MOVEMENT IN CORRIDORS: ENHANCEMENT BY PREDATION THREAT, DISTURBANCE, AND HABITAT STRUCTURE

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Abstract. Movement by stream fish is known to be strongly influenced by abiotic factors such as floods and temperature, but roles of biotic factors, such as predation threat, and interactions of abiotic and biotic factors are less clear. Predation threat is known to fragment populations of killifish, *Rivulus hartii,* in Trinidad rivers by rendering habitat inhospitable. We asked whether such spatial fragmentation was accompanied by reduced movement by fish in the predator-occupied zone of a river, relative to a zone free of the strong piscivore, *Hoplias malabaricus,* that causes the fragmentation. We used a 19-mo marking study in a river with a predator barrier, field experiments in the river, and mesocosms to evaluate four hypotheses: (1) the predator reduces prey movement in the river; (2) for the special case of prey leaving refugia, the predator increases movement; (3) movement positively correlates with water level in the predator's presence; and (4) complex physical structure in hazardous habitat promotes prey movement.

We marked 1467 *Rivulus* in the natural study areas and had 1015 recaptures. Contrary to Hypothesis 1 but in support of Hypothesis 2, prey showed greater movement along the river in the presence of the predator, regardless of whether the fish resided in a refuge at its previous capture. An experiment with introduced fish confirmed the findings that movement was elevated in the predator's presence. Effects of an abiotic factor (water level, Hypothesis 3) and a phenotypic trait (body size) depended upon whether the predator was present: movement was independent of water level and body size in the absence of the predator, but positively related to both variables in the predator's presence. Emigration from the river to tributaries was also independent of body size in the predator's absence, but positively size-dependent in the predator's presence. Complex physical structure (Hypothesis 4), in the form of cobble added to experimental pools, enhanced the transit of fish through hazardous pools.

This study shows that spatial fragmentation does not necessarily imply that movement between fragments will be impeded (dynamical fragmentation). Rather, it is possible that movement among spatial fragments may be enhanced by the same factor, predation threat, that produced the spatial fragmentation in the first place. Because of the context-dependent effects of an abiotic factor (water level) and a phenotypic variable (body size) on movement, the study also emphasizes the need to clarify the exact role of predation as an agent promoting or retarding movement, and it suggests a need for incorporating such parameters into models of movement and metapopulation dynamics.

Key words: corridor; diffusion; dispersal; fish; fragmentation; heterogeneity; Hoplias malabaricus; *predation; river;* Rivulus hartii; *tropical fish.*

INTRODUCTION

The movement of individuals through the landscape matrix is fundamental to a host of ecological processes, such as population spread and redistribution (Dobzhansky and Wright 1943, Crumpacker and Williams 1973, Higgins et al. 1996, Kot et al. 1996), metapopulation dynamics (Harrison 1994, Hanski et al. 1995, Hanski 1998), local species richness (Hanski and Gyllenberg 1993, Fahrig and Merriam 1994, Kruess and Tscharntke 1994), local and regional population dynamics (Kareiva 1990, Dunning et al. 1992), inbreeding depression (Fran-

kel and Soule 1981, Lacy 1987, Jimenez et al. 1994), and opportunities for local adaptation (Hastings and Harrison 1994). Although a great deal of progress has been made in the development of a quantitative methodology for the study of animal movement (Skellam 1951, Kareiva 1990, Turchin 1998), the roles of biotic and abiotic factors in affecting the movement of individuals are not well understood (Turchin 1998). Reviews (Doak et al. 1992, Meffe and Carroll 1994, Rosenberg et al. 1997) note the paucity of studies of the ecological influences on movement among patches, an observation that is especially applicable to the study of movement in aquatic ecosystems, which have generated an enormous literature (Matthews 1998).

The importance of abiotic and biotic factors in influencing rates of movement of fish along streams is

largely unknown and eclipsed by the search for environmental cues that synchronize the movement of large numbers of individuals, e.g., spawning migrations (Leggett 1977, Helfman et al. 1997), movement in response to floods (Guillory 1979, Ross and Baker 1983, Chapman and Kramer 1991), and mass seasonal movements in temperate regions (Hall 1972). In such mass movements of fish, interactions with other species and habitat structure seem unimportant in affecting movement rates or total distances moved. Reviewing movement data at a more local spatial scale, Gowan and Fausch (1996) assigned no role to species interactions in the movement of temperate zone fish, and Matthews (1998) stated ''movement patterns are 'autecological' with little or no apparent influence from other species.'' However, others have suggested a role for species interactions as a proximate cause of fish movement (Mense 1975, Fraser and Sise 1980, Mundahl and Ingersoll 1983, Matthews et al. 1994).

Predators are known to fragment stream fish on two spatial scales, and prey movement away from predators can contribute to both patterns. First, because predators can cause emigration from predator-occupied pools in streams, the presence of predators in a stream or river can produce a pattern in which prey fish are more abundant in riffles or other shallow areas than in the intervening deeper water (Fraser and Cerri 1982, Power et al. 1985, Power 1987, Schlosser and Ebel 1989, Fraser and Gilliam 1992, Gilliam et al. 1993). Second, at a spatial scale involving a river and its tributaries, the presence of predators in the river can cause low densities in the river and high densities in the tributaries, with behavioral shifts from the predator-occupied river contributing to that pattern (Fraser et al. 1995, 1999). The pattern of high tributary abundance but rarity or absence in rivers is often observed (Gorman and Karr 1978, Angermeier and Karr 1983, Matthews 1986, Schlosser 1987, Sheldon 1987, Beecher et al. 1988, Rahel and Hubert 1991, Townsend and Crowl 1991).

The demonstration of behaviorally induced spatial fragmentation of prey raises the question of whether nonlethal predator effects may also affect movement rates by transiting fish in streams and rivers, i.e., whether the spatial fragmentation is accompanied by dynamical fragmentation of the prey. In such communities, rivers function as a corridor for movement among tributaries containing populations that are otherwise isolated ecologically and genetically (e.g., Meffe and Vrijenhoek 1988). In the present study we contrast a fragmented zone of a watershed to an unfragmented zone to evaluate hypotheses on the effects predation and abiotic factors (hydrological disturbance and habitat structure) have on the movement rates of a small stream fish.

Our broad null hypothesis is that predator threat in a river has no effect on longitudinal movement in the river. In evaluating this hypothesis, we also ask whether hydrological regime (wet and dry seasons), river sub-
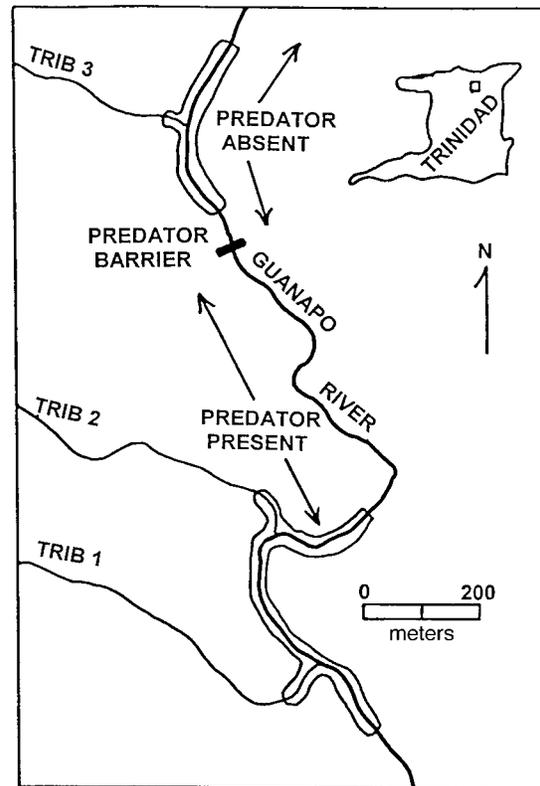

FIG. 1. Map of the Guanapo River study area in the Northern Range Mountains of Trinidad, West Indies, showing the locations of the predator-absent and predator-present zones.

populations (fish in isolated side pools along the river vs. fish in the river proper), or phenotype (sex, size) interact with predation threat to influence movement in the river corridor. We also evaluate whether complex physical structure along pool edges promotes movement through predator-occupied pools. We address these questions with a 19-mo study of individually marked fish in stretches of a river differing in predation threat, and with field experiments in the river and an experimental stream facility.

THE STUDY SYSTEM

The field marking study was done in the headwaters of the fourth-order Guanapo River in the Northern Range Mountains of Trinidad, West Indies (Fig. 1). The upper Guanapo River is divided into a predator-present zone and a predator-absent zone by a barrier waterfall, above which the strong piscivore *Hoplias malabaricus* (Erythrinidae) is absent, while the prey species, *Rivulus hartii* (Rivulidae), is present both above and below the waterfall. At the barrier, stark contrasts occur that are known to be induced by the predator (Fraser et al. 1995): above the barrier *Rivulus* is abundant and found throughout the river at densities comparable to the tributaries, but below the barrier *Rivulus* is rare in the river

and those present are restricted to extreme shallow river edges.

Fraser et al. (1999) postulated that three distinct habitat types were important in determining movement of *Rivulus* along the river, and from tributary to tributary, in the predator zone: (Habitat 1) river pools, (Habitat 2) intervening riffles between pools, and (Habitat 3) side pools within the river banks but isolated from the moving river current. Isolated side pools can occur in depressions in impervious rock outcroppings along the river usually elevated 0–2 m above the river, and can also occur via hydrological arrangement of alluvial river substrates that result in isolated pockets of still water. Although isolated from the threat of *Hoplias,* alluvial side pools can disappear and appear due to drying, wetting, and hydrological rearrangement, exposing resident *Rivulus* to predation threat as they enter the river proper. Above the barrier waterfall *Rivulus* is abundant in all three habitats. Below the barrier it is typically absent from river pools except sometimes among stones at the extreme edges, but pockets of *Rivulus* occur in Habitats 2 and 3, where it feeds and reproduces (Fraser et al. 1999).

HYPOTHESES

We used the contrasting river zones (predator present and predator absent) and experiments to test the following hypotheses.

Hypothesis 1.—Overall (averaged across season, sex, and body size), predators reduce longitudinal movement of prey fish that occupy the river proper (exclusive of fish in isolated side pools). The explanation is that the predator *Hoplias* occurs throughout the water column, including the shallow edges of pools and riffles in the river. Thus, a *Rivulus* moving anywhere in the river is likely to encounter the predator, and such threat may inhibit movement relative to the predator-absent zone. Especially, predator presence might discourage pool crossings.

However, a mesocosm experiment also gives some support to the opposite possibility, i.e., that the predator is, on balance, a net promoter of movement (Fraser et al. 1995). In that experiment, fish in transit in predator-absent treatments typically stopped in river pools, but in the predator-present treatments some *Rivulus* were induced to continue through the predator-threatened pools and ascend into a predator-free experimental tributary. Thus predators might increase travel distances by rendering pool habitat and some riffle habitat inhospitable, inducing travel to more acceptable locations. Thus we considered the two-tailed alternatives (predator as net inhibitor vs. predator as net promoter), against the null of no predator effect.

Hypothesis 2.—Predators increase longitudinal movement of prey fish that leave refugia (isolated side pools). The explanation is that in the event that an isolated side pool is lost via disturbance (drying, flooding), or that a fish emigrates from an isolated side pool, fish in the predator-present zone encounter hostile river habitat, and might travel long distances in search of suitable habitat. In contrast, fish in the predator-absent zone, where the predator does not degrade the habitat, will typically have suitable habitat nearby.

Hypothesis 3.—In the presence of the predator, movement in the river correlates positively with water level. The explanation is that during floods, complex riparian vegetation can become inundated, temporarily increasing complex edge habitat along predator-occupied pools, and potentially providing protective cover for transiting fish. Also, hydrological disturbance can render previously isolated side pools accessible to predators, and eliminate side pools via rearrangement of substrates, potentially inducing movement. We formulated no a priori hypothesis about seasonal variation in movement in the absence of the predator, but we do evaluate whether the effect of water level is contingent upon the predator's presence.

Hypothesis 4.—Complex physical structure in hazardous habitat promotes prey movement. Specifically, we hypothesized that complex physical structure at pool edges (e.g., cobble, woody debris) promotes movement of *Rivulus* through predator-occupied pools, relative to pools lacking complex edges.

METHODS

River study areas

The mark–recapture study was done in two study areas, one each in the predator-present zone and the predator-absent zone (Fig. 1). In the predator-absent zone fish were marked along a 150-m stretch of river, delimited up- and downstream by a section of fast riffles. The search area for marked fish included the 150 m marking zone, plus a maximum of 100 m upstream and downstream of the marking zone. The predator-absent zone contained six pools with rock walls on one side and sand–gravel beach on the opposite side. The pools were separated by raised riffles, which included areas of still water, backwaters, and pools of alluvial substrates. A tributary entered this zone from the west. We marked fish in the mouth of the tributary (Tributary 1) to a barrier waterfall 15 m upstream, and we searched for marked fish to an additional 50 m upstream of the barrier, finding no marked fish.

Because *Rivulus* are rarer in the predator-present zone than in the predator-absent zone, we used a longer stretch of river, 444 m, in which to mark fish in an effort to more nearly equalize sample sizes. As in the predator-absent zone, our search area included this marking zone and up to 100 m up- and downstream of the zone. The predator-present zone contained the same pool–riffle habitat as described for the predator-absent zone except that six of 10 pools contained steep rock walls on both sides. In addition, the predator-present zone contained two tributaries that entered from the west. We marked fish in both tributaries, up to 25 m,

and searched for marked fish for an additional 87 m beyond the marking area in Tributary 2 to the base of a barrier falls, and 25 m beyond in Tributary 3, also to a barrier falls. We never found the predator, *Hoplias,* in Tributary 3, but we observed *Hoplias* in Tributary 2 during several sampling periods between the river and the barrier waterfall at 112 m.

The movement study

To assess movement, we marked *Rivulus* at approximately two-month intervals from January 1996 to May 1997. We recaptured fish at the same intervals, including a final recapture in July 1997. *Rivulus* were collected from all habitats within the river banks, and in the lower reaches of each tributary. We marked a total of 1467 *Rivulus*:735 in the predator-absent zone, and 732 in the predator-present zone.

We searched for *Rivulus* after dark between 1830 and 0200 when *Rivulus* can be located visually and dip-netted. Each *Rivulus* was placed in a reclosable plastic bag at its point of capture, and its location marked with a labeled flag, permitting return of the fish to its exact microhabitat after processing. *Rivulus* were anesthetized in tricaine methanesulfonate (MS222), measured for total length (TL), sexed and marked by injection with a small dot (0.5 to 1 mm diameter) of elastic polymer that fluoresces under ultraviolet illumination (NW Marine Technology, Shaw Island, Washington, USA). We used seven body positions and five colors to generate a triplet code (each fish received exactly three dots of elastomer) that uniquely identified each fish. We marked fish >29 mm TL using a 3-mL tuberculin syringe with 29-gauge needles. We ran measuring tapes along the river from permanent starting points to record each fish's location.

We monitored the water level of the Guanapo River at the downstream study area with a programmable water level logger (Model WL-40, Remote Data Systems, Whiteville, North Carolina, USA), set to record water level at 4-h intervals. We downloaded the stored water level data at each sampling date. The study period included two dry seasons (about January through May) and two wet seasons.

Analysis

For each recapture, we arbitrarily assigned positive values to upstream moves and negative values to downstream moves, and calculated net movement per day as ([position at recapture] − [previous position])/[days since last captured]. Because our sampling interval was about two months, we present data as net movement per 60 days. We then analyzed such movement distributions by using the advection–diffusion framework for population movement in one dimension (Zabel and Anderson 1997, Turchin 1998, Skalski and Gilliam 2000), in which directional bias (the ''advection'' component), if any, is separated from population spread (the ''diffusion'' component), represented by the variance in distance moved. However, we never detected a directional bias (mean signed movement was never different from zero), and hereafter we concentrate on differences in variances of the movement distributions. When comparing two distributions, we tested for differences in the variances with an *F* test. When testing for effects of multiple factors (e.g., predator presence, sex) and/or covariates (e.g., body size, water level), we first squared the data (because variances are estimated as means of squared data), and conducted ANOVAs or ANCOVAs on those squared data, asking whether the mean-squared distance moved per 60 days differed among treatments. In such ANOVAs and ANCOVAs, we log-transformed the squared movement rates as $\log_{10}(x^2 + 1)$, and note that analyses of log-transformed squared data are essentially identical to analyses of log-transformed unsigned distances per day, because $\log(x^2) = 2 \log(|x|)$.

Owing to differences in the linear dimensions of the predator-absent and predator-present zones, we restricted analyses of movement to observed moves of <250 m, the maximum distance that a marked fish could move within the smaller zone and still be detected, which eliminated five long-distance recaptures recorded in the predator-present zone. We used the Cormack-Jolly-Seber module in the program MARK (20 July 1998 version)[4] to estimate the probability that we captured a fish given that it was present on a given date, and the apparent survival (probability that an individual had neither died nor left the study area). In applying that model, we focused on river-dwelling fish only, excluding capture histories of fish found in the tributaries, because our focus is on movement within the river.

Displacement experiment

To evaluate Hypothesis 2 (predators increase movement of fish leaving refugia), we analyzed movement by fish in the marking study that moved from isolated side pools to the river proper, and we also did a displacement experiment intended to simulate an event in which elimination of isolated side pools forced entry of fish into the river proper. Overall, the design of the displacement experiment included three factors, each with two levels: predator zone (predator absent, predator present), source of fish (river, tributary), and introduction habitat (pool, riffle). Our primary interest was in the effect of the predator-zone factor on movement. In addition, because we were interested in the behavior of fish entering the river from a tributary as well as a fish entering the river from an isolated pool along the river (tributary fish might be less experienced with predation threat than fish from the predator-zone river), we collected half of the fish for the displacement experiment from the river itself, and half from nearby

[4] URL: ⟨http://www.cnr.colostate.edu/~gwhite/mark/mark. htm⟩.

tributaries. Finally, the introduction-habitat factor (pool vs. riffle) addressed whether fish introduced into pools vs. riffles differed in distance moved; we were interested in whether there was an interaction between the predator-zone factor and the introduction-habitat factor. We used 40 uniquely marked *Rivulus* from each source (tributary, river) within each zone. Total length in millimeters for fish from the predator-absent zone was 49.7 ± 1.5 (mean ± 1 SE) (tributary origin) and 47.6 ± 0.8 (river origin), and for the predator zone was 48.0 ± 1.3 (tributary origin) and 47.6 ± 1.6 (river origin). To avoid mixing gene pools across zones, fish were introduced into the same zone from which they were caught. We chose, within each zone, 10 introduction sites, which included an approximately equal number of pools and riffles. We released four fish at each site, two from each source. Subjects were chosen arbitrarily without regard to sex or size. After four days we searched the river for introduced fish, choosing four days as the time interval because we felt it was a reasonable interval to represent movement induced by a disturbance event. As with the marking study, meter tapes were run along the river and the distance moved by each fish noted. We used a three-way ANOVA to analyze the log-transformed squared distances moved.

Effects of complex structure

We used our experimental stream facility, fully described in Fraser et al. (1995), to evaluate Hypothesis 4 (effect of complex structure on pool crossings in the presence of predators). The facility consisted of nine replicate streams (width = 0.42 m, length = 2.7 m) situated perpendicular to and elevated on a bank 0.8 m above a third-order tributary of the Arima River, Ramdeen Stream. Experimental streams received water piped from a first-order tributary of Ramdeen Stream, and each stream was joined to Ramdeen Stream by a cement and stone cascade. Ramdeen Stream flowed along the base of the nine cascades, and we enclosed part of Ramdeen Stream at the base of the cascades by building nine enclosures in the stream, each 2.36 m² and 10–15 cm deep, separated by wood partitions, and screened on the front (stream side) by window screening backed by heavy mesh. Henceforth we refer to the nine streams as "tributaries" and the nine base sections as "river pools." We formed groups of three contiguous river pools by cutting underwater slots in the two middle wood partitions of a group. Screens over the slots allowed passage of *Rivulus* while confining the larger *Hoplias* to the middle of the three pools. Arranging the nine tributary–river pools into groups of three river pools, with a tributary entering each end pool (middle tributary blocked), allowed us to conduct a maximum of three trials simultaneously.

Hypothesis 4 predicts that in the presence of the predator, pools with physical structure along the edge will allow passage of more *Rivulus* than will those lacking such structure. We tested this prediction with two experiments.

Experiment 1.—In the first experiment, we treated the middle river pool as a corridor pool between tributaries, and focused on whether the presence of structure in the corridor facilitated the tributary-to-tributary movement of *Rivulus* when the predator *Hoplias* was also present in the corridor. Moving from a starting tributary to the adjacent tributary required a movement sequence consisting of a lateral move (tributary to river pool), longitudinal moves across three river pools, and another lateral move (river pool to tributary). We asked whether more fish moved from a start tributary to the adjacent tributary in the presence of physical structure than in its absence, when the predator was present in the intervening pools. Structure, when present, consisted of 12 cobble-size river stones arrayed along one side of each pool. We collected 128 *Rivulus* (TL = 48.8 ± 10.7 mm [mean ± 1 SD]) and six *Hoplias* (TL = 159.1 ± 42.6 mm [mean ± 1 SD]) from Ramdeen Stream and adjoining tributaries. In each replicate (paired design), we chose two of the three tributary–river units randomly, and also randomly chose one of the two units to receive structure (cobble). We then stocked 32 *Rivulus* into the downstream tributary of each unit, and one predator *Hoplias* individual into the middle river pool of each unit. We used blocking screens to acclimate the fish for 12 h in their respective start locations prior to releasing them after dusk. The experiment was terminated after 21 d and the tributaries and river pools searched for *Rivulus*. We replicated this experiment five times over five months, drawing subjects from the community tank. We rotated the six *Hoplias* through the five replications.

We compared the proportion of the total fish recovered that had colonized the adjacent tributary in the structure–no structure pairs by a paired *t* test (pair = month), two-tailed, $\alpha = 0.05$. Proportions were arcsine square-root transformed for analysis.

Experiment 2.—In the second experiment we focused only on longitudinal movement by *Rivulus* and asked whether pool structure facilitated the movement of *Rivulus* along the river (river pool to river pool) when *Hoplias* was present in the intervening pool. In this experiment we closed off the tributaries in each unit, and stocked *Rivulus* directly into the most downstream of the three river pools. As before, we collected *Rivulus* from Ramdeen Stream and adjoining tributaries and stored them in a community tank ($N = 168$, TL = 46.9 ± 14.3 mm [mean ± 1 SD]). We rotated among six *Hoplias* (TL = 151.8 ± 48.9 mm [mean ± 1 SD]). We used 10 *Rivulus* and one *Hoplias* per replicate and replicated the experiment eight times. The time course for each replicate was 24 h, owing to the need to test only for pool crossing and not tributary colonization. We compared the proportion of the total fish recovered that had crossed into the third river pool in the two treatments by an unpaired *t* test, two-tailed, with $\alpha =$
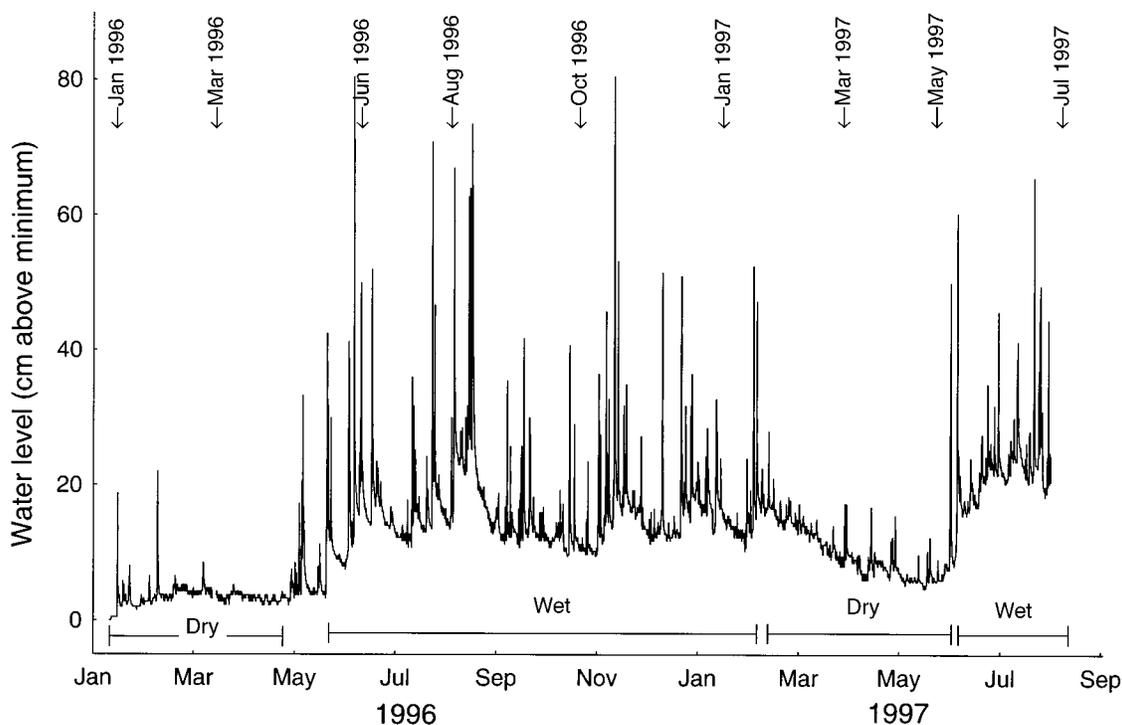
FIG. 2. Hydrologic regime during the study period (water level measured every 4 h), and spacing of fish sampling events (top row). The study period included two dry seasons and two wet seasons.

0.05. Proportions were arcsine square-root transformed for analysis.

RESULTS

Sample sizes, capture probabilities, and survival in the river

The movement study in the Guanapo River from January 1996 through July 1997 resulted in 1015 recaptures of the 1467 marked fish. Of these recaptures, 672 (392 predator absent, 280 predator present) were recaptures of individuals in the river or in isolated side pools along the river for which the previous capture was also in the river or isolated side pools. An additional 34 (13 predator absent, 21 predator present) were fish that had moved from the river corridor (including isolated side pools) to a tributary, or vice versa, and 309 (36 predator absent, 273 predator present) were recaptures of individuals in the tributaries for which their previous capture was also in the tributary. Across sampling dates, we collected more fish (>29 mm TL) per 100 m of river in the predator-absent zone than the predator-present zone (exclusive of fish in isolated side pools, 85.6 ± 5.5 vs. 15.4 ± 1.4 [mean $\pm$ 1 SE] per 100 m, respectively; in isolated side pools, 6.7 ± 1.7 and 6.4 ± 1.1 per 100 m, respectively). Capture probability in the river was estimated to be 0.441 (SE = 0.031) in the predator-absent zone and 0.437 (SE = 0.049) in the predator-present zone. Estimated apparent survival per month was 0.787 (SE = 0.013) vs. 0.757

(SE = 0.021) in the predator's absence and presence, respectively (z test, $P = 0.23$).

Hydrologic regime

The study period included two dry seasons and two wet seasons (Fig. 2), with the former characterized by low or falling baseline water levels and reduced frequency and intensity of spates.

Distributions of movement distances in the river corridor (Hypotheses 1 and 2)

To appraise Hypotheses 1 and 2, we categorized fish using the river corridor according to their use of isolated side pools. The ''NN'' isolation class included recaptures in which a given fish was found in a non-isolated location (not in an isolated side pool) at a given recapture, and also at its previous capture, ''NI'' fish switched from a non-isolated location to an isolated location, etc. ''NN'' recaptures (Fig. 3a) showed markedly greater variance in the distribution of movement distances in the predator's presence as compared to the predator's absence ($F_{144, 357} = 4.48$, $P < 0.001$), in contradiction to Hypothesis 1, which held that predation threat would reduce movement. Fish observed to move from isolated side pools to non-isolated locations (''IN'' recaptures, Fig. 3c) also showed greater variance in movement in the predator's presence ($F_{42,14} = 6.49$, $P < 0.001$), in support of Hypothesis 2, that fish moving from isolated side pools would ''scatter'' more in

a) NN: Fish non-isolated both times

b) NI: Fish that moved from non-isolated to isolated

c) IN: Fish that moved from isolated to non-isolated

d) II: Fish in isolated side pools both times
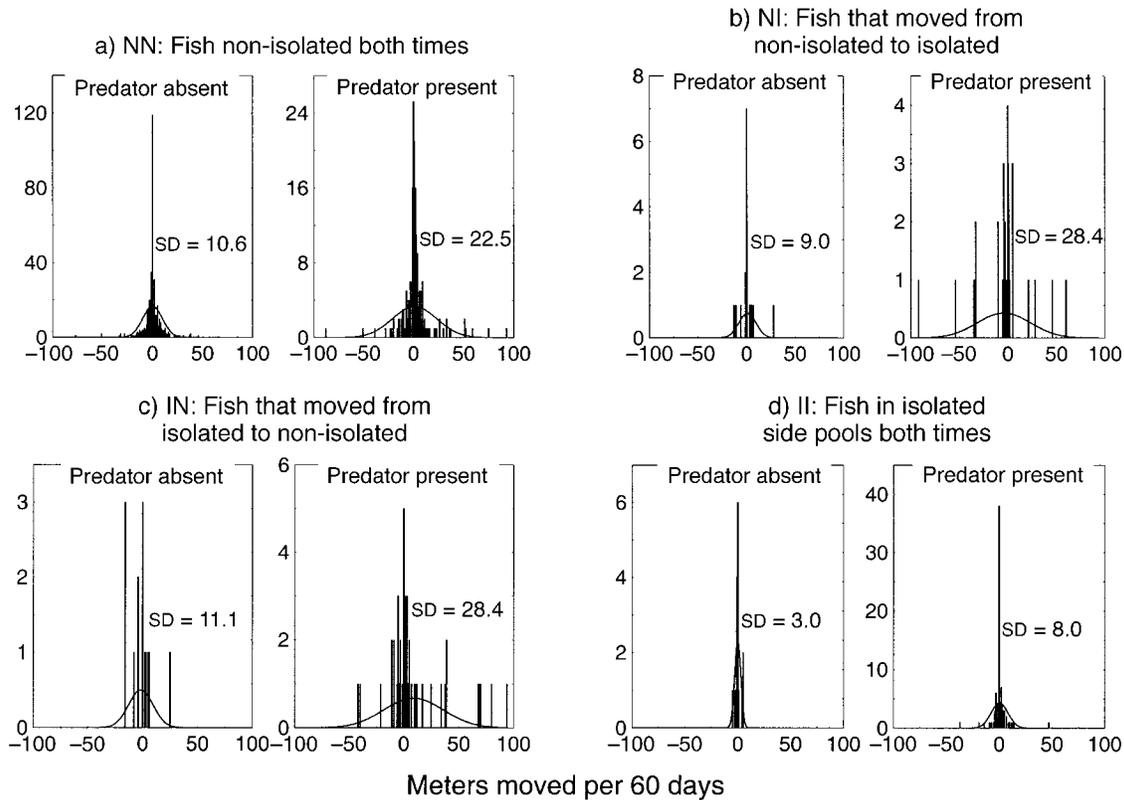
Meters moved per 60 days

FIG. 3. Movement distributions for recaptured fish, contrasting the predator-absent zone and the predator-present zone, and categorized by use of isolated side pools (refugia) along the river's edge. For example, "NN" fish were not in isolated pools at either the recapture or their previous capture, and "IN" fish were observed to switch from an isolated pool to the river proper or into a tributary. In every case, movement was greater in the presence of the predator than in its absence ($P < 0.001$ in each case). Maximum-likelihood fits of normal distributions are shown, and the distributions tended to be strongly leptokurtic.

the presence of the predator. The phenomenon of predator-promoted movement also extended to the other categories: NI recaptures (Fig. 3b, $F_{28,17} = 10.04$, $P < 0.001$) and II recaptures (Fig 3d, $F_{87,17} = 7.41$, $P < 0.001$).

Given these results, it is not surprising that the overall movement distribution pooling across isolation classes (Fig. 4) for the predator-present zone also shows greater variance than the distribution for the predator-absent zone ($F_{405,301} = 4.23$, $P < 0.001$). The cumulative distributions of the absolute value of movement (inset in Fig. 4; cumulative from the right) indicate that, regardless of the distance chosen, a greater proportion of fish moved at least that far in the predator's presence than in its absence. The distributions also showed some similarity: both distributions were distinctly leptokurtic (predator absent, kurtosis = 12.64, SE of kurtosis = 0.24; predator present, kurtosis = 16.13, SE = 0.28), and neither distribution showed a directional bias (predator absent -0.11 ± 0.52 [mean $\pm$ 1 SE], t test vs. zero, $P = 0.84$; predator present 1.89 $\pm$ 1.23, $P = 0.13$). Further, the enhanced movement in the predator-present zone was remarkably consistent across sexes (Fig. 5). A 2×2 ANOVA showed a predator effect ($F_{1,702} = 5.16$, $P = 0.018$), but no effect of

sex ($F_{1,702} = 0.27$, $P = 0.59$) and no interaction ($F_{1,702} = 2.50$, $P = 0.10$).

The second test of Hypothesis 2, the displacement experiment (Fig. 6), also revealed greater movement in the presence of the predator than in its absence (Fig. 6; $F_{21,34} = 8.48$, $P < 0.001$). Notably, a substantial portion of the fish introduced to the predator-absent zone remained within 5 m of their introduction point, unlike fish introduced into the predator-present zone. The full $2 \times 2 \times 2$ ANOVA yielded a main effect of predator ($F_{1,47} = 12.67$, $P = 0.001$) and an interaction of predator and introduction habitat ($F_{1,47} = 7.31$, $P = 0.010$); the other main effects (source of fish, introduction habitat) and interactions all yielded $P > 0.16$. The significant predator $\times$ introduction habitat term reflected the fact that fish introduced into pools moved further in the predator's presence than in its absence, but fish introduced into riffles, while showing the same trend, were not statistically distinguishable (LSD test, $\alpha = 0.05$).

Body size, movement, and emigration

We had formulated no a priori hypotheses regarding body size and movement. However, we found that
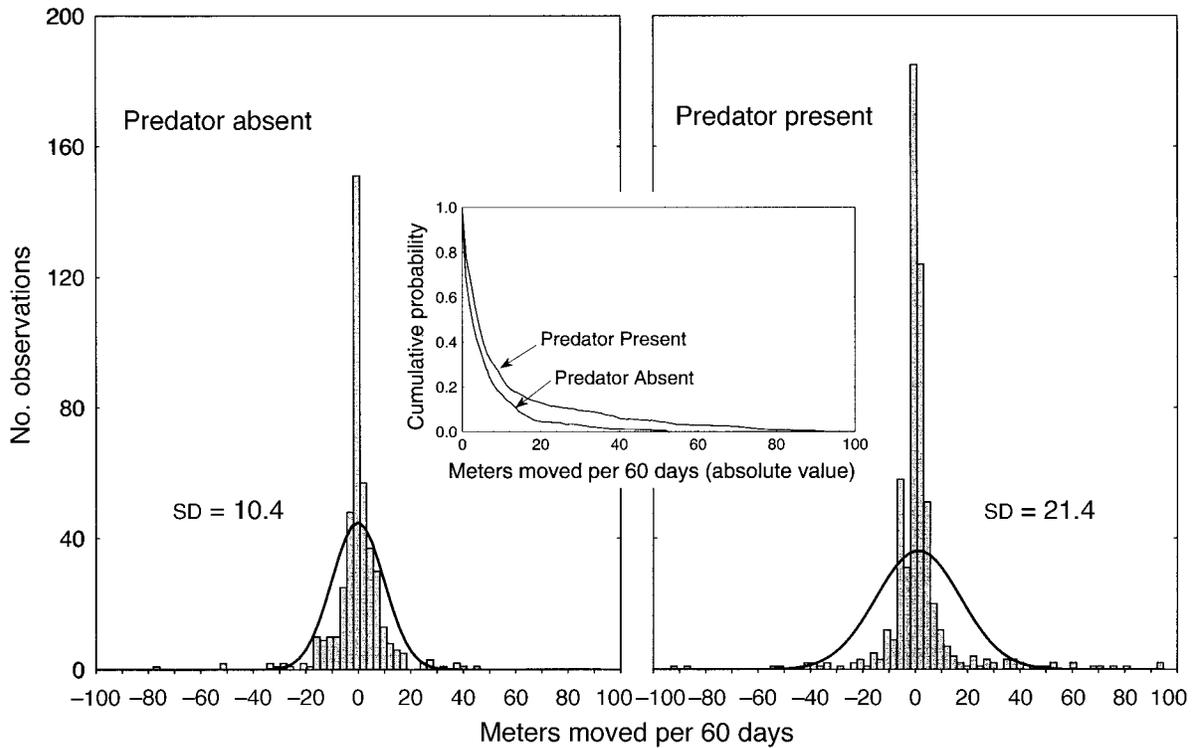
FIG. 4. Overall movement distributions in the predator's absence and presence, pooled across all the categories in Fig. 3. The inset shows that at any given distance, the presence of the predator corresponded with an increase in the proportion of fish moving at least that far.
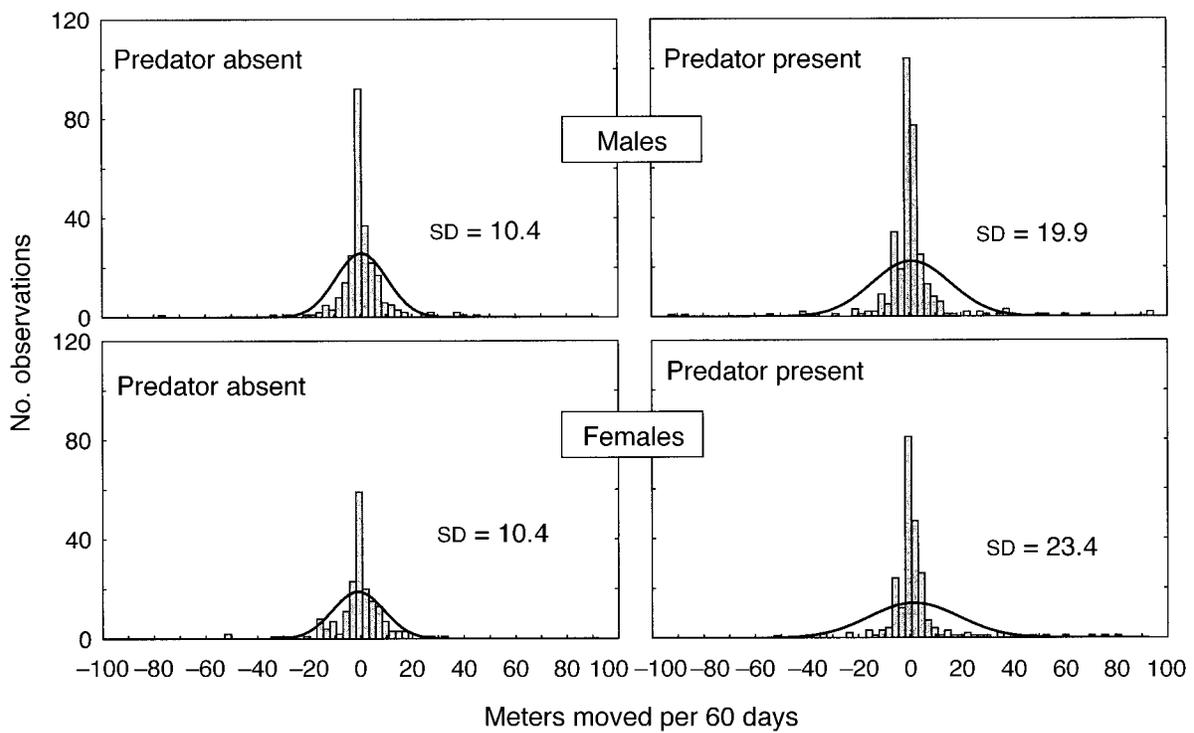

FIG. 5. Overall movement by predator regime and sex. Sexes did not differ in movement, and the enhanced movement in the predator's presence was consistent across sexes.
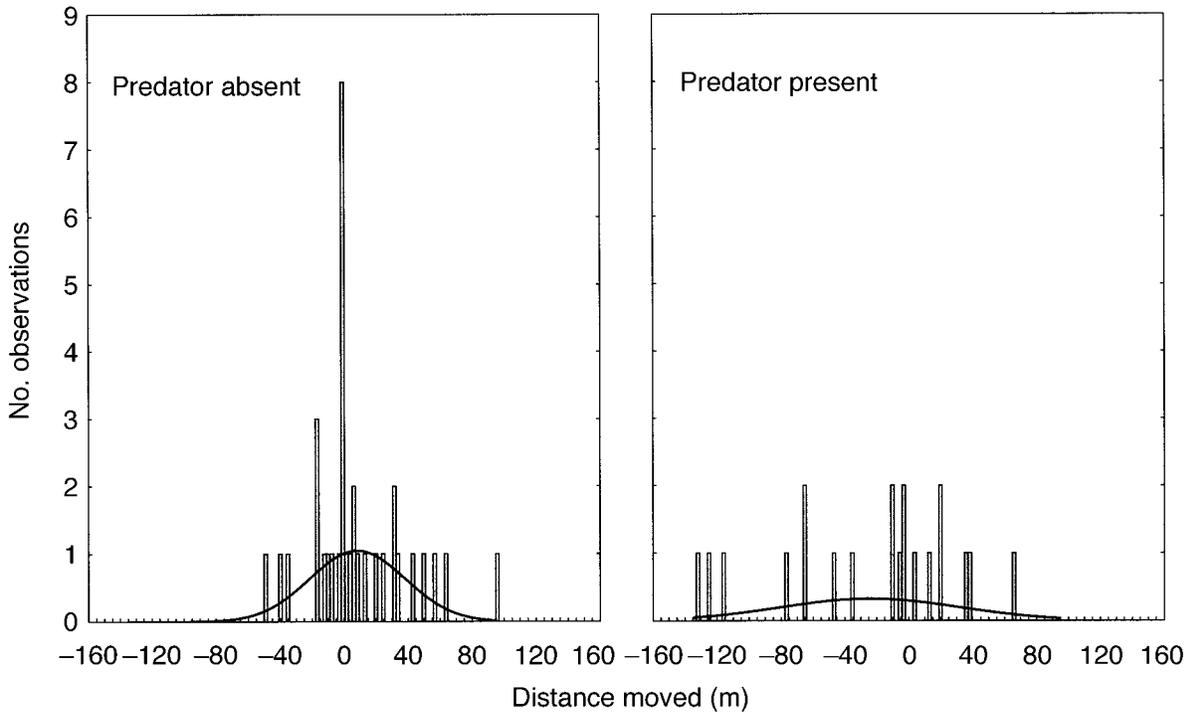
FIG. 6. The displacement experiment. As with naturally moving residents, fish introduced into the predator-present zone showed greater ''scattering,'' with more movement than those introduced into the predator-absent zone. Negative values indicate downstream movement.

movement was independent of body size in the predator's absence, but positively size-dependent in the predator's presence (Fig. 7). An ANCOVA with predator and sex as factors and total length at recapture as the covariate yielded a significant effect of predator ($F_{1, 701} = 5.67$, $P = 0.02$), no effect of sex ($F_{1, 701} = 0.31$, $P = 0.58$), and no interaction ($F_{1, 701} = 2.66$, $P = 0.10$). However, as suggested by Fig. 7, the effect of the covariate, body length, was nonhomogeneous with respect to the presence or absence of the predator ($F_{1, 700} = 11.02$, $P < 0.001$). Hence we did a separate ANCOVA analysis for each predator treatment (sex as a factor and length as covariate), finding a positive slope for the effect of length on movement in the predator-present zone ($F_{1, 299} = 8.79$, $P = 0.003$), vs. a non-significant negative relationship for the predator-absent zone ($F_{1, 403} = 1.60$, $P = 0.21$). The relationship between body size and movement was remarkably similar for males and females within each predator treatment (Fig. 7).

The positive relation between body size and movement in the predator-present zone corresponded with a positive relation between body size and emigration from the river in the predator's presence, but not in its absence. For each fish captured in the river corridor (including isolated side pools), we assigned a value of one if its next capture was in a tributary, and a zero if not. Logistic regression (logit) on those values (Fig. 8) yielded a positive relationship for the predator-present zone ($P = 0.006$), but not for the predator-absent zone ($P = 0.970$). The increasing probability with body size was also apparent if the probability of emigration was calculated for each 10-mm length interval (30–39 mm, 40–49 mm, etc.), reaching ~0.25 for the largest size class in the predator-present zone (Fig. 8). Overall, the probability that a fish in the predator-present zone of the river corridor would be found in a tributary on its next capture was 0.060 ($N = 298$, SE $= 0.014$), and the probability for the predator-absent zone was 0.027 ($N = 403$, SE $= 0.008$); these proportions differ by a t test on proportions (two-tailed, $P = 0.030$).

Water level and fish movement (Hypothesis 3)

To evaluate Hypothesis 3, we used a subset of the data, extracting only those recapture events in which a given fish was captured in consecutive samples, so that movement during that single interval could be associated with the mean water level during that interval. In agreement with Hypothesis 3, water level in the river correlated with increased movement in the predator-present zone (Fig. 9). For fish in the predator-present zone, the ANCOVA showed an effect of mean water level ($t_{198} = 2.49$, $P = 0.014$) and an effect of isolation class ($F_{3, 198} = 10.29$, $P < 0.001$), with homogeneity of the covariate effect across isolation class treatments ($F_{3, 195} = 0.642$, $P = 0.589$). We stated no hypothesis about the effect of mean water level on movement in the predator-absent zone, but found that neither iso-
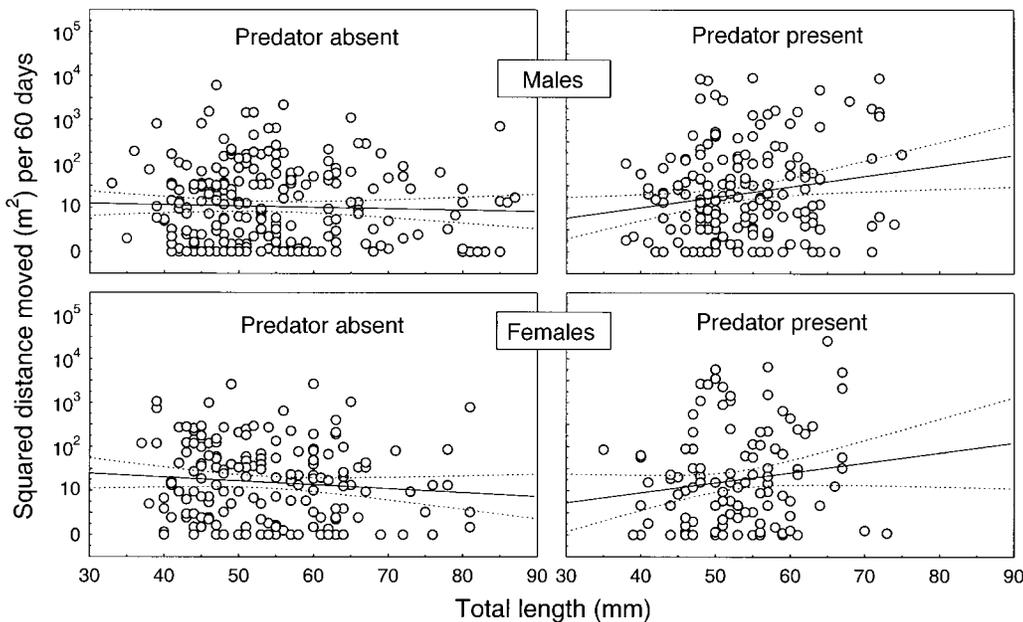
FIG. 7. Movement rate was independent of body size in the absence of the predator, but the presence of the predator induced a positive relationship in both males and females.

lation class nor mean water level significantly affected fish movement (isolation class, $F_{3, 282} = 1.75$, $P = 0.157$; mean water level, $t_{282} = 0.112$, $P = 0.911$, homogeneity of covariate, $F_{3, 279} = 1.898$, $P = 0.130$). Plotting movement for each sampling interval (Fig. 10) and comparing the pattern with the water levels in Fig. 2 also reflects the association of high water with greater movement in the presence of the predator, but not in its absence. In the dry season, movement in the presence of the predator falls to levels near or sometimes below that of movement in the predator's absence. In the first year of the study, the sample interval most clearly associated with low water level in the dry season (the March 1996 sample, reflecting January 1996

to March 1996 movement) was the only sample in the study in which fish moved less in the predator's presence than its absence ($t_{54} = 2.34$, $P = 0.023$). In the study's second year, the sample associated with the lowest water level was May 1997, and fish movement between March 1997 and May 1997 was indistinguishable between the predator-absent and predator-present Zones ($t_{137} = 0.989$, $P = 0.324$).

Complex physical structure and movement through predator-occupied pools (Hypothesis 4)

Both experiments showed that increased physical structure promoted movement through predator-occupied pools (Fig. 11). In Experiment 1, the addition of

FIG. 8. Emigration from the river as a function of body size (total length in millimeters). Emigration was independent of body size in the absence of the predator (solid line, logit regression, $P = 0.97$), but strongly positive in the predator's presence ($P = 0.006$). Probabilities are also shown, with $\pm$ 1 SE, for 10-mm intervals.
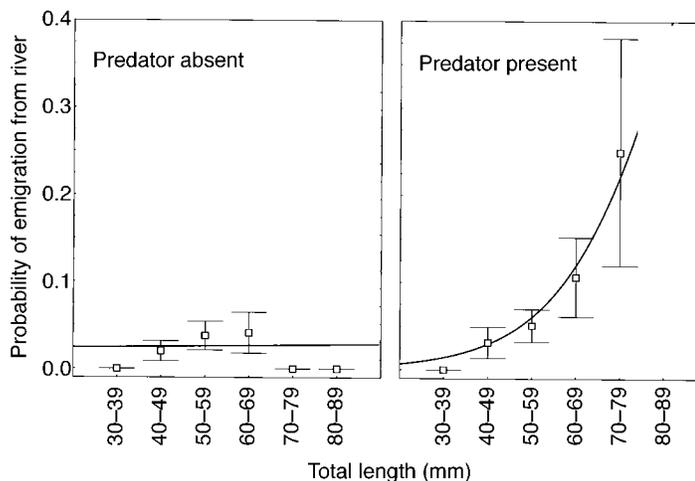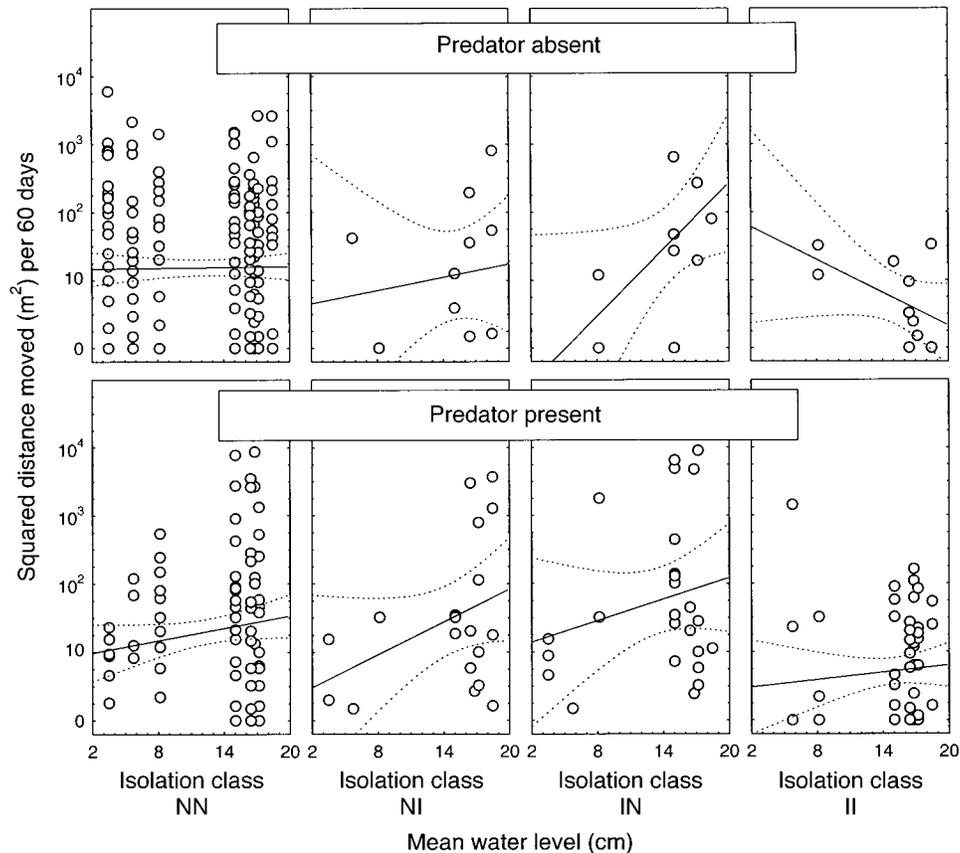
FIG. 9. Movement in relation to mean water level in the sampling interval. In the predator's absence, water level had no consistent effect on movement ($P = 0.91$), but the predator's presence corresponded with a positive relationship ($P = 0.01$). Isolation classes are as in the Fig. 3 legend. Dotted lines indicate 95% confidence intervals of the regression.

cobble increased the proportion of fish colonizing the adjacent tributary ($t_4 = 4.26$, $P = 0.013$), reflecting the net effect of both longitudinal movement and lateral movement (movement from the river to the tributary). Experiment 2, focusing specifically on longitudinal movement, detected a similar facilitation of movement ($t_{14} = 2.17$, $P = 0.048$).

DISCUSSION

Our most salient conclusion is that spatial fragmentation does not necessarily imply that movement between fragments will be impeded (dynamical fragmentation). Rather, it is possible that movement among spatial fragments may instead be enhanced by the same factor, predation threat, that produced the spatial fragmentation in the first place. Our previous work (Fraser et al. 1995) anticipated this result, arguing that predators can render some intervening habitat inhospitable, and hence encourage further movement by animals that enter such areas. However, in view of an alternative, that the predator might be a net retarder of movement by discouraging entry into such hostile sites in the first place (Hypothesis 1), we were unwilling to form a conclusion regarding the overall net effect of the predator

on movement without a long-term study across seasons, with attention to the natural history of our system, including the isolated pools along the river's edge and hydrological disturbance.

Our mesocosm experiments (Fraser et al. 1995 and the present paper) were well replicated, but the present field mark–recapture study was not replicated across multiple watersheds. As with many such field studies in which replication across sites is not feasible, one may question whether we are documenting differences due to the predator in the two zones, rather than some unknown additional factor. We are confident that movement differences in the two zones result from the predator's presence or absence. First, we chose the Guanapo River for the study specifically because a single predator barrier occurs in the fourth-order zone of the river, and concurrent with the barrier is the abrupt decline in *Rivulus* density and the dramatic behavioral shift to edge areas, which we have previously established to be caused by the predator (Fraser et al. 1995). Second, the displacement experiment complements the observational study of wild marked fish, yielding the same result. Third, the present work was preceded by rep-
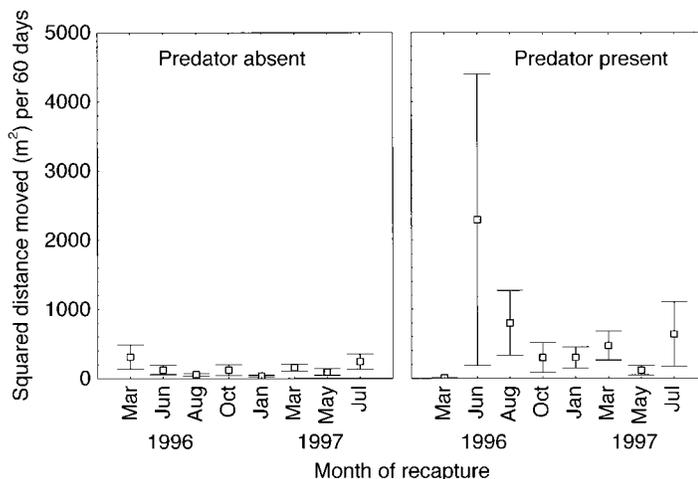
FIG. 10. Movement across time. Movement in the predator's presence showed more seasonal variability than in the predator's absence, and movement in the predator's presence was depressed during dry seasons (March 1996, May 1997), as also indicated by Fig. 9. Error bars show ± 1 SE.

licated mesocosm experiments (Fraser et al. 1995), again yielding the same result.

Our results show that the predator can be a net promoter of movement along the river and perhaps of gene flow among tributaries, but we do not generalize to say that we would always expect that result. For example, Storfer (1999) suggests that sunfish in streams may act as a barrier to gene flow in the streamside salamander (*Ambystoma barbouri*), and that result can be expected if the sunfish impose a high mortality rate on potential dispersers, or if potential dispersers strongly avoid entering sunfish-occupied pools. Fraser et al. (1995, 1999) point to ways in which predators can be either

net promoters or net retarders of movement. Predators can promote movement by removing suitable habitat (resulting in rapid transit across such habitat, once entered) or by initiating movement by direct attack or approach, but can also block movement by killing prey or by discouraging entry to dangerous sections along the corridor. Rosenberg et al. (1998) make some similar points, showing faster movement through poor habitat, and emphasizing the effect of movement speed between two points and the mortality rate in determining the probability of safe passage through a corridor. Schultz (1998) and Haddad (1999) also document faster movement when dispersing animals enter inappropriate hab-
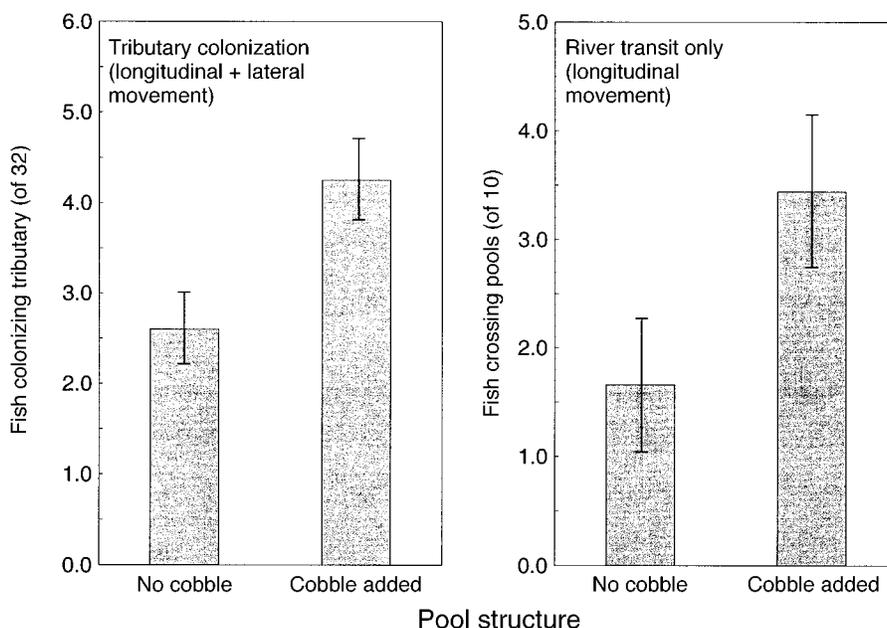

FIG. 11. Increased complexity of physical structure (addition of cobble at pool edges) promotes movement through predator-occupied pools, whether measured as tributary-to-tributary moves over a long time period (21 d; left figure) or as crossings of a single pool over a short time period (24 h; right figure). Errors bars show ± 1 SE.

itat. Haddad (1999) emphasizes the role of boundary crossing in creating a more predictive theory of inter-patch movement, and Wiens et al. (1993) point to mortality, probability of encountering a boundary, and probability of boundary crossing as key processes in communication among patches.

Given our result that the predator promoted movement by the prey, any inhibitory effect on movement was empirically outweighed by the promoting effects. We have little data on the diel temporal patterning of movement in *Rivulus,* but numerous anecdotal observations suggest that *Rivulus* may sometimes move in the day when *Hoplias* is relatively inactive (Fraser and Gilliam 1992). Also, like many riverine fishes (Minckley and Meffe 1987, Scrimgeour and Winterbourn 1987, Matheney and Rabeni 1995), and as suggested by our physical structure experiments (Hypothesis 4), *Rivulus* may take advantage of flooded river margins and skirt potentially high-risk pools during periods of high water. We found little movement by *Rivulus* in the first part of the dry season of 1996 (first recapture), but high movement by the time of the second recapture, just after a series of four spates that marked the end of the 1996 dry season; overall, movement in the predator's presence correlated with higher water (Hypothesis 3, Fig. 9). The diversity of hydrological conditions encountered during the period of this study, and possibly the diel activity patterns of *Rivulus,* facilitated movement in the predator-present zone.

In contrast to the view that movement patterns are primarily autecological (Matthews 1998), this study illustrates the interplay of an interspecific biotic factor (predation threat) and an abiotic factor (water level) in affecting movement. By the autecological view, the finding that water level affected movement in the predator-occupied part of our study watershed would not be surprising. However, the crucial point is that the abiotic, apparently autecological factor, water level, was rendered influential only in the presence of another species, the predator *Hoplias.* In the predator's presence, a phenotypic trait, body size, also became a predictor of both movement along the river (Fig. 7) and the probability of emigration from the river into tributaries (Fig. 8).

Landscape ecology tells us that properties of a population at a particular location are influenced not only by the properties of the habitat at which they occur, but also the properties of adjacent habitat (Danielson 1991, Pulliam 1996, Schlosser 1998, Haddad and Baum 1999). In our study, the river subpopulation in the predator-present zone not only exported a greater proportion of its population to tributaries relative to the predator-absent zone, but it also exported its larger individuals disproportionately. This result suggests that the presence of the predator could restructure source–sink relationships between the river and its tributaries. Tributaries adjacent to a predator-occupied river might show properties of pseudosinks (Watkinson and Suth-erland 1995), in which emigration from the river, especially of large individuals, produces crowding in the tributaries, with net immigration into the tributaries exceeding emigration from the tributaries. In this scenario, the predator-occupied river, despite its lower population density than the tributary, would be a source population, and the tributaries a pseudosink (here, we follow Pulliam [1996] in reserving the term "sink" or "true sink" for sites in which local populations decline to zero if immigration is removed, a case unlikely to apply to tributaries in our system). Diffendorfer (1998) casts doubt on the existence of source–sink relationships among animals that assess habitat quality, arguing instead for balanced dispersal among sites, characterized by an equal exchange of numbers of individuals between any two sites. In size-structured populations, such as fish populations, a different concept of source–sink or balanced dispersal relationships may be needed, as the export of large individuals from the river in the presence of the predator might be balanced in competitive impact or reproductive value by export of more than one small individual, resulting in unbalanced dispersal by criterion of counting individuals, but balanced dispersal by some broader criterion of mass or reproductive potential. In such situations, decisions on what to measure (individuals, mass, reproductive potential) can be critical in asking whether a predator's presence alters source–sink relationships.

In both the predator's presence and its absence, overall movement distributions were distinctly leptokurtic, and the distribution in the presence of the predator was more leptokurtic than in the predator's absence. The genesis of leptokurtic distributions should have impacts on the way that one would model population spread. In our system, the leptokurtosis apparently arises from a variety of sources, which contribute sub-distributions with different variances to the total distribution. Among those sources are (a) temporal heterogeneity (water level or season), (b) spatial heterogeneity (isolated side pools and the river proper), and (c) morphological phenotype (body length). In principle, a simple diffusion process might describe the data well within any single source of heterogeneity, with possibly normally distributed movement distributions within each combination, and a leptokurtic distribution resulting when such normal distributions with unequal variances are summed (Skalski and Gilliam 2000). Further, Sokolowski et al. (1997) have related movement to a genetic polymorphism, and we have discovered a source of phenotypic variation in *Rivulus* in which a laboratory assay for "bold" vs. "shy" behavior contributes to the heterogeneity of movement in field releases (D. F. Fraser and J. F. Gilliam, *unpublished data*). It is not clear when, or whether, models that take a composite leptokurtic distribution as a starting point, such as those by Kot et al. (1996), can adequately describe spread and redistribution in populations in which temporal,

spatial, and/or phenotypic heterogeneity generates the leptokurtic distribution in the first place.

Predation threat enforces a fragmented population structure on *Rivulus* by rendering river pools uninhabitable and restricting occupancy by *Rivulus* to raised riffles, cobble edges between pools, and sometimes cobble interludes within pools (Fraser et al. 1995). We observed that very small cobble patches ($<$5 m long) in the predator's presence did not always contain *Rivulus,* but very large patches ($>$15 m long) along riffles always had *Rivulus* and might be source habitat (see also Fraser et al. 1999). The maintenance of *Rivulus* on very small patches depends on immigration rates, which are influenced not only by the movement rates we document here, but also by proximity to sources and overall population density; the predator's presence increases the probability that a given individual will move at least x meters (Fig. 4, inset), but the total number of individuals moving at least x meters also depends on the number of fish present locally to do the moving. Therefore, although movement of individuals is greater in the predator's presence, we would expect that the lower population density in the predator's presence can result in some suitable patches remaining uncolonized for long periods. Further, the ubiquity of *Rivulus* in pools and riffles in the absence of the predator means that potential colonists are always nearby regardless of the location of an empty, colonizable patch, but in the predator's presence potential colonists can be nearby if the patch is near a riffle, but comparably distant if the patch lies along a pool. We surmise that such effects can produce longer times to recolonization of patches in the predator's presence despite the greater movement, and also more spatially variable and possibly more temporally variable patterns of recolonization events.

The extent to which predation enforces a fragmented spatial structure in other aquatic systems is unknown. Although we found that the predator increased movement of individuals, it is also plausible that predation threat in a different system, e.g., one with both nocturnal and diurnal predators, could be a net retarder of interpatch moves. In either case, this study points to the need for clarifying the scope of predation, and other interspecific interactions, as agents affecting movement and patch colonization probabilities, and suggests a need for incorporating those probabilities into the parameterization of metapopulation models.

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