian host (Ginetsinskaya 1961). The metacercariae were easy to observe and often distorted the eye considerably. Both eyes of each fish captured during the capture-mark-recepture protocol were examined, and the presence or absence of the parasite was recorded. In addition, all fish were examined for the presence or absence of distinctive black spots. These are the encysted metacercariae of the diplostomulid group commonly referred to as 'neascus', which have migrated to the body wall of the host. Again the final host is a bird, and the first intermediate host is a gastropod (Olsen 1974). The stage within the fish usually takes about three weeks to develop in North America (Olsen 1974). Because we did not dissect out the parasites in each fish, our estimates should be considered as a relative, rather than an absolute measure of prevalence. To reduce our measurement error, estimates of the presence or absence of parasites were limited to fish greater than or equal to 30 mm in total length. Because we have not identified the parasites to species, it is possible that each metacercarial type is represented by more than one species. The gender of each fish was determined by the examination of anal-fin morphology (Turner 1941). Some immature males could not be differentiated from females, and may have been included with the females. The non-destructive nature of the study in Quebrada Jicote prevented the necropsies that would be required for a finer analysis.

Statistical analysis

Friedman's test for repeated measures was used to examine variation in prevalance across sampling dates (Winer 1971, Conover 1980). Logistic regression analysis was used to test for the effects of pool, host length, and gender on the prevalence of all three parasites (Kleinbaum et al. 1988). The X^2 goodness of fit analysis was used to test for differences in prevalence among pools (Sokal & Rohlf 1981).

Results

The three digeneans found in *P. gillii* infected only a moderate proportion of the host populations (mean prevalence across pools and one standard deviation was 22.2% ± 15.7, 16.4% ± 15.3, and 5.0% ± 8.9 for clinostomatid, 'diplostomulum', and 'neascus' parasites, respectively). Prevalence values were slightly higher when fish were combined across all pools (27.8%, 26.3%, and 15.3% for clinostomatid, 'diplostomulum', and 'neascus', respectively). Higher prevalence values in the combined sample relative to the mean values across pools reflects the contribution of few pools with large populations (from which many fish were sampled) and high parasite prevalence (e.g., Pool 11, Pool 33 in Quebrada Jicote). The clinostomatid, which was the only digenean for which intensity of infection was scored, tended to be aggregated in distribution (variance to mean ratio = 26.18).

Minor variation in prevalence between sample periods existed, though differences were not significant (Friedmans test $X^2 = 3.6$ for the clinostomatid; $X^2 = 0.29$ for the 'diplostomulum'; $X^2 = 2.55$ for the 'neascus', $p > 0.25$). Based on plots of prevalence and sample period, no general trend for any of the three parasites was apparent over the short time frame of collections, either when pools were analyzed separately or combined. We grouped all sample periods for each pool together for further analyses.

Clinostomatid parasitization in Quebrada Costa Rica

The prevalence and mean intensity of the clinostomatid infection in fish from Quebrada Costa Rica differed among pools ($X^2 = 35.3$, $p < 0.001$; $F_{5,265} = 10.15$, $p < 0.001$, respectively, Fig. 1a, b). These differences showed no obvious relation to the downstream directional gradient of the pools (Spearman rank correlation; prevalence: $r_s = 0.086$, $p = 0.87$; intensity: $r_s = 0.086$, $p = 0.87$). Prevalence and mean intensity of infection varied with host gender and body length (Fig. 2a, b). Although larger females showed higher prevalence and mean intensity of infection, no such length relationships were found in male fish. Males tended to be smaller than females. To compare similarly sized fish, we arbitrarily divided the fish from all pools into four size classes. Most males (94%) were less than 50 mm in total length.

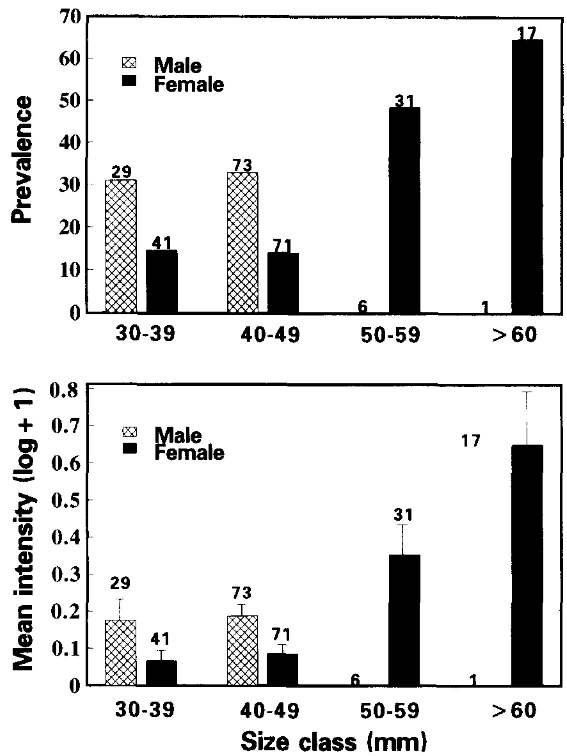

Fig. 2. The relationship between length of *Poecilia gillii*: a – prevalence (percent infected) and b – mean intensity of the clinostomatid metacercariae in Quebrada Costa Rica for all pools combined. Standard errors for intensity are indicated. The numbers above each column are the sample sizes for each size class. No males above the second size class were infected.

For fish smaller than 50 mm, males were 2.3 times as likely to be infected as females (32.4% vs. 14.3% for males and females, respectively; $X^2 = 9.86$, $p < 0.005$, Fig. 2a). In addition, the mean intensity of infection was 2.3 times higher for males smaller than 50 mm than for females in the same size class ($t = 2.83$, $p < 0.005$, Fig. 2b). For the larger size classes, sample size was very small for males (since they were less abundant than large females). The small number of large males examined were free of parasites, whereas larger females exhibited an increase in prevalence (females < 50 mm vs. females ≥ 50 mm; $X^2 = 27.6$, $p < 0.001$, Fig. 2a) and mean intensity ($t = 6.37$, $p < 0.001$, Fig. 2b) over the smaller size classes. Logistic regression was used to examine the effects of pool, length, gender, and the interaction between length and gender on the probability of infection. When the effects of body size and host gender were removed, there were still significant pool effects on clinostomatid prevalence (Table 1).

'Diplostomulid' parasitization in Quebrada Jicote

Prevalence of both the 'diplostomulum' and 'neascus' metacercariae differed significantly among the 14 pools ($X^2 = 154.4$, $p < 0.001$ for 'diplostomulum'; $X^2 = 273.7$, $p < 0.001$ for 'neascus'; Fig. 3a, b). 'Diplostomulum' prevalence showed no relationship with distance from the most upstream pool ($r = 0.017$, $p = 0.95$). However, the position of the pools within the unidirectional downstream gradient related to 'neascus' prevalence, with a general decline in prevalence in downstream pools ($r = -0.56$, $p = 0.038$). Larger fish were more parasitized, and body size effects remained significant when pool and gender effects were removed (Table 1). Again, most males were less than 50 mm in total length. The prevalence of infection of both parasites in fish less than 50 mm (TL) was higher in males than in females ('diplostomulum'; 27.3% and 21.2% for males and females, respectively; $X^2 = 7.2$, $p < 0.05$; 'neascus': 17.4% and 11.8% for males and females, respectively; $X^2 = 9.3$, $p < 0.005$). When pool and body size effects were removed, there were still weak gender effects on 'neascus' prevalence ($p = 0.095$); however, there were no significant gender effects on 'diplostomulum' prevalence (Table 1). Larger females exhibited a significant increase in the prevalence of the two parasites ('diplostomulum': 21.2% and 75.3% for females < 50 mm and females ≥ 50 mm, respectively, $X^2 = 136.3$, $p < 0.001$; 'neascus': 11.8% and 42.3% for females < 50 mm and females ≥ 50 mm, respectively, $X^2 = 67.4$, $p < 0.001$). Only four large males (≥ 50 mm) were examined. All were infected with 'diplostomulum', whereas only one of the four fish was infected with 'neascus'. Mean body size of fish differed among pools ($F_{13,1668} = 4.8$, $p < 0.001$). Although pool differences in body size may account for some of the heterogeneity in prevalence among pools, logistic regression analysis indicated that significant pool differences remained after the effects of body size were removed (Table 1).

Four variables (fish density, pool area, dissolved oxygen, and relative net periphyton production) were used in a stepwise multiple regression to partition ecologically important correlates of the prevalence of 'diplostomulum' and 'neascus' metacercariae in Quebrada Jicote pools. Host population density was positively correlated with 'diplostomulum' prevalence and was the only significant correlate (arcsine √ prevalence = – 0.32 + 0.28*log density; $r^2 = 0.38$, $p = 0.020$). In a simple correlation matrix, again, host population density was the only significant factor (density $r = 0.61$, $p = 0.020$; area $r = 0.32$, $p = 0.27$; periphyton $r = 0.18$, $p = 0.54$; oxygen $r = -0.33$, $p = 0.25$). In a stepwise multiple regres-

Table 1. Logistic regression analyses for the effects of pool, total length, gender, and the interaction of length and gender on the prevalence of parasitism by the metacercariae of three digeneans: a clinostomatid, and two diplostomulid parasites ('diplostomulum' and 'neascus').

Treatments	Clinostomatid		'Diplostomulum'		'Neascus'	
	X^2	p	X^2	p	X^2	p
Sample size	270		1671		1676	
Log length	3.47	0.063	12.37	< 0.001	18.37	< 0.001
Gender	7.88	0.005	0.23	0.634	2.78	0.095
Pool	27.86	< 0.001	131.78	< 0.001	78.63	< 0.001
Length by gender	7.67	0.006	0.06	0.809	3.48	0.062

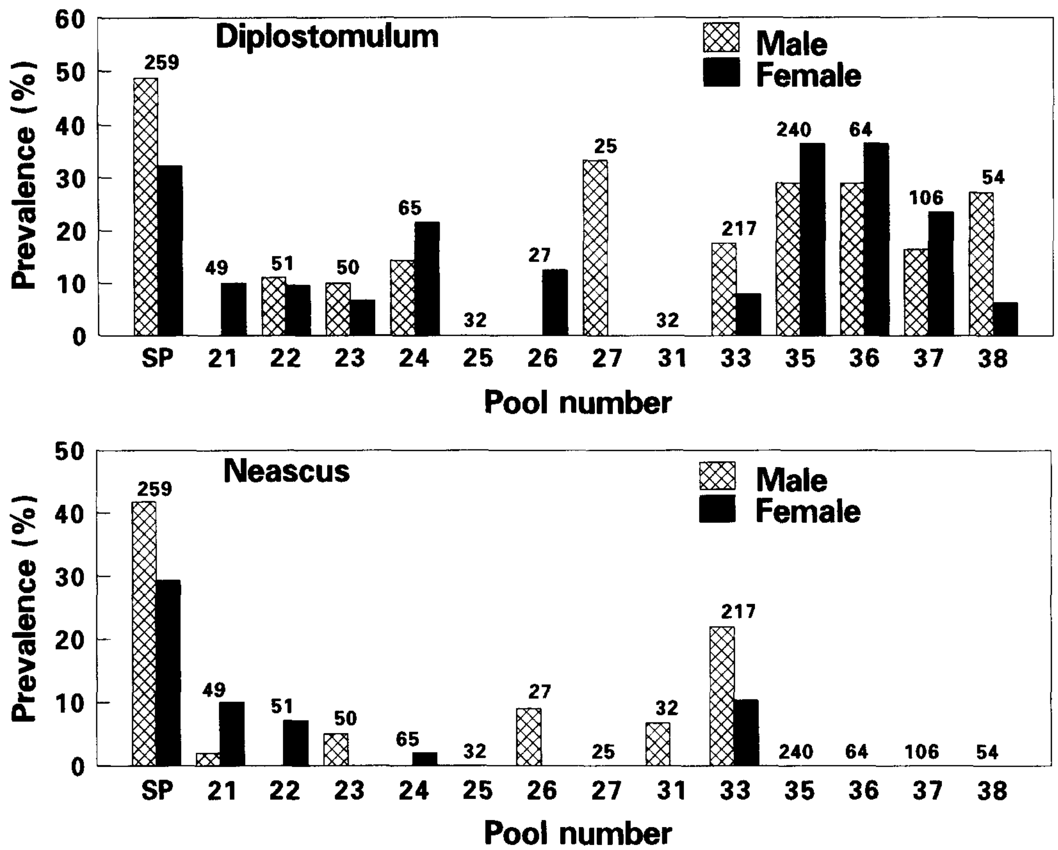

Fig. 3. The prevalence of (a) 'diplostomulum' and (b) 'neascus' parasites found in *P. gillii* in Quebrada Jicote, separated by host gender. Sample sizes appear above each pool number. The pool numbers for Quabrada Jicote are the same as those used in Chapman & Kramer (1991b) and the map therein; SP refers to the Source Pool. Pools 21–27 are pools from sector 2 of Q. Jicote and Pools 31–38 are pools from Sector 3.

sion, pool surface area was positively correlated with the prevalence of 'neascus' and was the only significant correlate (arcsine √ prevalence = $-0.32 + 0.16*\log$ pool area; $r^2 = 0.62$; $p < 0.001$). Correlations between the four independent variables and the prevalence of 'neascus' produced similar results; pool area was the only significant factor (area $r = 0.79$, $p < 0.001$; density $r = 0.04$, $p = 0.90$; periphyton $r = 0.06$, $p = 0.85$; oxygen $r = -0.15$, $p = 0.61$).

Discussion

Previous studies have revealed variation in prevalence of parasites of fishes among lakes (Dogiel 1961, Kennedy 1985, Bell & Burt 1991), rivers (Kennedy 1990), and among sampling stations in large bodies of saltwater, such as the North Sea (Pilcher et al. 1989). In addition, variation in susceptibility to disease has also been found among fish populations from different rivers (Price 1985, Gjedrem & Aulstad 1974). In this study, we demonstrate that significant spatial heterogeneity in the prevalence and intensity of fish parasites exists on even smaller scales, among dry season pools in intermittent streams.

The effect of pool area on 'neascus' prevalence may reflect whether the final hosts, fish-eating water birds, could use all pools equally. During the course of the study, potential avian hosts were generally observed in the larger pools. For the 'diplostomulum', host density was the only significant predictor of prevalence of parasites within pools. Organisms under stress or in poor body condition are generally less resistant to parasites (Zuk 1990). If higher densities contribute to higher levels of stress, pools with higher densities of fish might be expected to be more heavily parasitized.

There has been much recent interest in the potential importance of stochastic events in determining the composition of parasite communities (Kennedy 1985, 1990). Intermittent streams are often subject to severe flash flooding which may substantially alter host-parasite dynamics. In our study, there was no evidence to suggest that clinostomatid and 'diplostomulum' prevalence were influenced by their position in the unidirectional downstream gradient; however 'neascus' prevalence was negatively correlated with distance from the most upstream pool. Chapman & Kramer (1991a) studied the rainy season dispersal of *Poecilia gillii* in the wet season preceding our dry season collection of parasite data, during which time there were two major floods. The first flood was very severe, and pools lost an average of 75% of their populations. Most of the lost fish died by becoming trapped in desiccating pools. Population loss varied from 12% in the Source Pool to an average of 68% in the middle sector, to an average of 93% in the most downstream pools. If 'neascus' had been present prior to the first very severe flood, the high loss of fish from most pools in Sector 3 may have contributed to the absence of this parasite in these downstream pool populations in the following dry season. Although populations increased in the post-flood period, the severe flood may have lead to the local disappearance of parasitized fish or the first intermediate host in Pools 3–5 to 3–8.

Fish body size and age have often, though not always, been found to be positively associated with the prevalence and/or density of parasite infection (Dogiel 1961, Amin 1985, Madhavi & Rukmini 1991). In Quebrada Jicote, the prevalence of both 'diplostomulum' and 'neascus' was positively correlated with the length of *P. gillii.* Body size effects remained significant when the effects of pool and fish gender were removed. In Quebrada Costa Rica, female and male fish differed in the way they were parasitized by the clinostomatid. Larger females were more heavily parasitized than smaller females. For fish smaller than 50 mm, male *P. gillii* were more likely to be infected by the clinostomatid, and had a greater intensity of infection than similarly sized females. This was not true for larger size classes; however, sample size was small for very large males.

In these streams, pools are only temporarily separated, joining during the floods in the rainy season. Thus, *P. gillii* populations, having undergone growth in divergent parasite conditions, are mixed before being divided into different pools again. The patchiness in parasitism among microhabitats may be relevant to the maintenance of heritable genetic variation in host and parasite populations. Models have shown that the temporary partitioning of habits into microhabitats where selection acts differently, before 'random' mating among individuals from all microhabitats, can maintain genetic diversity (Levene 1953, Levins & MacArthur 1966). Genetic variation in host resistance has been demonstrated in other systems (Price 1985, Wakelin & Blackwell 1988), but remains to be investigated at the present site.

This study has demonstrated significant environmental heterogeneity in parasite infection at a small scale, among temporarily disconnected pools, and that ecological variables also correlate with parasite prevalence. This demonstrates that environmental parameters may affect parasitism in groups of fish isolated in dry season pools, and suggests which patterns need further experimental testing.

Acknowledgements

Funding for this work was provided by an NSERC Post-Graduate and Post-Doctoral Fellowship to LJC and CAC, a McConnell Memorial Fellowship to LJC, a FCAR doctoral scholarship to MC, and NSERC Operating Grants to D.L. Kramer, L. Lefebvre, and G. Bell. We would like to thank M. Bryant and V. Visman for help with dissections. J. da Silva, M. Bradford, J. Schikoff and two anonymous reviewers improved the manuscript with their comments. We would also like to thank D. Brooks for helping to identify the parasites.

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