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Ecology, Volume 76, Issue 5 (Jul., 1995), 1461-1472.

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PREDATION AS AN AGENT OF POPULATION FRAGMENTATION IN A TROPICAL WATERSHED¹

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Abstract. Stream fish sometimes show multimodal distributions, with high densities in the tributaries of a river but rarity or absence in the river itself. To assess if predation can produce such a fragmented distributional pattern on a large geographic scale, we determined the density and habitat use of a prey fish in two tropical stream watersheds, each with a barrier waterfall that split the drainage into a region with a strongly piscivorous fish and a region lacking a strong piscivore. In contrast to sites with the strong piscivore, the prey fish in areas above barriers showed a dramatic expansion into the main river, thereby spatially consolidating an otherwise fragmented distribution. Manipulation of piscivores in a third-order stream flanked by a series of first-order experimental streams also showed that the prey distribution expanded into the third-order stream when piscivores were excluded, and that the presence of the piscivores in the third-order stream reduced prey densities both by killing the prey and by inducing the prey to ascend cascades to enter the tributaries.

Because the predator created spatial fragmentation of the prey population, we examined prey-fish dispersal in the experimental stream facility to ask whether the predator could reduce prey movement into and beyond the predator-occupied sites. As hypothesized, the experiment revealed that predators could block prey dispersal by killing prey. However, the experiment also suggested that predators may increase prey movement between tributaries by inducing shifts out of river sites. The results suggest that realistic models of dispersal by prey would need to account for effects of both predator consumption and prey behavioral responses to the predator.

Key words: corridors; experimental stream; fish; fragmentation; habitat use; *Hoplias*; niche shift; patchiness; predation; predation threat; *Rivulus*; tropical stream.

INTRODUCTION

The geographic distributions of many organisms show multimodal patterns of abundance. In one model, such a pattern occurs because intervening areas consist of physically unsuitable habitat, e.g., water surrounding terrestrial islands or deforested areas surrounding forest fragments (Model I). In an alternative model (Model II), unoccupied intervening areas have suitable physical habitat, but gaps or saddles in the distribution of the organism still occur due to negative biotic interactions, such as competition and predation (Brown 1984, Jeffries and Lawton 1984, Wiens 1989, Ross 1991). Such multimodal patterns of abundance are often present in river systems with dendritic drainage patterns, yet little is known about their causes (Schlosser 1987). These systems may contain species having their highest densities in tributaries, but with saddles of low densities or complete absence in intervening river sites (Sheldon 1968, Li et al. 1987). For such

populations Model II would be supported if a population expands into the main river when predators or competitors are removed, and Model I would be supported if the prey population fails to expand, remaining spatially fragmented.

Here, we have identified a tropical aquatic system in which these processes can be studied on a large scale, that of the entire drainage. In a previous study of predator effects on a local scale (within a pool, or between two adjacent pools within a stream), Fraser and Gilliam (1992) found that a predator, the piscivorous fish *Hoplias malabaricus*, suppressed female reproduction, reduced growth rates, and increased death rates of the killifish *Rivulus hartii* when the predator entered a stream pool. The predator also caused some prey to shift between pools within a stream. More recently we surveyed the fish community throughout much of an entire watershed, the Heights of Guanapo in Trinidad (Gilliam et al. 1993), where we found *Rivulus* at high densities in predator-free first- and second-order tributaries, but at low densities in the main, fourth-order river which is occupied by *Hoplias*. The survey, how-

¹ Manuscript received 18 November 1993; revised 26 September 1994; accepted 28 September 1994.

ever, failed to adequately test a prediction of the predation hypothesis, that steep gradients in *Rivulus* densities should occur at points of contact with *Hoplias*. Because *Hoplias* did not ascend tributaries in this drainage, it was not possible to examine points of contact within stream orders, except for one site on the fourth-order Guanapo River, which was not examined in detail in that study. Thus, the question of whether predation, a biotic factor (Model II), is sufficient to cause the broad distributional pattern of *Rivulus* in the drainage remained unanswered.

Furthermore, Model I, the alternative hypothesis that predation may have little or nothing to do with the distributional pattern of *Rivulus*, is also plausible. Indeed, Model I is supported by the fact that *Rivulus hartii* and other members of the genus *Rivulus* are usually viewed as occupants of small headwaters and isolated waters (Tee-Van 1922, Hoedeman 1958, Kristensen 1970, Luling 1971, Huehner et al. 1985). A physical variable, such as flow rate, could limit the distribution of *Rivulus*, and *Rivulus* could represent a "small water" fish that would not alter its distribution if the predatory species were removed from the main river. Support for the alternative hypothesis would suggest that predator effects, although influencing vital rates and use of space within a stream, do not account for the broader distributional pattern of *Rivulus*.

The purpose of this study was to test the broad hypothesis that predation can produce the observed distributional patterns of *Rivulus* in the Heights of Guanapo drainage. We predicted that the saddles of low density in the intervening river would disappear, and the otherwise fragmented distribution of *Rivulus* should consolidate, if predators were removed. To test this prediction we chose another watershed, the Paria drainage system, where a barrier waterfall occurs in the lower portion of the drainage, in a fifth-order section of the main river, blocking the upstream movement of potential predators and leaving almost the entire drainage free of piscivorous fish. We predicted that *Rivulus* would expand into portions of the predator-free fourth- and fifth-order Paria River (predator-released). We also tested this prediction in the Guanapo drainage, where the previous study had revealed that the upper limit of the distribution of *Hoplias* coincided with a barrier waterfall. We asked if the density and microhabitat use of *Rivulus* increased as predicted above the barrier. The previous study suggested such a pattern, but did not measure density in detail near the barrier, or examine differences in habitat use.

Because our earlier studies suggested that intimidation was a significant component of the predation process in this predator-prey interaction, we also did an experimental manipulation (Density gradient experiment) to test the hypothesis that *Rivulus* actively avoids *Hoplias*-occupied waters, thereby producing a density gradient between the river and connecting tributaries. We built a series of first-order, experimental

field streams connecting to a third-order stream, and manipulated the density of *Hoplias* in the third-order stream. We asked whether (1) *Hoplias* can induce a behavioral shift by *Rivulus* out of the third-order stream into the connecting first-order tributaries when a steep cascade intervenes at the junction of the two, and (2) such behavioral shifts and/or consumption by *Hoplias* can produce a difference in *Rivulus* density between the first- and third-order sites, as compared to densities in the absence of *Hoplias*.

Finally, because the presence of *Hoplias* in a river has the potential to reduce movement between tributaries, with implications for regional population dynamics and genetic divergence, we did a second experiment in the field streams (Movement experiment) to test the prediction that *Hoplias* would restrict movement by *Rivulus* between tributaries when a predator occupied sites between them.

METHODS

Study area

The study was done in two opposing watersheds, separated by a high ridge (660 m), in the Northern Range Mountains of Trinidad (Fig. 1). The south slope watershed, the Heights of Guanapo, contains a major drainage that we previously surveyed for fish in 1990. Topography and vegetation relevant to the present study are described in Gilliam et al. (1993). The north slope drainage, the Paria River system, is a forested and relatively undisturbed drainage, similar to the Guanapo River drainage, but differing from the Guanapo in having its first upstream barrier to piscivorous fish, a 10 m high waterfall, Paria Falls, within 500 m of its mouth at the Caribbean Sea. Although the strongly piscivorous goby, *Eleotris pisonis* (food habits in Nordlie 1981), occurs in the 500-m stretch below Paria Falls, only *Rivulus hartii*, guppies, *Poecilia reticulata*, and the small gobies *Sicydium punctatum* and *Gobiesox strumosus* are known to occur above this waterfall, leaving almost the entire Paria River free of any strongly piscivorous fish. In addition to the fish, the most conspicuous members of the Paria River fauna are prawns belonging to the genera *Macrobrachium* and *Atya*. *Macrobrachium* spp. are carnivorous and known to prey on small fish like the guppy (Endler 1978). In aquaria, *Macrobrachium crenulatum* readily eats the eggs and fry of *Rivulus* (D. F. Fraser, unpublished data). While the feeding habits of *Atya* in Trinidad are unknown, members of the genus in Puerto Rico are entirely herbivorous and detritivorous (Pringle et al. 1993).

The Guanapo, in contrast to the Paria, has its first barrier waterfall >40 km from its ocean mouth, and a host of species, including the strong piscivore *Hoplias malabaricus* (food habits: Costa 1987, Prejs 1987, Winemiller 1989, Fraser and Gilliam 1992), occur in 8000 m of fourth-order river that we surveyed in 1990. The

Guanapo barrier consists of a massive, quartz boulder lodged in a notch in a section of the river with canyon-like walls, creating a 2.3-m waterfall. The 1990 and several subsequent surveys reveal no strongly piscivorous fish above this barrier.

Field procedures

To address the predictions that the density of *Rivulus* in the main rivers would increase and that *Rivulus* would expand its use of the main river habitat in the absence of the predator *Hoplias* or *Eleotris*, we chose eight river section (sites), five in the Guanapo and three in the Paria River, for censuses of the *Rivulus* population. Study sites above barrier waterfalls are designated predator-released sites (R), whereas study sites below barrier falls are designated predator sites (P). Thus, P1–P4 are predator sites (P1–P3 Guanapo, P4 Paria) and R1–R4 are predator-free sites (R1–R2 Guanapo, R3–R4 Paria) (Fig. 1). Study sites, all in fourth- or fifth-order rivers, were chosen by the criteria: (1) entering tributaries demarcate their up- and downstream ends, (2) they contain pools and riffles, and (3) they are accessible to investigators. The study sites, i.e., sections of river that were intensively surveyed, varied in length from 113 m to 793 m ($\bar{X} \pm 1SE = 351.5 \pm 88.2$ m).

We censused seven sites twice, once at the beginning of the dry season in January 1993 and once near the beginning of the wet season between May and July 1993. We censused the eighth site, R4 (Paria, predator release), once in January 1993.

River censuses of *Rivulus* were done visually after dark, using headlamps and underwater flashlights. Our census procedure, involving two searchers and a recorder, included walking through each designated section and recording the exact location of each *Rivulus* encountered including: (1) distance from the downstream end of the section (in metres), (2) distance from the shore line, (3) depth of water at the fish's position, and (4) location (bottom, middle, top) of the fish in the water column. We also estimated the total length (TL) and recorded the sex of each fish (*Rivulus* < 25 mm TL were classified as immature and are not reported). In addition to characteristics of the fish, we also recorded the dominant habitat type in the section, e.g., pool, riffle, or backwater, and whether the location of the fish was isolated from the main stream, as in an isolated flood pool. Finally, we mapped the stream, measuring the length and width of pools and stretches between pools. We censused *Hoplias* and other fish species, using the same procedure, but did not enumerate *Poecilia*, which were usually abundant in all sections. Counts of *Rivulus* in tributaries were made by censusing *Rivulus* in \geq two pools, rather than by the more comprehensive procedure that we used in the rivers.

In addition to the eight study sites (P1–P4, R1–R4), a ninth site (R5) was visited in a preliminary stage of

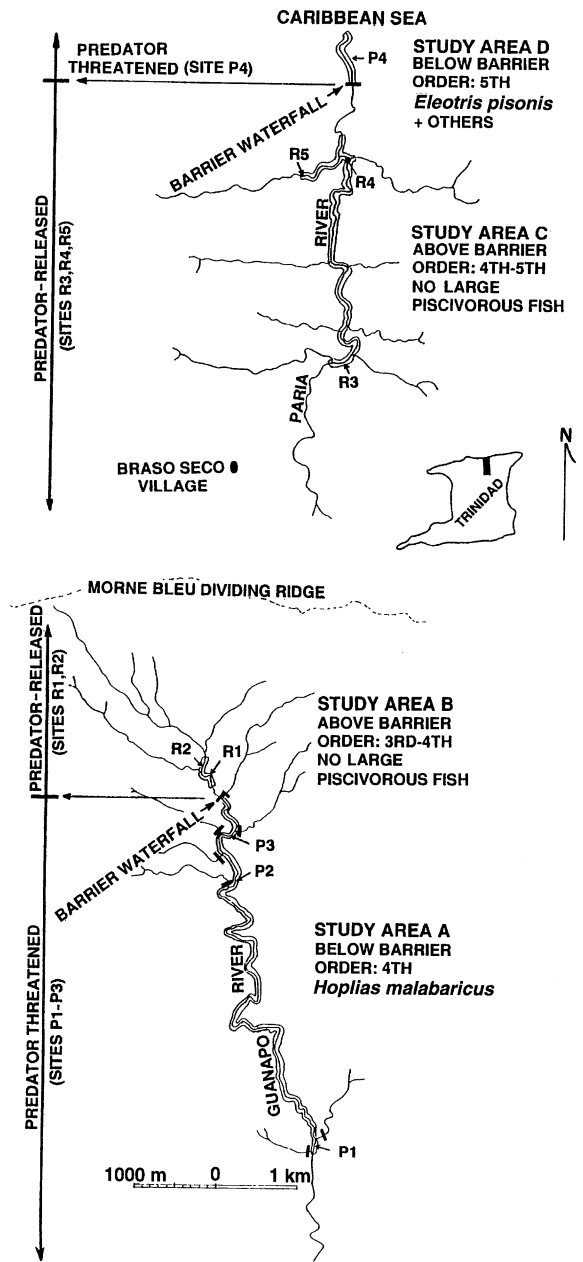


FIG. 1. Map of opposing Heights of Guanapo (south slope) and Paria (north slope) drainages in the Northern Range Mountains of Trinidad. Predator-released study sites (R1–R5) occur above barrier waterfalls; predator-present study sites (P1–P3) occur below barrier waterfalls. Locations of barrier waterfalls are indicated by solid bars. The species listed in study areas A and D are large piscivorous fish.

the project (January 1992), and data on microhabitat use in one pool were collected by the above visual methods.

Visual censusing, as opposed to seining and electrofishing, was necessary to obtain exact position data on each fish, and night censusing was preferable to daytime censusing, because *Rivulus* are readily observed

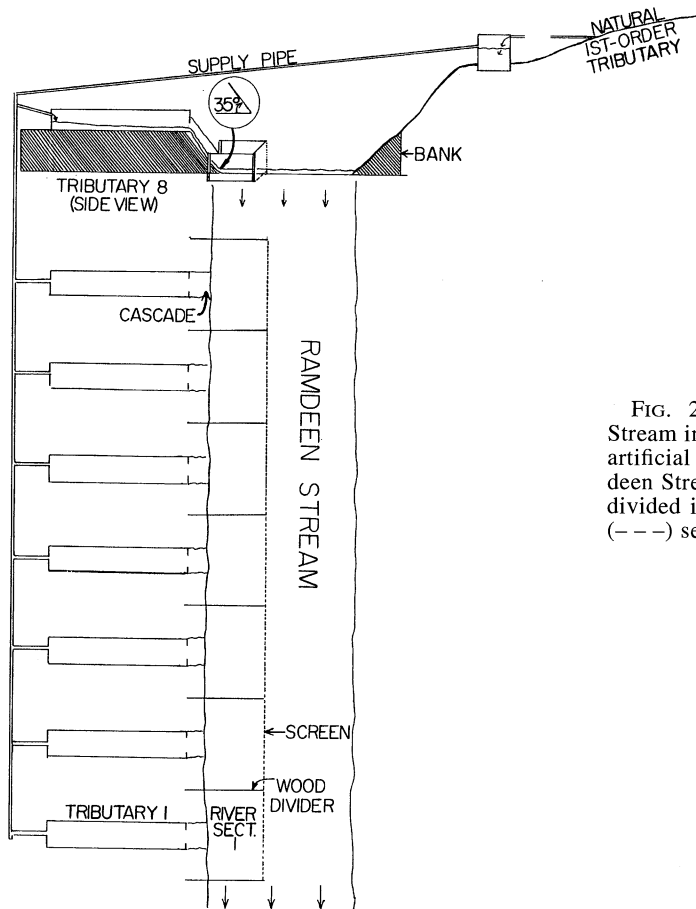


FIG. 2. Experimental stream facility at Ramdeen Stream in the Arima Valley, Trinidad. Eight "first-order" artificial tributaries are connected to the third-order Ramdeen Stream by a steep cascade. Ramdeen Stream is subdivided into eight sections by wood partitions. A screen (---) separates the river sections from the main stream.

on the bottom or in the water column at night but are less conspicuous during the day. *Hoplias* is active at night and readily observed on the bottom or in the water column, but remains more concealed and presumably less active in daylight (D. F. Fraser and J. F. Gilliam, unpublished data). *Rivulus* is both a diurnal and nocturnal forager, and both *Rivulus* and *Hoplias* are solitary, sit-and-wait, or stalking predators. Investigator search rates varied depending upon the density of *Rivulus*, typically ranging between 30 and 120 m of stream per hour.

Experimental stream facility

We built eight replicate, experimental streams (width = 0.42 m, length = 2.7 m; gradient = 0.2 cm/m; flow volume = 0.01 m³/min) situated perpendicular to and elevated on a bank (0.8 m high) above a natural, third-order tributary of the Arima River, Ramdeen Stream, previously described in Fraser and Gilliam (1992). Each experimental stream received water piped from a first-order tributary of Ramdeen Stream (Fig. 2). Four months prior to starting the experiments, we translocated substrate from the natural first-order stream into the experimental tributaries. Organic materials from the canopy accumulated in the tributaries, so that by the

end of the 4-mo period they appeared to mimic the natural tributary in substrate characteristics and accumulated organic debris. Because almost all tributaries in the Heights of Guanapo (Fig. 1) have waterfalls close to their junctions with the main river, we joined each experimental stream to the third-order stream by a cement and stone cascade ($N = 8$, slope = 34.6 ± 0.90 degrees, height = 0.80 ± 0.27 m [means ± 1 SE], Fig. 2). Ramdeen Stream flows along the base of the cascades but is divided into eight sections (2.36 m² each) by wood partitions. The eight sections are contiguous and separated from the main flow by a terminal end-screen consisting of window screen backed by a heavy mesh screen. The 1.4-mm² mesh of the window screen prevented colonization by fish indigenous to Ramdeen Stream. Because of the wood partitions, the individual sections resembled backwaters in the natural stream, such as those that occur behind logs, rocks, or tree roots. The sections received both inflow from the main stream, and outflow from the tributaries.

The presence of a cascade between the first-order tributary and the third-order stream added realism to the system. *Rivulus* could not simply swim from a location containing a predator to a nearby predator-free one, as we have previously observed (Fraser and Gil-

liam 1992), but had to ascend, by making jumps or flips, the 0.8 m high cascade (barrier fall), to escape from a predator-occupied section. Water in the cascades varied from a thin sheet to a maximum depth of 5 mm, considerably less than the body depth of the fish.

During the 4-mo pre-stocking period, we left the experimental tributaries unscreened to verify that *Rivulus* could ascend the waterfall of each tributary. By the end of this period, *Rivulus* were found in each tributary, indicating that each was accessible to *Rivulus*. In addition, we found numerous fry, further indicating that *Rivulus* treated the tributaries as natural first-order streams. *Rivulus* was the only fish species that colonized the tributaries. Prior to stocking the streams, we visually searched and then electrofished each tributary and the third-order sections to remove any resident fish, including the newborns.

Density gradient experiment

The hypothesis predicts that, in the absence of *Hoplias*, *Rivulus* will expand its use of the main river. Using the experimental stream facility, we manipulated *Hoplias* to test the prediction that *Hoplias* could produce strong differences in the density of *Rivulus* between first- and third-order streams. We also asked if behavioral shifts by *Rivulus* and killing by *Hoplias* both play a role in producing the differences.

In reporting these experiments, we refer to the first-order experimental streams as the "tributaries" and the third-order Ramdeen Stream as the "river", because these experiments are intended to reflect the natural situation in which *Rivulus* is found in tributaries and predators in the main river. An experimental unit consists, then, of one tributary connected by a cascade to one river section.

We did two 55-d trials between 16 January and 12 May 1993, with each trial consisting of four experimental units free of predators and four with *Hoplias* in the river section below the cascade (*Hoplias* density in enclosure = 0.42 individuals/m²). Thus, each treatment (predator present, predator absent) was replicated eight times. To analyze for position effects, e.g., variation in canopy cover over tributaries, we blocked by tributary number (tributary 1 and 2 formed a block, tributary 3 and 4 another, etc., totalling eight blocks across the two times), and used a random procedure to choose one river section within each block to receive one *Hoplias*, taken from Ramdeen Stream (first trial: four *Hoplias* of TL 149.8 ± 17.6 mm, second trial: four *Hoplias* of TL 175.3 ± 17.0 mm [means ± 1 SE]). Although we had no evidence that *Hoplias* could or would ascend the cascades, we nevertheless screened the tributaries with 1.2-cm *Hoplias*-proof mesh just beyond the top of the cascades.

Rivulus were caught in Ramdeen Stream, in excess of the number used, and maintained in laboratory aquaria for several days prior to stocking into the tributaries. During this period the fish were marked with

acrylic paint injected at the caudal peduncle. All *Rivulus* were marked uniquely for the tributary into which they were stocked. Following marking we treated the holding tanks with antibiotics and observed the fish for several days. Only fish that appeared healthy, and which had visible marks, were selected for the experiment.

In each experimental unit we stocked 4 *Rivulus* into the tributary (first trial: 32 *Rivulus* of TL 48.9 ± 1.6 mm, second trial: 32 *Rivulus* of TL 52.6 ± 1.6 mm [means ± 1 SE]) and 8 *Rivulus* into the river section (first trial: 64 *Rivulus* of TL 54.9 ± 1.3 mm, second trial: 64 *Rivulus* of TL 49.5 ± 0.9 mm). The sex ratio was 1:1 in all replicates. We stocked *Rivulus* first, and 24 h later *Hoplias*.

Two censuses were made for each replicate. The first was a night visual count of *Rivulus* on the 10th day (10th day chosen arbitrarily) of the experiment to assay for predator-induced ascent by *Rivulus* up the cascade separating the river and tributaries. At the end of each trial (55 d) all tributaries and third-order river sections were again searched for *Rivulus* at night using headlamps, and all fish were removed, including any fry. We followed the visual search by electrofishing, but undisturbed *Rivulus* are easily located at night, and >95% were captured during the visual search. We also verified the presence of *Hoplias*.

Movement experiment

In the movement experiment, we modified the experimental stream facility to group the eight tributaries into four pairs, removing the wooden partition in the river between members of each pair. Thus, *Rivulus* could potentially disperse from a given tributary, move into the river, and possibly disperse to the adjacent tributary in that pair. We asked whether a predator in the main river altered dispersal from tributaries. In each replicate, seven adult *Rivulus*, marked uniquely for each tributary, were introduced into each tributary (14 total *Rivulus* per replicate), and we randomly chose two of the four tributary pairs for stocking a single *Hoplias* into the river (the predator treatment). The remaining two pairs served as predator-free controls. Each treatment was replicated a total of six times by doing three 25-d trials over the period 18 May to 29 August 1993. The first trial differed from the second and third in that 16 *Rivulus* were stocked into a single tributary in each pair, rather than 14 *Rivulus* split between the two tributaries in each pair, so we analyzed the data by proportions to standardize for the difference in numbers stocked. *Hoplias* (127 mm and 177 mm) were assigned randomly to river sites in each trial. The same two fish were used in each trial. As in the previous experiment, screens at the top of each cascade allowed passage by *Rivulus*, but assured that *Hoplias* could not enter a tributary.

At the end of each trial each marked *Rivulus* was scored as (i) found in its "home" tributary (its stocking

site), (ii) colonized the river site, i.e., moved from its home tributary to the river, (iii) colonized the adjacent tributary, or (iv) dead. These data are ordered categorical data (Agresti 1990) with the order iv, i, ii, iii representing increasing degree of dispersal (iv arbitrarily put before i). We answered the following questions using these data: First, did the predator affect survival rate of the potential colonizers (proportion not scoring iv)? Second, of the survivors, did the predator affect the proportion dispersing (excluding iv, proportion not scoring i)? Third, of those dispersing, did the predator affect the proportion dispersing to the farthest site, the adjacent tributary (excluding iv and i, proportion not scoring ii)? Mann-Whitney U tests, two-tailed, were used to compare treatments.

RESULTS

Field censuses

The field censuses showed that *Rivulus* density increased greatly in larger waters when released from the threat of predation (Study Areas B and C, Fig. 1), thus supporting the main hypothesis. The density of *Rivulus*, measured as the number of fish per 100 m of river course, was significantly greater in the predator-free (R1–R4) sections above the barrier falls than in the predator-occupied (P1–P4) sections below the barrier falls (t test on log-transformed data, two predator levels, $N = 4$ study sites per predator level, $t = 3.44$, $P = 0.014$; densities averaged across dates for sites with > 1 sampling date). *Rivulus* density was 23 times higher in January and 34 times higher in May–July where predators were absent than where predators were present (predator-occupied sections January: 3.22 ± 1.71 *Rivulus*/100 m; May–July: 6.36 ± 3.69 *Rivulus*/100 m; predator-free sections January: 72.8 ± 35.8 *Rivulus*/100 m; May–July 1993: 214.8 ± 119.4 *Rivulus*/100 m [means ± 1 SE]). The same conclusion applies if we consider only fish found in pools, or only fish found in areas between pools, including runs, glides, and riffles. Combining times and considering only pools, *Rivulus* was 109 times more abundant where predators were absent than where present (predator-occupied sections 2.19 ± 0.8 *Rivulus*/100 m, predator-free sections 238.9 ± 84.5 *Rivulus*/100 m; t test as above, $t = 4.17$, $P = 0.006$). Similarly, considering only fish found in areas between pools, *Rivulus* was 10.5 times more abundant where predators were absent than where present (predator-occupied sections 6.15 ± 2.63 *Rivulus*/100 m, predator-free sections 64.2 ± 24.3 *Rivulus*/100 m; t test as above, $t = 3.44$, $P = 0.014$). Although *Rivulus* was rare in the main river in the presence of the predator, we note qualitatively that *Rivulus* would often be found in nearby rain or flood pools isolated from the river, and that a locally high density (57 *Rivulus*/100 m or 0.07 inds./m²) occurred in some riffles of P3, the first major riffles below the barrier.

We found *Hoplias* in 5 of 19 Guanapo River pools

in January and in 4 of 19 in July. When *Hoplias* was present in a pool, we found from 1 to 3 individuals there (density = 0.013 ± 0.002 *Hoplias*/m² [means ± 1 SE]).

The magnitude and consistency of the difference in population levels above and below the barrier falls in the two drainages are shown in Fig. 3, where data are shown as fish per unit area in pools to allow comparison to tributaries. In the Guanapo River, *Rivulus* density increased sharply above the barrier falls (Fig. 3a). We also confirmed that the exact boundary between abundant and rare *Rivulus* populations in the Guanapo River corresponded precisely with the barrier. We found *Hoplias* in the plunge pool directly below the boulder that forms the barrier. Immediately above the boulder, *Rivulus* was common, whereas immediately below the boulder *Rivulus* was absent. Above the boulder, densities in the Guanapo River were similar to densities in tributaries joining the river (inset Fig. 3a), but below the boulder *Rivulus* densities were much lower in the river than in the tributaries joining the river (inset Fig. 3a), illustrating the steep gradient in density between the river and tributaries in the predator-occupied stretches, but not elsewhere.

The same pattern, a contrast in density of *Rivulus* above and below the barrier, also occurred in the Paria drainage, where we found *Eleotris pisonis* (125 mm TL) immediately below the Paria Falls. *Rivulus* did not occur in the plunge pool below the falls, nor in any of the downstream section between the falls and the river mouth at the sea (Fig. 3b). However, in contrast to the predator-free sections of the Guanapo, the density of *Rivulus* was relatively low throughout the Paria River. We also noted qualitatively that *Macrobrachium crenulatum* and *M. carcinus* were very abundant above the barrier with numbers and mass clearly higher than those of *Rivulus*. The 500-m section of Paria River immediately above the Paria Falls, where the river passes through a canyon, was not fully surveyed, but we noted that *Macrobrachium* densities were high and *Rivulus* density low in that reach.

In the Guanapo, we found a decided shift in the distribution of *Rivulus* within pool habitats above and below the barrier. Below the barrier, *Rivulus* was always near pool edges (Fig. 4a), but above the barrier we found *Rivulus* throughout pools (Fig. 4b). We found the identical pattern above the barrier in the Paria River, Fig. 4c and d (*Rivulus* was never found below the barrier). These data refer to nocturnal distributions; we did not quantify daytime distributions, but note qualitatively that *Rivulus* tended to be near or under cover in the daytime, and shifted to more exposed positions at dusk.

Density gradient experiment

Experimental manipulations of *Hoplias* in river sites revealed that *Hoplias* can produce strong differences in *Rivulus* density between tributary and river sites

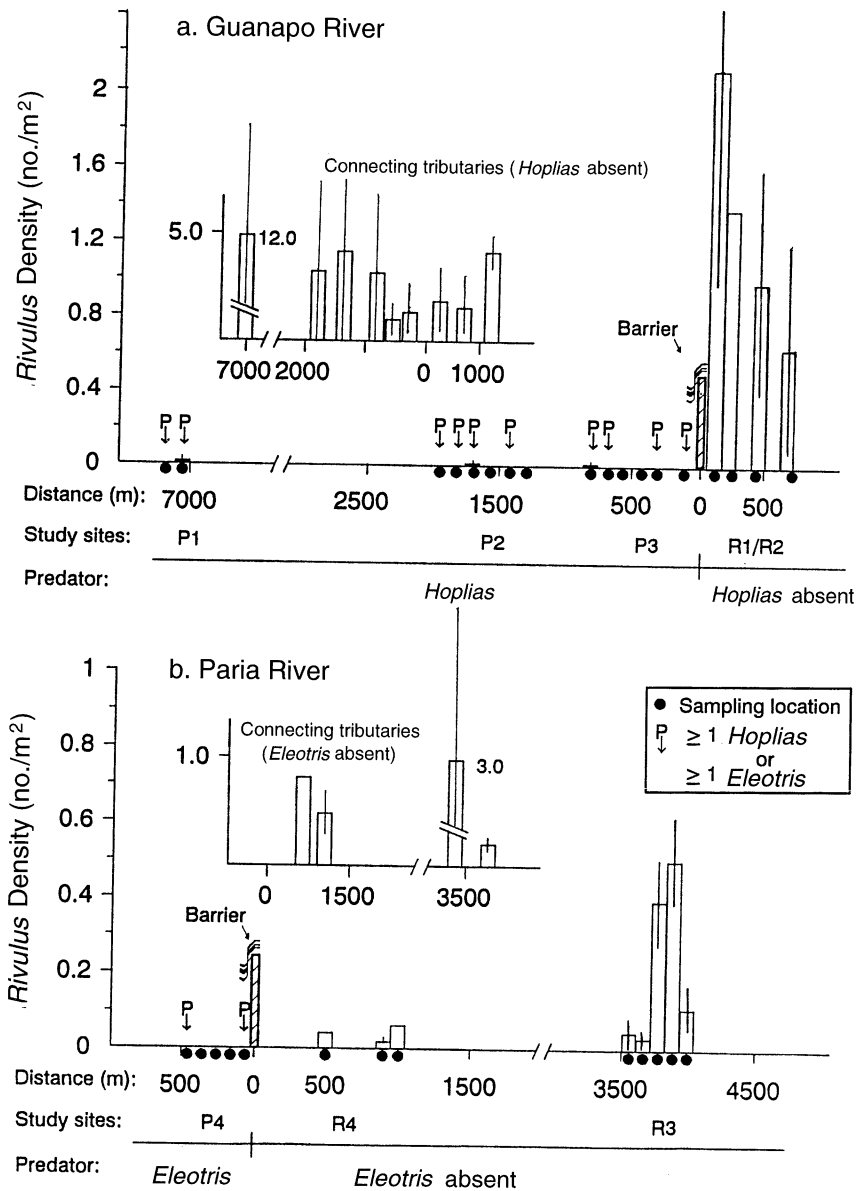


FIG. 3. Density of *Rivulus hartii* in pools, grouped by 100-m sections of river. Error bars are ± 1 SD of the mean densities when >1 pool or >1 sampling time occurred for that section. *Rivulus* densities increased in the main Guanapo and Paria Rivers above barrier waterfalls. *Rivulus* densities were high in predator-free tributaries throughout the Guanapo drainage, including those that entered below the barrier (quartz boulder), and below which *Rivulus* densities in the main river were low. Densities are for fish ≥ 25 mm in total length.

(Fig. 5). When *Hoplias* was excluded from the river (predator-free), *Rivulus* density was similar in the tributary and river sites; however, when *Hoplias* was present in the river sites, *Rivulus* showed large differences in density. Defining the difference as $D = (\text{density in river}) / (\text{density in tributary} + \text{density in river})$, where $D > 0.5$ indicates higher density in the river than the tributary, and $D < 0.5$ indicates the opposite, the experiment yielded the following values (means ± 1 SE). $D = 0.56 \pm 0.04$ by mass and $D = 0.57 \pm 0.04$ by number in predator-free conditions, and $D = 0.13 \pm$

0.04 by mass and $D = 0.22 \pm 0.04$ by number when predators were present (ANOVA on arcsine-transformed D : predator effect $P = 0.0003$, block effect $P = 0.31$ by mass; predator effect $P = 0.0005$, block effect $P = 0.046$ by numbers). This difference reflects all population processes, i.e., deaths, growth in mass, and movement by stocked fish, and births, growth in mass, and movement by recruits born during the experiment. Considered separately, both the recruits and stocked fish showed the same pattern as did the whole population (D of stocked fish (by mass) = 0.55 ± 0.05

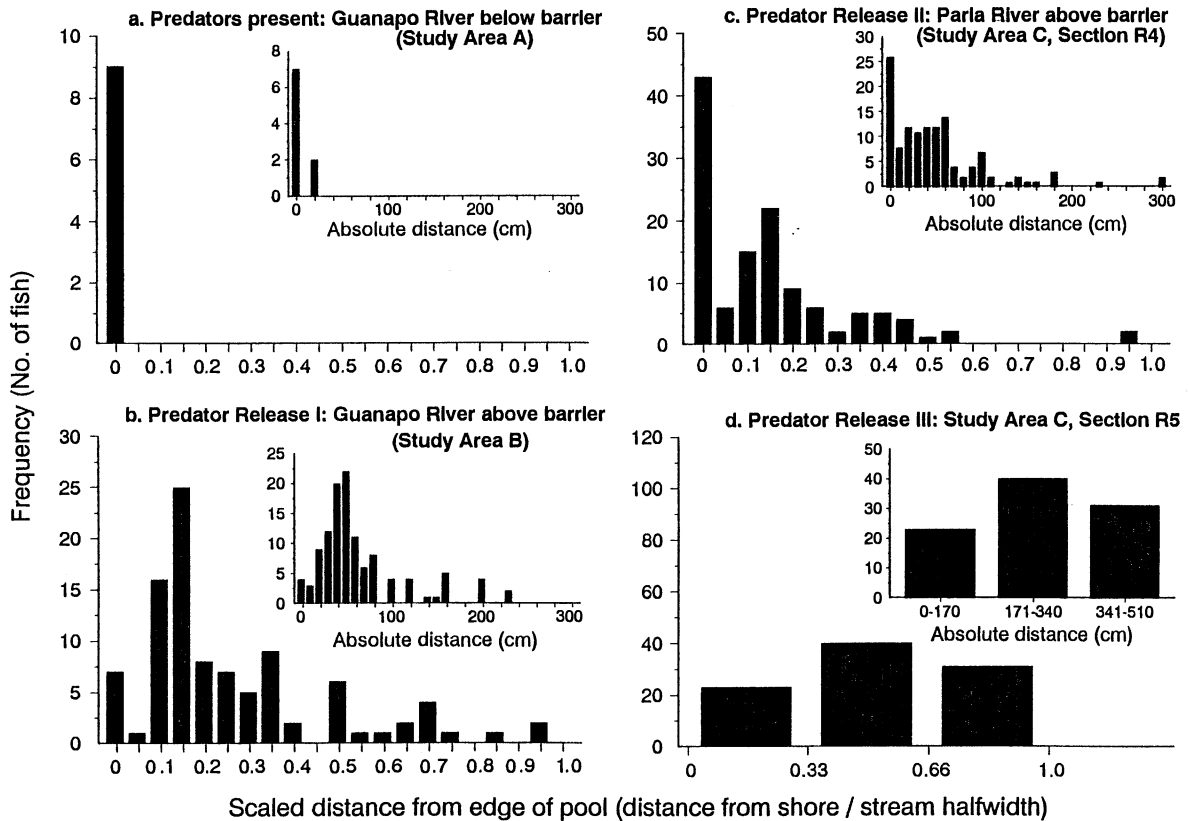


FIG. 4. Nocturnal distribution of *Rivulus*. Distance from pool edges where *Rivulus* were found in predator pools of the Guanapo River (none were found in the predator pools of the Parla River) and predator-free areas of the Guanapo and Parla Rivers. When piscivorous fish are absent *Rivulus* shifts its use of the habitat to include both edges and the deeper, open waters of large pools.

in predator-free conditions, D of stocked fish = 0.10 ± 0.04 when predators were present; ANOVA as above, predator effect $P = 0.0005$, block effect $P = 0.28$; D of recruits = 0.68 ± 0.04 in predator-free conditions, D of recruits = 0.22 ± 0.05 when predator was present; ANOVA as above, predator effect $P = 0.0017$, block effect $P = 0.23$). Production and growth of newborn *Rivulus* occurred in the experimental units (screening at the river excluded immigration of *Rivulus*). *Rivulus* <30 mm TL comprised 48% by number and 10% by mass of all fish collected at the end of the 8-wk trials.

The 10th-day census revealed a behavioral contribution to the difference, showing that *Rivulus* left *Hoplias*-occupied waters and ascended the cascades to enter the tributaries. Fig. 6 shows that significantly more *Rivulus* (only stocked *Rivulus*, as recruits had not yet appeared) were present in the tributaries when *Hoplias* was present in the river than when it was absent (number of stocked *Rivulus* in tributary after 10 d [means \pm 1 SE]: predator present 5.9 ± 1.0 *Rivulus*, no predator 3.5 ± 0.8 *Rivulus*, $N = 8$, ANOVA predator effect $P = 0.04$, block effect $P = 0.13$), indicating a net shift out of the river induced by the predator.

In addition to the behavioral shifts, mortality also played a role in establishing the density difference in Fig. 5. Defining mortality as number stocked fish minus number of marked fish recovered, the no-predator treatment yielded 2.1 ± 0.8 fish (means \pm 1 SE), and the predator treatment 6.5 ± 1.2 fish (ANOVA on number killed, $P = 0.016$, block effect $P = 0.36$).

Movement experiment

The purpose of the movement experiment was to determine if predators constitute a barrier to dispersal. The presence of the predator in the river reduced the proportion of prey surviving the experiment (proportion surviving with predator 0.39 ± 0.10 [means \pm 1 SE], = 0.81 ± 0.05 without the predator; $N = 6$ replicates per treatment, $U = 36.0$, $P = 0.002$) (Fig. 7). Summing across all replicates, 72 of 88 stocked prey survived when no predator was in the river, but only 25 of 88 prey survived when the predator was present. By killing some of the fish that entered the river, the predator acted as a barrier to dispersal from a tributary. In addition, of the surviving prey, the predator decreased the proportion that dispersed from the home tributary (0.11 ± 0.06 with the predator, 0.53 ± 0.07

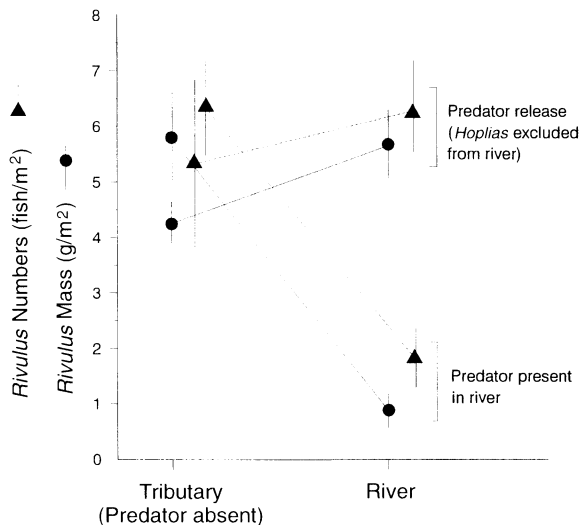


FIG. 5. Mass and numbers of *Rivulus* in the first-order experimental tributaries and their corresponding third-order river sections at the end of eight weeks. $N = 8$ for all treatments; data show means ± 1 SE. With the predator, *Hoplias*, excluded from the river, *Rivulus* densities there were similar to those in the tributaries, but when *Hoplias* was present in the river, *Rivulus* densities showed a steep gradient between the river and tributaries. Numbers per m^2 are for all *Rivulus*, including recruits (total size range 13 mm to 86 mm total length).

without the predator; $N = 5, 6$ replicates, as one predator replicate had no survivors; $U = 30.0, P = 0.004$). Summing across replicates, 36 of the 72 survivors were found outside of the home tributary in the non-predator treatment, but only 5 of the 25 survivors were found outside of the home tributary in the predator treatment. Of the fish dispersing, however, the predator increased the percentage dispersing to the adjacent tributary rather than staying in the river ($100 \pm 0.00\%$ with the predator, $0.00 \pm 0.00\%$ without the predator; $N = 3, 6$ replicates, respectively, as 3 predator replicates had no dispersers; $U = 18.0, P = 0.024$). Summing across replicates, 5 of the 5 surviving dispersers entered the adjacent tributary when a predator was in the river, but 0 of the 36 surviving dispersers entered the adjacent tributary when the predator was not present.

In summary, the predator can block dispersal by killing prey and/or by causing prey to return to the home tributary, but enhance tributary colonization by inducing prey to climb a cascade to escape the river site.

DISCUSSION

The dramatic expansion of *Rivulus hartii* into fourth- and fifth-order rivers, when released from predation, strongly supports the hypothesis (Gilliam et al. 1993) that predation plays a significant role in the large-scale distributional pattern of *Rivulus*. Further, the manipulative experiments demonstrated that behavioral shifts from the larger waters may have contributed to this

pattern. Where previous studies have shown that predator-induced behavioral shifts in use of space by stream fish can produce patterns of abundance on local scales within pools or pool-riffle combinations (Fraser et al. 1987, Power 1984, 1987, Schlosser 1987, Harvey et al. 1988), the present study shows that these patterns can also extend to geographic scales, over entire drainages.

While we focus on predation threat from *Hoplias* in the Guanapo, it is important to note that other species are also blocked by the falls, i.e., covary with *Hoplias*. In addition to *Hoplias*, the characid *Hemibrycon taeniurus* and the cichlid *Aequidens pulcher* are both absent above the barrier waterfalls in the Guanapo River (Gilliam et al. 1993: Fig. 2). *Hemibrycon* is very patchily distributed in the Guanapo River, and it was not observed in any of our study areas except in the plunge pool immediately below the barrier falls. *Aequidens*, however, is common throughout the Guanapo and hence is a potential competitor of *Rivulus*. For this reason, the predator enclosure/exclosure experiments are useful in showing that *Hoplias* is a sufficient agent to produce density gradients. We do not know whether competition from *Aequidens* may also be an agent sufficient to have produced the sharp boundaries. We note that the negative effect of guppies, *Poecilia reticulata*, on *Rivulus* is sufficient to produce a decline in *Rivulus* densities (Gilliam et al. 1993), but nothing so sharp and intense as occurs where *Hoplias* and *Aequidens* occur. While not denying the existence of competition, the results of our field and experimental studies, taken

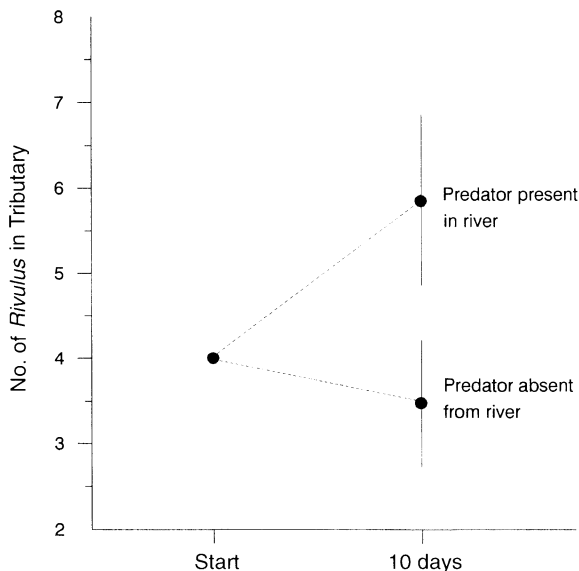


FIG. 6. Initial behavioral shifts of marked *Rivulus* between stream orders in the gradient experiment. $N = 8$ for all treatments; data show means ± 1 SE. When the predator, *Hoplias*, was present in the third-order river, some *Rivulus* shifted into the first-order tributary by ascending a steep, intervening cascade.

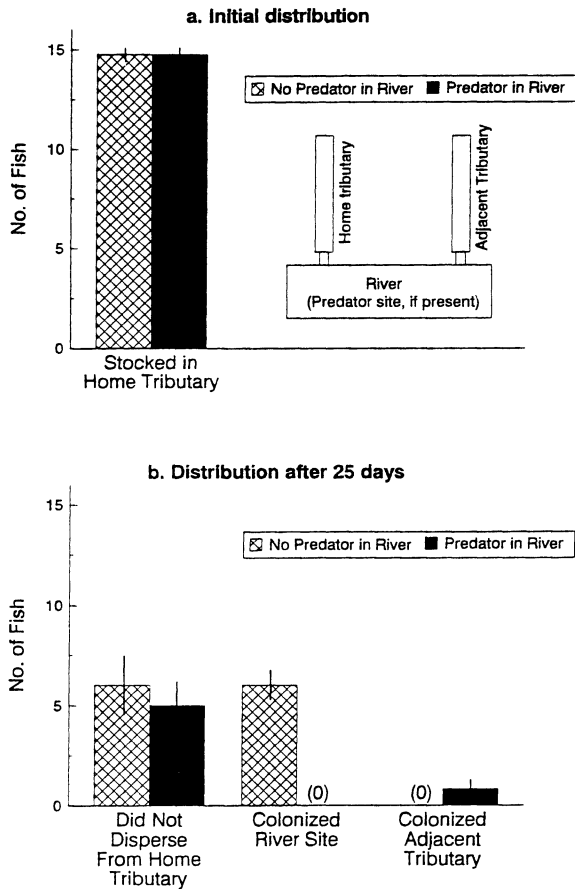


FIG. 7. Dispersal of *Rivulus* from the initial site stocked after 25 days in the Movement Experiment. Diagram at lower right in upper graph shows field site layout. When the predator *Hoplias* was present in the main river, *Rivulus* failed to colonize the river site, but did show a tendency to disperse farther, beyond the predator, to colonize the adjacent tributary.

together, are strong and consistent with the predation hypothesis, and we are confident that we can predict impacts of some hypothetical future events. For example, if the quartz boulder that forms the upper limit to *Hoplias* in the Guanapo were dislodged by erosion, we would predict that subsequent upstream invasion by *Hoplias* would cause *Rivulus* to contract from the main river and become spatially isolated into tributaries as currently is the case below the barrier. Similarly, we predict that stocking of *Hoplias* or other strong piscivores into the Paria or Guanapo drainages by humans would have similar, strong impacts on *Rivulus* distributions.

The present study shows that *Rivulus* is a flexible species capable of occupying many habitats ranging from shallow, isolated pools to large rivers, but that biotic interactions can constrict the distribution and abundance of *Rivulus* from otherwise suitable areas. In the Guanapo drainage, these interactions produce a multimodal pattern of abundance with the highest *Ri-*

vulus densities in the absence of other fish, separated by distinct saddles in density where predators occur (in the Paria drainage, preliminary evidence suggests a different pattern; see below). Strong biotic effects do not preclude the existence of abiotic influences, e.g., stochastic climatic events that might influence population trajectories, but at least for this tropical stream, a comprehensive view of the effects of stochastic climatic events and physical properties on stream fish communities would need to examine the effects of such events on species interactions rather than on how they affect assemblages directly (Meffe 1984).

The Density Gradient experiment showed a role for predator intimidation in causing the steepness of the *Rivulus* density gradient between the river and tributaries, as well as between the river and nearby flood pools in the Guanapo drainage. In the absence of predatory threat, *Rivulus* showed little tendency to ascend the steep cascade at the base of each experimental tributary, but the results clearly showed that predation threat was a strong stimulus to induce *Rivulus* to shift out of the river. The same phenomenon was seen in the Movement Experiment, where the predator induced prey to climb the cascade of the adjacent tributary. Thus, it is plausible that threat contributes to the steepness of the density gradient and the contraction of the population under predation in the Guanapo. It seems unlikely that killing alone could account for the almost complete elimination of *Rivulus* from large, structurally complex river pools; although *Hoplias* is common throughout the Guanapo below the barrier falls, its pool density is actually quite low (means \pm 1 SE = 0.01 \pm 0.01 *Hoplias*/m²).

Movement among fragments.—In the Movement experiment we initially hypothesized that *Hoplias* would block the tributary to tributary movement of *Rivulus* relative to the no-predator controls. However, the opposite occurred; more *Rivulus* colonized adjacent tributaries when the predator was present than when it was absent. As noted above, *Rivulus* in unthreatened treatments had little impetus to ascend the steep cascades, although many did descend from their home tributary and colonize the river. However, when *Rivulus* descended from their home tributary in the predator treatment, some were consumed, some presumably returned to their home tributary, while others ascended the adjacent cascade. The latter move may have been facilitated by the proximity of the tributaries (2 m) in this small-scale experiment, but it is plausible that predators may enhance movement between nearby tributaries, because they increase the probability that the prey will move out of the river into a tributary. Because the probability of predatory death should increase with distance, predators might diminish movement between more distant tributaries, while enhancing movement among nearby tributaries, as in this experiment. We note that *Hoplias* density was higher in the experiment than in the Guanapo (0.42 *Hoplias*/m² in tributaries vs. 0.01 *Hoplias*/m²

in the Guanapo River pools), and mortality rates in the experiment presumably represent mortality rates over longer distances in the Guanapo. The fate, then, of a *Rivulus* attempting to move between tributaries in predator-threatened Guanapo River will depend on such factors as distance between tributaries, the density of predators, and the presence of refuge corridors, such as cobble edges and organic debris, in and along the river. We found many stretches in the Guanapo where steep vertical walls would afford little safety for a migrating *Rivulus*, and we never found *Rivulus* in these locations. Clearly the physical structure of the habitat should affect the probability of encountering predators (Fraser and Cerri 1982) as well as the prey's rate of movement.

Although *Rivulus* is rare in and beside predator-occupied river sections, *Rivulus* can be found along river edges (e.g., among cobble), in isolated flood pools, or in rain pools in rock depressions. In considering gene flow between tributaries, rather than flow of individuals, a key question is whether such sites represent stepping stones in and along the river that allow reproduction and a new source of migrants between tributaries. Detectable genetic fragmentation due to predators would require strong blocking effects, given that one or a few migrants per generation among sub-populations may be sufficient to prevent substantial genetic divergence (e.g., Franklin 1980, Varvio et al. 1986).

In addition to the predator-influenced active movement discussed above, passive transport of juveniles or eggs in floods may displace *Rivulus* downstream, independent of predator-altered movement. Nothing is known of such processes in Trinidad streams, but Harvey (1987) has identified spates as transporters of larval fish in temperate streams. Possible counterbalances to downstream transport are exploratory dispersal upstream and predator avoidance. For fish above barriers, upstream movements are not risky because piscivore-occupied sites are always downstream. Downstream movements, however, are dangerous: *Rivulus* moving downstream over the barrier falls in either drainage face a high probability of death (piscivorous fish in both rivers were located immediately below the barrier falls). Similarly, *Rivulus* in predator-occupied river sites can locate a predator-free site by moving up tributaries, but downstream movements keep the fish in predator-occupied zones. We do not know whether an upstream bias exists in exploratory movement, but the hypothesis is testable using mark-recapture techniques.

Distributional patterns of Rivulus in the Paria drainage.—An unanswered question arising in this study concerns the distribution of *Rivulus* in the Paria drainage. As we outlined in the introduction, the genus *Rivulus* has usually been viewed as a "small water" fish, with its distribution often restricted to headwaters and isolated shallow, even temporary, pools. We, however, found *Rivulus hartii* in large water sites above barrier falls in both drainages. *Rivulus* was also abundant in

the headwaters of Guanapo tributaries (Gilliam et al. 1993), but we have noted qualitatively that some of the Paria's tributaries were conspicuously devoid of *Rivulus*; sites in tributaries which appeared likely sites for *Rivulus* occupancy, based upon our experience in the Guanapo and elsewhere, often had few or no *Rivulus*. This pattern may be owing to a possible negative impact from prawns of the genus *Macrobrachium*, which are abundant in the Paria and other drainages on the northern versant of the Northern Range Mountains. The Guanapo drainage, on the southern versant, is more remote from the sea and has few *Macrobrachium*, although it does contain a low density of *Macrobrachium carcinus*. The Paria contains dense populations of *M. carcinus* and *M. crenulatum*, which, as noted above, are potential predators of *Rivulus*. They may also be potential competitors through both exploitative and interference competition.

Overall, the picture that emerges from our studies of *Rivulus hartii* in Trinidad is that biotic interactions within the fish community are strong and consistent. Recent emphases on abiotic stochastic influences on temperate stream fish communities have been controversial (Capone and Kushlan 1991). Our studies suggest that broad generalizations that stream fish communities are more structured by stochastic rather than deterministic factors than other community types, e.g., lake fish, would be premature.

ACKNOWLEDGMENTS

We thank Kathleen Egid, Edward E. Emmons, Peter Atwood, and Gregory Rys for their help in the field. We are grateful to Ed Emmons and Rashied Baboe for their help in the construction of the experimental stream facility. Mary Alkins-Koo, Julian S. Kenny, and Christopher Starr of the University of the West Indies discussed our work with us, offered helpful advice, and gave us access to the facilities of the Department of Zoology. We thank Roopchand and Faye Ramdeen for permission to conduct studies on their land, and Victoria Soo Poy and Gerard and Oda Ramsawak of the Mount St. Benedict Guest House for giving us access to the laboratory facilities at the Guest House. We thank Cavell Brownie for statistical advice. We thank Scott Cooper and an anonymous reviewer for their careful comments on the manuscript. Our work was supported by grants from the National Science Foundation (DEB 9208102 and DEB 9221788).

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