

Floods, Habitat Hydraulics and Upstream Migration of *Neritina virginea* (Gastropoda: Neritidae) in Northeastern Puerto Rico

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ABSTRACT.—Massive upstream migrations of neritid snails (Neritidae: Gastropoda) occur in tropical and subtropical streams worldwide, but their seasonality and proximate causes are unknown. We monitored massive upstream migrations of *Neritina virginea* for 99 weeks, and conducted a detailed study of snail density, size, and hydraulic descriptors in lower Río Mameyes, northeastern Puerto Rico. The study assessed the 1) timing and seasonality of upstream migration, 2) size composition of migratory aggregations, 3) patterns of habitat use, and 4) role of floods on upstream migration. Massive upstream migrations (500–3000 ind/m²) were observed in 44 of 99 weeks of observation. While *N. virginea* aggregations occurred at random time intervals, they were clumped during rainy periods. Migratory aggregations consisted mostly of small individuals (5–7 mm). Greater mean density was consistently observed in a stable riffle than in an unstable run (115.7 and 17.8 ind/m², respectively), but mean density increased and mean size reduced in both reaches during the first 7 upstream migratory events. *N. virginea* density and size dynamics differed between reaches as a function of habitat hydraulics. While juveniles used the stable riffle as a permanent habitat and preferred passageway, they also used an adjacent, unstable reach after storm events. Density variation was correlated with days postflood (>3.5 m³/s) in both reaches. Our observations indicated that massive upstream migrations of *N. virginea* juveniles occur at least once a month, presumably as habitat-dependent responses to floods.

KEYWORDS.—Neritid snails, diadromy, physical habitat, disturbances, Neotropical streams

INTRODUCTION

In coastal and insular streams and rivers, migrations between marine and fresh waters (i. e., diadromy) are common among aquatic fauna (Ford and Kinzie 1982; McDowall 1998). Many species of fish, shrimp, crayfish, and crabs exhibit this type of migration (Baker 1978). Nevertheless, migratory events have been less frequently reported in gastropod mollusks; although it is known that at least 13 families include migratory species (Huryn and Denny 1997). Among tropical gastropods, the family Neritidae comprises several freshwater genera (subfamily Neritinae) whose individuals migrate upstream in massive aggregations. Such migrations of freshwater neritids were reported in Hawaii (Ford 1979; Ford and Kinzie 1982), Costa Rica (Schneider and Frost 1986; Schneider and

Lyons 1993), Japan (Nishiwaki et al. 1991a; Hirata et al. 1992), French Polynesia (Resh et al. 1990, 1992; Liu and Resh 1997), and Puerto Rico (Covich and McDowell 1996; Pyron and Covich 2003).

Recently, mark-and-recapture studies in northeastern Puerto Rico suggested that neritid gastropods are more active and travel longer distances during given periods of the year and that upstream migration may be seasonal (Pyron and Covich 2003). However, other one-year mark-and-recapture study on a neritid gastropod in southern Japan showed no seasonal occurrence of upstream migrations, or seasonal changes in mean distance movement (Nishiwaki et al. 1991a). These findings contrast with another study in the same area, showing that maximum travel distance varies over the year, being greater during the period of high water temperature between April and August (Hirata et al. 1992). Records of gastropod density and egg laying in French Polynesia (Resh et al. 1991, 1992) and Japan (Nishiwaki et al.

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1990b; Hirata et al. 1992) also suggest a seasonal occurrence of such migrations, but the controlling factors remain unknown. There are no additional long-term, high-frequency studies dealing with upstream migrations of neritid gastropods, although other aspects such as life history (Ford 1979), growth rates, and fecundity (Shigemiyama and Kato 2001), habitat selection (Liu and Resh 1997; Ohara and Tomiyama 2000), and predators (Teixeira 1994; Resh et al. 1999) were studied elsewhere.

Schneider and Lyons (1993) proposed that upstream migrations of neritids in a Costa Rican stream were related with increased fish predation in the estuary. Small-sized individuals were more abundant within migratory groups, and they were also more responsive to the presence of predators, as similarly observed in other freshwater gastropods (e.g., Alexander and Covich 1991). The distribution of predatory fish (Allan 1995), and the quantity and quality of periphytonic food (Johnson and Brown 1997; Biggs and Smith 2002) can also be correlated with the spatio-temporal variations in discharge and water velocity. Thus the occurrence of upstream migrations might ultimately be a function of stream discharge and channel hydraulics. For example, laboratory experiments using clams demonstrated that emigration is displayed only after increased water movement, even when density-dependent competition is strong under slow water movement (Powers and Peterson 2000). In natural conditions, the flash flood disturbance can be an important control of stream community dynamics (Hart and Finelli 1999; Lake 2000). Several studies document that invertebrate abundance is a function of the elapsed time after storm flows in both tropical and temperate streams (Grimm and Fisher 1989; Flecker and Feifarek 1994; Ramírez and Pringle 1998). Recent studies also suggest that the effects of storm flow on benthic fauna are mediated by habitat stability (reviewed by Lake 2000). Habitats experiencing greater scouring such as runs and plane beds (Matthaei et al. 1999a, b) show lower abundance and persistence of benthos than more resistant riffle and pool habitat (e.g., Gjerløv et al. 2003).

Measuring habitat stability in flashy tropical streams is logistically difficult. Fortunately, channel hydraulics may be used to estimate the forces experienced by streambed elements and organisms (Nowell and Jumars 1984; Statzner et al. 1988; Davies and Barmuta 1989; Way et al. 1993). If measured close to the streambed, standard Reynolds number (Re) and roughness Reynolds number (Re^*) indicate if microflows are turbulent ($Re > 2000$), laminar ($Re < 500$), rough ($Re^* > 70$), or smooth ($Re^* < 70$). Similarly, Froude number (Fr) indicates if near-bed flows are supercritical (i.e., erosive, $Fr > 1$) or subcritical (i.e., depositional, $Fr < 1$). Typically, flood stable habitats have larger streambed elements, and more turbulent and rough flows. Unstable habitats generally have fine-grained substrates and experience nearly laminar or smooth flows at baseline discharge (Nowell and Jumars 1984; Davies and Barmuta 1989; Naiman 1998; Montgomery and Buffington 1998; Matthaei et al. 1999a, b).

In this study we tested the following hypotheses: 1) upstream migration events of neritid gastropods are seasonal, 2) migratory aggregations consist of small-sized individuals, 3) individuals use turbulent, rough flows as passages during upstream migrations and as permanent habitats, and 4) influence of flood regime on the distribution of neritid gastropods depends on habitat hydraulics and stability.

MATERIALS AND METHODS

Study organism

The presence of the freshwater neritid *Neritina virginea* (Linné 1758) in several islands of the Caribbean has been noted in many studies, some from the middle of last century (Russel 1941; Aguayo 1966; Humfrey 1971). Other species have also been reported in the region (Russel 1941; Aguayo 1966; Humfrey 1971), but may be color variants of *N. virginea* (Cosel 1986; Diaz and Puyana 1994; J. F. Blanco, unpublished data). While the presence of *N. virginea* in the Caribbean is well documented, massive upstream migrations have been recently documented in two streams (e.g., Mameyes

and Espíritu Santo) in northeastern Puerto Rico (Covich and McDowell 1996; Pyron and Covich 2003).

Study area

This study was conducted in a lower segment of Río Mameyes, draining the Luquillo Experimental Forest (LEF), located in northeastern Puerto Rico (Fig. 1a). The upper part of the watershed, managed by the United States Forest Service, is covered by tropical wet forests (Scatena 1989). The lower part of the watershed is suburbanized, but has extensive abandoned pastures (Ramos 2001). Río Mameyes is considered the most conserved stream in Puerto Rico, and is gauged by the US Geological Survey (USGS). The highest discharge is typically observed during the two rainy seasons of the year: May and August-December (Fig. 1b).

The study site is located beneath Bridge

1771 of road PR Route 3 (18°22'27"N, 65°45'50" W, elevation: 5 m above sea level) over the Río Mameyes, where two reaches, separated by an elevated and stabilized island formed after the construction of the bridge in 1982. Most of the river's flow runs through a ~11 m wide the main reach (MR: a riffle at right and looking downstream). Channel depth is nearly constant across the section (<40 cm), and the streambed consists of mid-sized boulders (<50 cm) and cobbles. The right bank of the reach is a concrete-lined bridge abutment. Less water flows through a side reach (SR) that occurs on the opposite side of the bridge. This reach is 3 m wide, less than 30 cm deep, and is influenced by deflected flow from a channel bend located 5-m upstream. The streambed consists of cobbles in the deepest part and of gravel in the shallowest part. The MR and SR join about 40 m downstream, and this point becomes a decision-making area for the migratory organisms moving upstream.

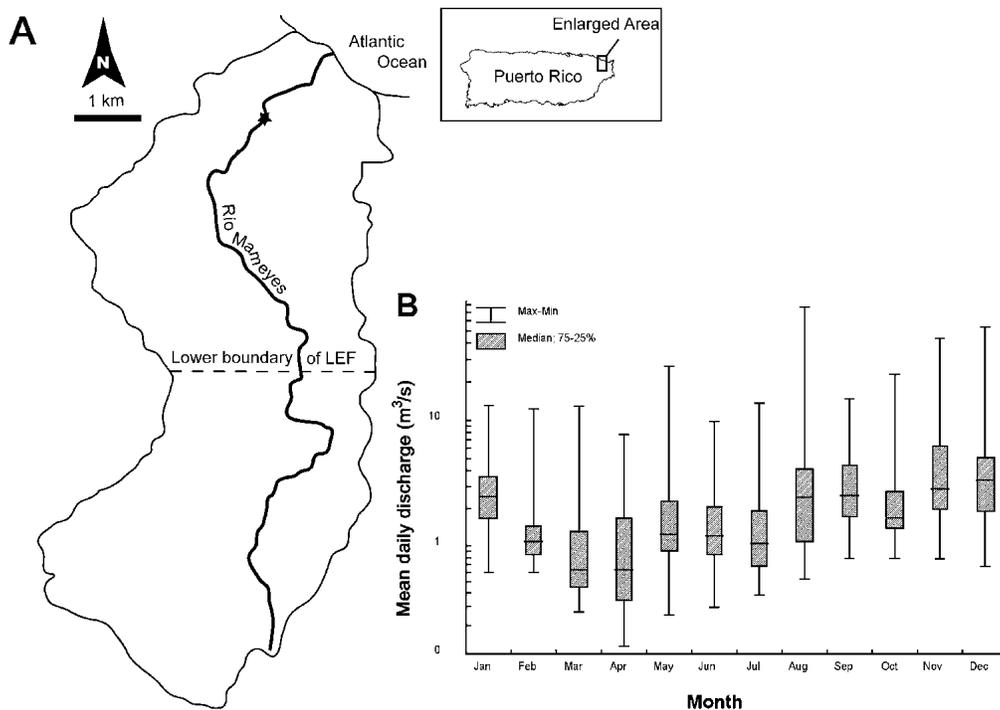


FIG. 1. A. Location of the study site (square) under PR Route 3 Bridge 1771 in Río Mameyes, Northeastern Puerto Rico. B. Discharge regime at the study site (note logarithmic y-axis) based in the 1998–2001 record (USGS gage 50066000 located 50 m upstream the bridge). LEF = Luquillo Experimental Forest.

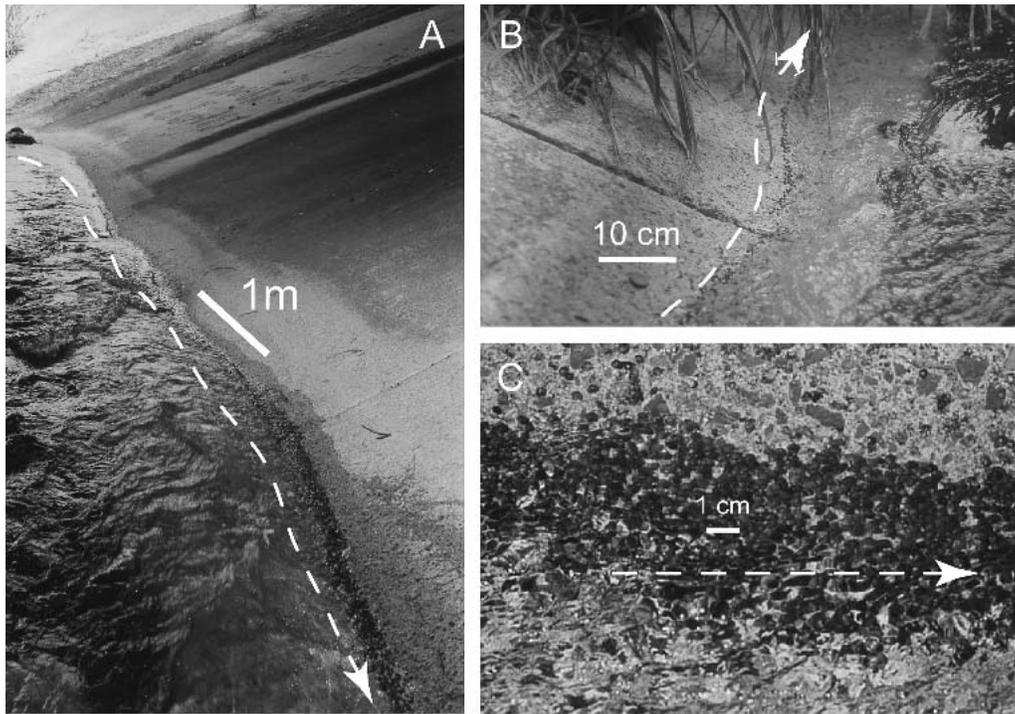


FIG. 2. Massive upstream migrations underneath the bridge PR Route 3 at the MR in Río Mameyes. A. Long trail after a large flood. B. Short trail after small flood. C. Close-up showing individual *N. virginea* in trails. Note individual displacement (broken arrow) against the flow.

Sampling

Occurrence of massive upstream migrations (Fig. 2) of *N. virginea* was monitored weekly to fortnightly between August 2000 and July 2002 for 99 weeks of observations. On 44 of these weeks high densities (> 500 ind/m²) of small individuals that were arranged in trails or groups were observed migrating on the bridge abutment in MR (Fig. 2).

In addition to the long-term monitoring, we conducted a detailed weekly study between August and December 2000. Sampling was restricted to periods when the instantaneous stream discharge was lower than 10 m³/s. Individuals were counted within 0.5 × 0.5 m quadrats (n = 10) placed on the streambed in MR and SR under the bridge during each sampling. All individuals within each quadrat were collected to measure aperture width using a caliper (0.05 mm). Individuals were divided into the following size groups: <4.00 mm

(spats), 4.00-6.00 mm (early juveniles), 6.00-8.00 mm (late juveniles), and >8.00 mm (adults). This grouping was based on preliminary field observations indicating distinctive behavior relative to individual size (cf., Pyron and Covich 2003). Spats had small and smooth, dark-brown shells, and were usually found underneath rocks. Juveniles exhibited greenish coloration with a variable pattern of axial lines or small yellow "tongues." These juveniles were very mobile and were commonly found on the sides of rocks. Adults exhibited the same coloration as juveniles, but moved randomly and were more common on the top of rocks. Sexual maturation was not considered for the grouping because it may be variable in tropical neritids (Ford 1979), and it is not easy to determine in small sized individuals (J. F. Blanco, pers. obs.).

Water velocity was measured 2 cm above substratum (shear velocity) with an electromagnetic flow meter (Flo-mate™, Marsh-McBirney) in points spaced 0.5 m across the

section of each reach. Three to five water velocity measurements (averaged over 30 s) were made at each point. During a single survey at the beginning of the study, the dominant substrate type was visually categorized as boulders, cobbles, pebbles, gravel, and finer particles. Discharge data for the sampling period were obtained from the USGS gage 50066000 (<http://waterdata.usgs.gov/pr/nwis>), located 20 m upstream from the study segment.

Data analysis

Since streamflow regime in the study area varies moderately with season, we hypothesized that the occurrence of massive migrations of gastropods may also vary throughout the year. Several insect studies in tropical streams suggest that intra-annual population dynamics may be correlated with seasonal variation in either stream discharge or rainfall (McElravy et al. 1982; Wolda and Flowers 1985; Masteller and Flint 1992; Masteller and Buzby 1993). For this reason, circular statistics were used to test for uniform distribution and uncover any seasonality (Batschelet 1982; Zar 1999). A Rao's spacing test was first conducted for two one-year periods: August 2000-July 2001, and June 2001-July 2002. Since we made weekly observations, each one-year period was equaled to 52 weeks. Also, each year was considered to be a round of 360° and, for that reason, this value was divided into 52 intervals of 6.9° (equivalent to one week). Accordingly, each upstream migration event had an exact location, expressed in degrees, into the one-year round. Based on the spacing of the migratory events, a U-statistic was computed and compared to a normally distributed theoretical value (Batschelet 1982). The null hypothesis that upstream migration events were uniformly distributed throughout the year would be rejected if the computed U value was greater than the theoretical value. In addition, the mean vector length (r) was computed as a measure of angular dispersion of upstream migratory events on one-year rounds. Mean vector varies between 0 and 1, and therefore, low values indicate wide dispersion, and high values indicate nar-

row dispersion, and greater concentration of observations.

Dispersion was high ($r < 0.2$) in both one-year rounds (2000-2001 and 2001-2002) because the distribution of migratory events was not unimodal. Visual exploration of our data suggested that upstream migration peaked at least once every calendar semester, and therefore our original data set was further subdivided into the following four periods: August-December 2000, January-June 2001, July-December 2001, January-June 2002. Within each of the new four periods, the mean angle (ϕ) and the mean vector length (r) were computed as metrics of central tendency and dispersion, respectively.

To determine under what hydrologic conditions upstream migrations occur, we used a discriminant function analysis (DFA, Statsoft 2003). The mean monthly discharge, monthly minimum and maximum, coefficient of variation, and number of floods greater than 3.5 and 18 m³/s were calculated using the daily stream discharge record for the 99 weeks (Fig. 3). These descriptors of discharge regime were used to step-wise discriminate among months with ≤ 1 , 2, and ≥ 3 weeks of migrations using the Statistica® software (Statsoft Inc.). Size-frequency distributions were also derived for several migratory aggregations and a One-Way ANOVA was used to test if mean individual size in migratory aggregations changed over time.

To determine the temporal variation in habitat use and hydraulics we conducted the following analyses. The flows at each reach were classified as either chaotic or non-chaotic, whether or not the rocks were exposed above the water surface. Secondly, Reynolds (Re), and Froude (Fr) numbers (Allan 1995; Appendix) were calculated to further classify the flows in both reaches at each sampling date. Temporal variation of flow type between reaches was explored by a Two-way ANOVA (reach \times date) using shear velocity, Re and Fr as response variables. A second Two-way ANOVA was calculated after pooling the sampling dates into three groups according to instantaneous discharge: two, three and five times the mean discharge (2-2.5, 3.0-3.5,

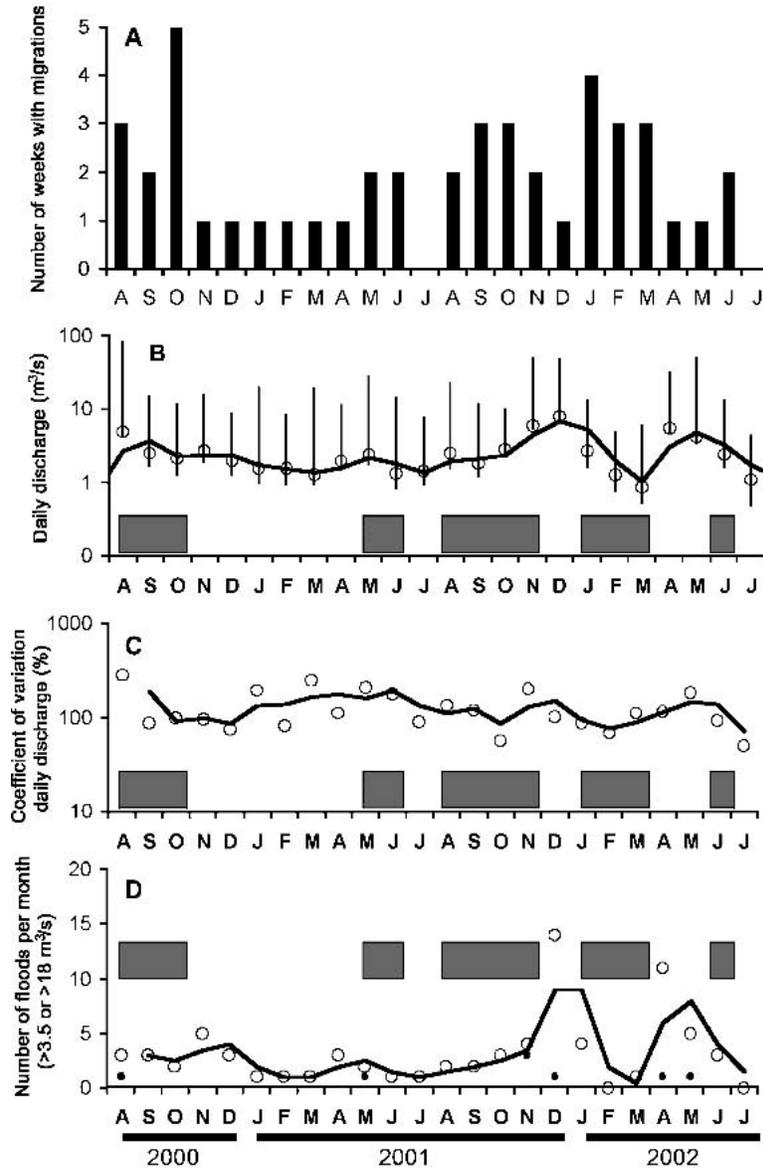


FIG. 3. A. Number of weeks per month when massive upstream migrations (Fig. 2) were observed at the MR. B. Mean monthly discharge (circles) between August 2000 and July 2002. Minimum and maximum daily discharges are indicated with a vertical line. Note logarithmic y-axis. C. Coefficient of variation of daily discharge throughout the month. D. Number of floods greater than 3.5 (open circles) or 18 (filled circles) m³/s per month. Boxes in B to D indicate periods when massive migrations occurred at least during two weeks. The thick lines show the running average.

and >5 m³/s, respectively). Two-way ANOVA was preferred over Repeated Measures ANOVA because the same plots and the two reaches were not always sampled on the same day. To assess habitat stability we used the percent of change

over time for the above hydraulic variables. More stable habitats are considered to have smaller changes over time, as already demonstrated in streams in temperate deserts (Grimm and Fisher 1989) and forests (Gjerløv et al. 2003).

Densities and sizes of *N. virginea* collected from August to December 2000 were transformed logarithmically to meet homoscedasticity for statistical tests. The homogeneity of variance of non-transformed data over time and between study reaches were also tested in a one way fashion using Levene's test and in multiple-ways using the Box-M and Sen and Puri's tests. A Two-way ANOVA was used to test differences of density and size between reaches and sampling dates (Zar 1999), and we used a G-test to determine uniformity of size groups over time within each reach (Sokal and Rohlf 1994).

To determine proximal causes of upstream migrations, mean gastropod density and its coefficient of variation (CV) were regressed against commonly used descriptors of the frequency and magnitude of flow-related disturbances (Allan 1995; Clausen and Biggs 1997; Biggs and Smith 2002). These parameters included mean discharge during the last 24 hrs (QMED24), instantaneous discharge (QINST), number of flashfloods during the previous week (#Q/WK), and number of days since a flood of given magnitude (DAYSSINCEQ). Intense rains frequently impact northeastern Puerto Rico and produce flashfloods that are readily identifiable by the sudden rising and falling limbs relative to the base flow (Fig. 5c). Flashfloods in Río Mameyes are characterized by instantaneous discharge $>3.5 \text{ m}^3/\text{s}$ (duration 20% of time) (Atkins et al. 1999). Large tropical storms and hurricanes may produce storm flows occurring less than 1% of time and promoting overbank flows and streambed scouring (Scatena and Larsen 1991). We included intermediate and large storm flows (instantaneous discharge: >18 and $>36 \text{ m}^3/\text{s}$, duration: <1 and 0.5% of time, respectively) to account for large and infrequent disturbances.

The interdependency among flood regime parameters was explored using correlation analysis. Weekly snail density records were not autocorrelated as migratory aggregations observed in one week moved upstream and were replaced by a new aggregation the following week. Step-wise Multiple Regression Models (Zar 1999) were independently derived for the mean

and the CV of gastropod density at each reach. Similar regressions were computed using gastropod mean size and percent of individuals per cohort as response variables. Finally, we explored several simple linear and non-linear regressions models between the elapsed time after storms and our biotic variables since this variable has been repeatedly used as a good predictor of lotic macroinvertebrate abundance in previous studies (e.g., Grimm and Fisher 1989; Flecker and Feifarek 1994; Ramírez and Pringle 1998).

RESULTS

Seasonality of massive upstream migrations

Forty four migratory aggregations of *N. virginea* were observed throughout the 99 weeks of sampling, 20 during the first year and 24 during the second (Fig. 3a). Migrations did not occur uniformly during either year: August 2000 to July 2001 (Rao's spacing test: $U = 3220$, $n = 20$, $P < .01$; mean vector, $r = .02$) and June 2001 to July 2002 ($U = 3900$, $n = 24$, $P < .01$; $r = .11$). When migration records were analyzed over 6-month periods, clustering was more evident. During the first year, most migrations were observed in October 2000 (mean angle: $\phi = 359$) and in May 2001 ($\phi = 179$). In contrast, during August to December 2001, and January to July 2002, massive migration events occurred at least monthly ($r = .1$ and 0, respectively). Nonetheless, migrations occurred at least during three weeks from September through October 2001, and January through March 2002.

The occurrence of massive upstream migrations of *N. virginea* was strongly related to stream discharge (Fig. 3b-d). The best discriminant function (Wilk's $\lambda = 0.16$, $F_{16,24} = 2.28$, $P = .032$) included the mean daily discharge, and the maximum and minimum discharge for both the observed and the previous month. The coefficient of variation of daily discharge of the previous month, and the number of floods (daily discharge $>3.5 \text{ m}^3/\text{s}$) during the observed month were also included. Multivariate distance between the groups of ≤ 1 and 2 weeks with migrations was not significant (Mahalanobis squared distance $MSD =$

8.79, $F_{8,12} = 2.23$, $P = .16$). In contrast, there was a significant distance between the groups of 2 and ≥ 3 weeks with migrations ($MSD = 8.79$, $F_{8,12} = 3.15$, $P = .036$). The months with ≥ 3 weeks with migrations showed a mean discharge ranging between 1 and 2 m^3/s , and they were preceded by months with higher mean discharge than months with ≤ 1 weeks with migrations (2.0 and 1.3 m^3/s , respectively) (Fig. 3b). The maximum discharge ranged between 3.8 and 8.1 m^3/s in months with ≥ 3 weeks with migrations, while the other groups (≤ 2 weeks) showed up to $>20 m^3/s$ (Fig. 3b). Months with ≥ 3 weeks with migrations were preceded by months with intermediate maximum (8-10 m^3/s), higher minimum discharges (0.4-0.7 m^3/s) (Fig. 3b), and less variable daily discharges (interquartile range of CV = 70-120%). Daily discharge was significantly greater in months with ≤ 3 weeks with migrations (CV: 88->200%, Fig. 3c). Months with ≥ 3 weeks with migrations presented between 1 and 3 floods, those with fewer migrations presented between 1 and 6 (Fig. 3d).

The mean daily discharge in the Río Mameyes is typically greater during May, and between August and December (Fig. 1b). High discharge was observed from August to January 2000, and from April to May 2001 (Fig. 3b), matching observed patterns of massive migrations in the period 2000-2001 (Fig. 3a). In contrast, the second year was atypically wet and had high mean monthly discharges from August 2001 to January 2002 and April and May of 2002 (Fig. 3b). In summary, massive upstream migrations occurred during periods of receding waters after high discharge periods (August-October 2000; May-June, and August-November 2001; January-March 2002).

We determined gastropod size composition of migratory aggregations based on groups collected in seven sampling dates between August 2000 and June 2001. Aggregated individuals ranged between 2.43 and 12.90 mm, but 50% fell in the 5-7 mm range. The overall average size was 6.05 ± 1.13 mm, but mean size was significantly different among migratory groups (One-way ANOVA: $F_{6,860} = 20.3$, $P < .0001$, Fig. 4). The variance of size also changed

among migratory aggregations ($F_{6,860} = 11.68$, $P < .0001$).

Habitat hydraulics and stability

Daily stream discharge showed a marked variation during August to December 2000 (Fig. 5c). Over this period, 14 flood days were evident and had magnitudes from 2 to approximately 100 m^3/s . Five events were greater than 10 m^3/s (Fig. 5c). The two study reaches had marked differences in terms of hydraulics (Table 1) and stability to those flashfloods and storm flows. The MR showed slightly faster, but significantly more variable water velocities than the SR (Two-way ANOVA: $F_{1,489} = 1.04$, $P = .31$, mean \pm s.d., MR: 0.30 ± 0.30 m/s, SR: 0.27 ± 0.20 m/s; homogeneity of variance test: $F_{1,489} = 11.48$, $P < .001$). The fast water velocities at both reaches promoted turbulent (mean $Re > 2000$), but non-erosive ($Fr < 1$) flows during discharges $< 3.5 m^3/s$. During relatively small storms ($> 5.0 m^3/s$), turbulence increased with velocity in both reaches, but more dramatically in the SR (among discharge periods: $F_{2,485} = 10.75$, $P < .001$, discharge period and reach interaction: $F_{2,485} = 2.88$, $P = .057$). Flows became more erosive ($Fr \sim 1$) in parts of both reaches, particularly at the SR when discharge was greater than 5.0 m^3/s . The fast flows along with larger streambed elements (cobbles and boulders) in the MR promoted chaotic and rough microflows (mean $Re^* > 30000$) at intermediate discharge ($< 3.5 m^3/s$). Flows were less chaotic and smoother (mean $Re^* > 10000$) in the small roughness elements of the SR (pebbles and cobbles) in the streambed. At high discharge, however, rough microflows increased faster in the SR than at the MR. The degree of change of the above variables between low discharge and storm flow dates was in the range of 100-200% in the SR and of 100-150% in the MR and indicates that scouring in the SR during flashfloods and storm flows may be greater because of the smaller substrates.

Upstream migration, gastropod density, and size

Snail density varied significantly over time ($F_{8,156} = 5.75$, $P < .0001$, Fig. 5a-b),

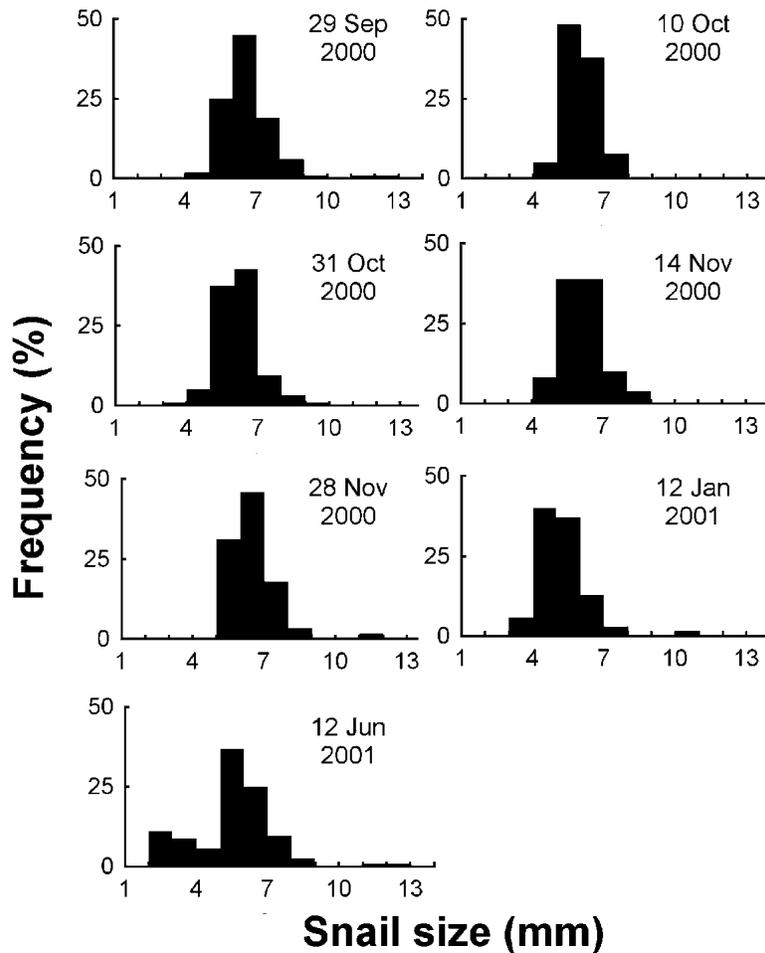


FIG. 4. Size-frequency distributions of *N. virginea* in migratory aggregations during 7 seven dates between August 2000 and June 2001.

and increased 2 to 10 times during migrations (200-800 ind/m²). This was particularly evident at SR (interaction, $F_{8, 156} = 2.37$, $P < .019$). Mean density was significantly higher at the MR than SR, where it dropped to nearly zero during non-migration periods (mean \pm s.d., MR: 115.7 ± 118.4 ind/m², $n = 86$, SR: 17.8 ± 33.8 ind/m², $n = 78$; $F_{1, 8} = 99.95$, $P < .0001$). At least, seven migratory events were observed in the MR (Sep 5, 19, Oct 3, 17, Nov 7, 14 and 28, Fig. 5a). Only five were observed in the SR (Fig. 5b) and all occurred after floods (Fig. 5c).

Shell size changed significantly between August and December 2000 (Fig. 6), as evidenced by the oscillation of the variance

($F_{9, 1229} = 37.92$, $P < .01$). Shell size variation was smaller at dates when gastropod density was higher (i. e., during massive migratory events). By analyzing each reach separately, mean size did not change over time at the MR ($F_{8, 931} = 0.63$, $P = .75$). Variance did change over time ($F_{8, 931} = 26.07$, $P < .01$). At the SR both mean size and variance changed significantly over time (means: $F_{8, 290} = 13.17$, $P < .0001$; variances: $F_{8, 290} = 8.58$, $P < .0001$). Mean size also showed differences between reaches, being smaller at the MR than at the SR (mean \pm s.d., MR: 6.3 ± 2.8 mm, $n = 940$, SR: 7.6 ± 2.4 mm, $n = 299$; $F_{1, 1237} = 54.55$, $P < .0001$; homogeneity of variance test: $F_{1, 1237} = 3.02$, $P = .082$).

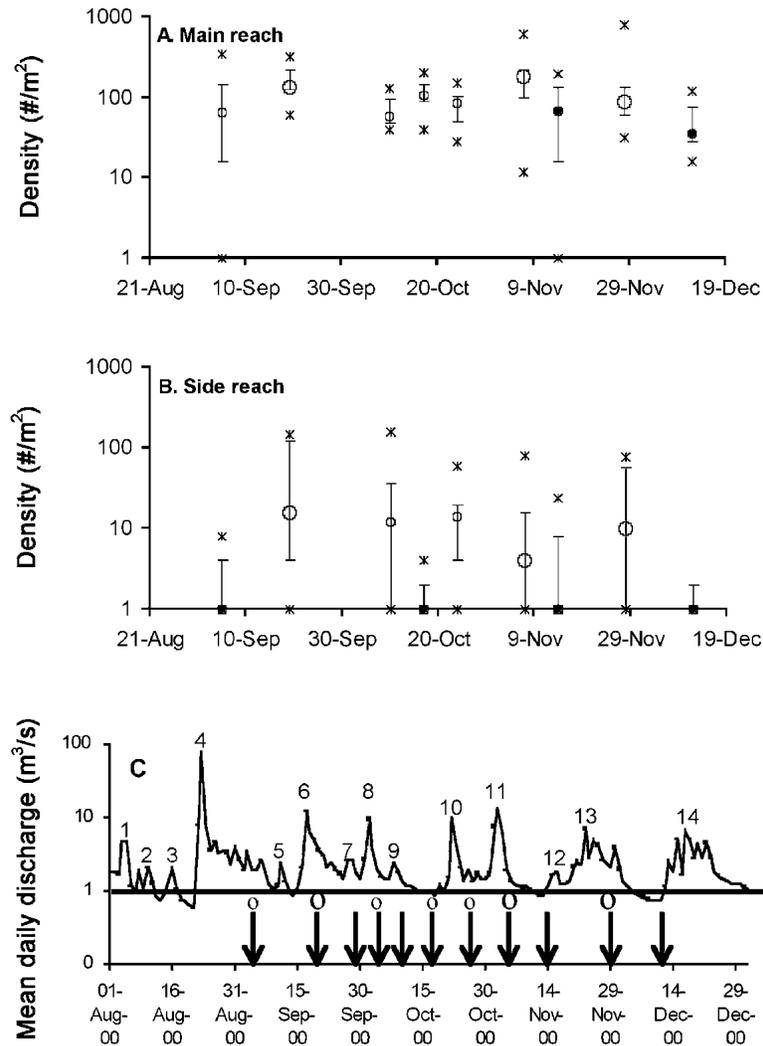


FIG. 5. Variation in *N. virginea* density at the Main and Side reaches (A and B, respectively). Circles: median. Whisker: interquartile range. Asterisks: extremes. Migrations are indicated with open circles, where size is proportional to the size of migratory aggregations. Closed circles indicate non-migratory events. C. Mean daily discharge between August 1 and December 31, 2000. Arrows: sampling dates. Open circles: migratory events. Numbers: flashfloods and storm flows. Horizontal line: Overall median discharge (1.5 m³/s) based in historical record for USGS gage 50066000. Note logarithmic y-axes.

Differences in mean size between reaches were related to differences in size structure of the snail population (Fig. 6, G-test for goodness of fit to uniform size distribution, MR: $G_{adj}(24) = 333.66$, $P < .05$, SR: $G_{adj}(16) = 120.23$, $P < .05$). While juveniles were dominant in both reaches, the early cohort dominated in the MR and late cohort in the SR. Adults were smaller in the MR, but more frequent and less variable over time

(10-30% of sample); while at the SR they were less frequent and more variable over time (0-100% of sample). Finally, spats were frequently recorded at the MR, but never observed at the SR.

Discharge regime and upstream migration

The variables used to characterize disturbance regime were not redundant, providing different information to be correlated to

TABLE 1. Hydraulic characteristics of the reaches in lower Río Mameyes, Puerto Rico. Low daily discharge: 2.0-3.5 m³/s. Intermediate daily discharge (flashfloods): >5 m³/s. N = 8 sampling dates.

Variable	Statistic	Main reach	Side reach		
Bankfull width (m)		11	3		
Base flow depth	Mean	30	20		
<i>D</i> (cm)	Min-Max	10-50	5-30		
Dominant substrate		Boulder Cobble	Cobble Pebble		
Substratum roughness <i>k</i> (cm)	Mean	20	5		
Near-bed flow type ¹		Chaotic flow	Non-chaotic flow		
		<i>Low discharge</i>	<i>Intermediate discharge</i>	<i>Low discharge</i>	<i>Intermediate discharge</i>
Shear velocity ² <i>U*</i> (m/s)	Median	0.19	0.29	0.20	0.37
	Interquartile	0.10-0.40	0.15-0.45	0.12-0.36	0.14-0.52
	Min-Max	0.00-1.10	0.00-1.65	0.00-0.50	0.00-1.14
Reynolds number ³ <i>Re</i>	Median	3800 (T)	5800 (T)	3800 (T)	7400 (T)
	Interquartile	1500-7600	3000-9000	2000-7200	2800-10400
	Min-Max	0-24000 (L-T)	0-33000 (L-T)	0-10500 (L-T)	0-23000 (L-T)
Froude number ⁴ <i>Fr</i>	Median	0.43 (sC)	0.66 (sC)	0.44 (sC)	0.84 (sC)
	Interquartile	0.17-0.86	0.34-1.03	0.34-0.8	0.31-1.18
	Min-Max	0.00-2.71 (sC-SC)	0.00-3.72 (sC-SC)	0.00-1.18 (sC)	0.00-2.58 (sC-SC)
Roughness Reynolds number ⁵ <i>Re*</i>	Mean	38000 (R)	58000 (R)	10000 (R)	18500 (R)
	Interquartile	10 ⁴	10 ⁴ -10 ⁵	10 ³ -10 ⁴	10 ³ -10 ⁴
	Min-Max	0.0-2.2 × 10 ⁵ (S-R)	0.0-3.3 × 10 ⁵ (S-R)	0.0-2.5 × 10 ⁴ (S-R)	0.0-5.7 × 10 ⁴ (S-R)

¹Near-bed flow type according to a comparison of depth (*D*) and substratum roughness (*k*): $D < 3k$ chaotic; $D > 3k$ non-chaotic.

²Interquartile range indicates temporal variation and min-max range indicates spatial variation.

³Mean flow type according to Reynolds number: >2000 Turbulent (T); <500 Laminar (L).

⁴Mean flow type according to Froude number: >1 Supercritical (SC); <1 Subcritical (sC).

⁵Microflow type classification according to Roughness Reynolds number (*Re**): $Re^* > 70$ hydraulically rough (R); $Re^* < 5$ hydraulically smooth (S).

variation in gastropod density and size in the studied reaches (Table 2). Instantaneous discharge (QINST) was weakly correlated to median discharge during the last 24 hours (QMED24), suggesting that the hydrography is very flashy. In addition, QINST decreased with time after flashfloods ($Q > 3.5 \text{ m}^3/\text{s}$) and small storm flows ($Q > 18 \text{ m}^3/\text{s}$), but was less correlated with very large storm flows ($Q > 36 \text{ m}^3/\text{s}$) that were less frequent. Elapsed time since a flashflood or a small stormflow event (DAYSSINCEQ) was negatively correlated with the number of events during the previous week (#Q/WK). Finally, DAYSSINCEQ3.5 and DAYSSINCEQ18 were strongly correlated, because most high flow events occurring during a week

are flashfloods that override the effects of small storm flows.

The mean gastropod density and its coefficient of variation (CV), as well as mean size and frequency distribution of the different cohorts were correlated with the flood regime at Río Mameyes. However, the relationships differed between reaches. At the MR, no single disturbance variable played a major role on the dynamics of gastropod variables. The #Q>3.5/WK and #Q>18/WK showed stronger positive effects on the percent of juveniles, while negative effects on the percent of spats and adults. In contrast, at the SR, more descriptors of disturbance regime were related to gastropod variables. Both QINST and #Q>3.5/WK were positively related to

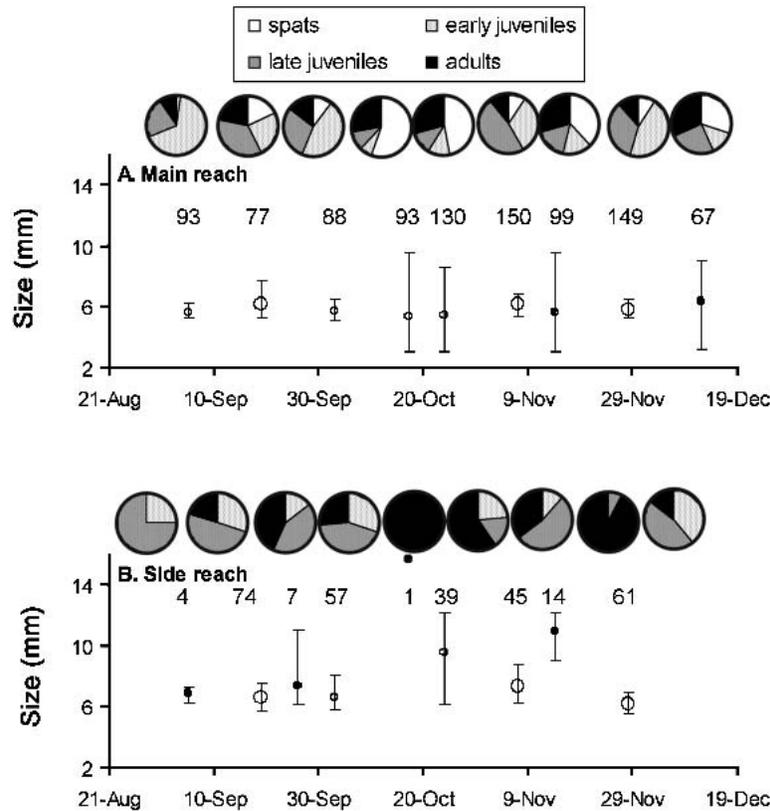


FIG. 6. Size variation in *N. virginea* at the Main and Side reaches (A and B, respectively). Circles: median. Whisker: interquartile range. Migratory events indicated by open circles. Closed circles indicate non-migratory events. Pies above of each sampling date correspond to percent of spats, juveniles, and adults. Numbers indicate the sample size for each date.

mean density, patchiness, and the percent of juveniles, but negatively related to the percent of adults. DAYSSINCEQ18 and DAYSSINCEQ3.5 also influenced these biotic variables. As a single variable, DAYSSINCEQ3.5 explained the largest proportion of variation in mean density at both the MR ($r^2 = .52$) and the SR ($r^2 = .69$) (Fig. 7). At the MR, mean density increased above background levels (~ 100 ind/ m^2) and peaked approximately five days after event >3.5 m^3/s . Density then approached background levels within the next five days. In contrast, at the SR the highest mean density was recorded right after a flashflood and then decreased exponentially.

While most of the single disturbance-regime variables were weak in explaining the dynamics of gastropod variables, they had a strong, combined, habitat-

dependent effect (Table 3). At the MR, mean density increased with $\#Q>18/WK$ and decreased with $\#Q>36/WK$. At the SR, mean density increased with high QINST. Patchiness of density (described by CV) increased with $\#Q>3.5/WK$ and was reduced by $\#Q>36/WK$ at MR. In contrast, more variables influenced CV at the SR. Mean size was not determined by any disturbance variable at the MR, but it was slightly influenced by the $\#Q>3.5/WK$ at the SR.

The distribution of individuals in size cohorts showed a tight correlation with the disturbance regime variables (Table 3). At the MR, the percent of spats increased with reduced QINST, $\#Q>3.5/WK$ and DAYSSINCEQ3.5. At the SR, spats were not found. The percent of early juveniles was explained by similar variables in both reaches. This per-

TABLE 2. Correlation indices among the disturbance regime variables and *N. virginea* density, mean (coefficient of variation, CV), size, and percent of individuals in different size categories. Values are indicated for both reaches in lower Río Mameyes. Median discharge in the previous 24 h (QMED24), instantaneous discharge (QINST), number of overbank flows (>36 m³/s) during the past 7 days (#Q>36/WK), number of storm flows (>18 m³/s) during the past 7 days (#Q>18/WK), number of flashfloods (>3.5 m³/s) during the past 7 days (#Q>3.5/WK), number of days since an overbank flood (DAYSSINCEQ36), number of days since a storm flow (DAYSSINCEQ18), number of days since a flashflood (DAYSSINCEQ3.5). Bolded: r² > 60%. N = 9 sampling dates.

Variable	QMED24	QINST	#Q>36/WK	#Q>18/WK	#Q>3.5/WK	DAYSSINCEQ36	DAYSSINCEQ18	DAYSSINCEQ3.5
QMED24	-	0.69	0.56	0.27	0.45	-0.46	-0.58	-0.52
QINST		-	0.39	0.31	0.59	-0.49	-0.82	-0.81
#Q>36/WK			-	0.79	0.57	-0.65	-0.67	-0.55
#Q>18/WK				-	0.82	-0.41	-0.64	-0.58
#Q>3.5/WK					-	-0.36	-0.77	-0.78
DAYSSINCEQ36						-	0.77	0.55
DAYSSINCEQ18							-	0.92
DAYSSINCEQ3.5								-
Mean density	-0.21	0.22	0.15	0.62	0.54	-0.26	-0.43	-0.42
CV of density	-0.30	-0.15	-0.33	0.17	0.37	0.37	0.10	0.14
Mean size	-0.22	-0.03	-0.28	-0.28	-0.35	0.55	0.41	0.28
% Spats	-0.36	-0.36	-0.24	-0.52	-0.65	0.07	0.31	0.22
% Early juveniles	0.42	0.30	0.20	0.39	0.60	-0.13	-0.25	-0.11
% Late juveniles	0.11	0.28	0.27	0.65	0.59	-0.07	-0.37	-0.38
% Adults	-0.32	-0.28	-0.32	-0.65	-0.77	0.24	0.40	0.30
Mean density	0.48	0.91	0.38	0.44	0.55	-0.46	-0.81	-0.79
CV of density	0.19	0.58	0.42	0.46	0.50	-0.11	-0.56	-0.54
Mean size	-0.37	-0.53	-0.34	-0.50	-0.68	0.10	0.46	0.40
% Early juveniles	0.47	0.74	0.24	0.38	0.71	0.02	-0.51	-0.58
% Late juveniles	0.23	0.30	0.24	0.44	0.54	-0.04	-0.20	-0.12
% Adults	-0.35	-0.51	-0.26	-0.46	-0.66	0.02	0.34	0.32

Main reach

Side reach

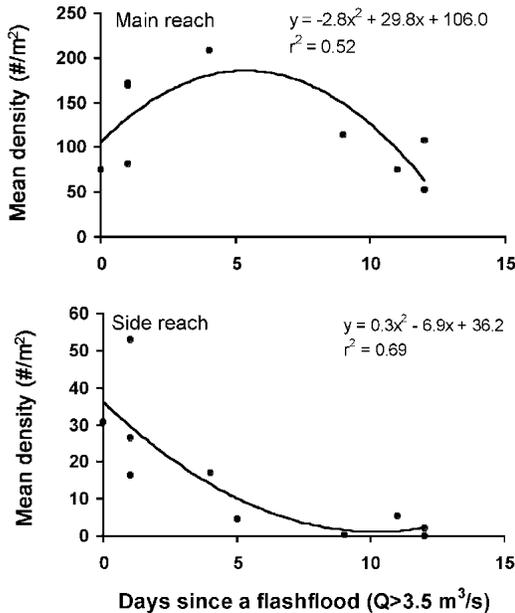


FIG. 7. Mean density variation of *N. virginea* with elapsed days after a flashflood ($Q > 3.5 \text{ m}^3/\text{s}$) at the main and side reaches. Different non-linear regression models were fitted for each reach. Note different scales in y-axis.

cent increased with QINST, #Q>3.5/WK, and DAYSSINCEQ3.5. However, DAYSSINCEQ36 better promoted an increase of early juveniles at the SR. The variation in percent of late juveniles was not as strongly determined by disturbance regime as in the previous cohort, and the models were reach-dependent. At the MR, it increased with #Q>18/WK and decreased with #Q>36/WK, while at the SR it increased with QINST and DAYSAFTQ3.5 and decreased with #Q>3.5/WK. The percent of adults was weakly determined by #Q>3.5/WK at the MR, but it was strongly determined by that variable as well as QINST, DAYSSINCEQ18, and DAYSSINCEQ3.5 at the SR.

DISCUSSION

Seasonality of massive upstream migrations

In this study we observed 44 massive upstream migrations of the neritid gastropod *Neritina virginea* over a two year period.

The migrations occurred at least once a month and were closely correlated to receding flows after periods of high discharge. In general, massive migrations were most frequent during the two high discharge periods of the year (May, and August to November). Nonetheless, prolonged periods of high discharge can presumably promote upstream migrations until the onset of the dry season, as they did in 2002. Given that successive storm flows are a proximate cause of migrations, the massive migrations of *N. virginea* tend to be seasonal but with a variable periodicity. Our results contrast with a previous one-year, mark-and-recapture study in a regulated stream in southern Japan stream, where non-seasonal migration was documented (Nishiwaki et al. 1991a). In our study, young juveniles (5-7 mm) dominated migratory aggregations. Similar findings were obtained for neritids in Puerto Rico (Pyrone and Covich 2003), Costa Rica (Schneider and Lyons 1993), and Hawaii (Ford 1979). Given the dominance of those intermediate-sized individuals, upstream migration may also be density-dependent and related to differences in resource-holding capacity among sizes, as was hypothesized for other migratory fauna (Baker 1978, Powers and Peterson 2000). This strategy, which is most likely used to avoid predators, has also been observed in *N. virginea* (J. F. Blanco, unpublished data). In addition, reduction of periphyton due to floods is common (e.g., Biggs and Smith 2002) and may also be responsible for triggering migrations (Johnson and Brown 1997).

Habitat hydraulics, and upstream migration

In the lower Río Mameyes, we recorded migratory aggregations in two habitats that differ in hydraulics and stability. At low and intermediate discharges, the MR showed faster and highly variable water velocities, highly turbulent flows (high Re), and highly rough microflows (Re^*), due to the boulders and cobbles dominating the streambed. The SR also showed fast, but less variable water velocities, less turbulent flows (Re), and smoother microflows (Re^*), due to finer streambed substrate (cobble and pebble). However, during storm flows

TABLE 3. Multiple (linear) regression models on flow-disturbance regime and dynamics of several variables associated to upstream migration of *N. virginea* in two reaches at lower Río Mameyes. F-values, probability of the regression, and adjusted determination indices (R^2) are included for each dependent variable at each reach. Standardized slopes (β) are shown between brackets next to each independent variable; those significantly different from zero are indicated with an asterisk. $n = 10$ sampling dates. Disturbance regime variables: median discharge in the previous 24 hrs (QMED24), instantaneous discharge (QINST), number of over bank flows ($>36 \text{ m}^3/\text{s}$) during the past 7 days (#Q>36/WK), number of storm flows ($>18 \text{ m}^3/\text{s}$) during the past 7 days (#Q>18/WK), number of flashfloods ($>3.5 \text{ m}^3/\text{s}$) during the past 7 days (#Q>3.5/WK), number of days since an over bank flood (DAYSSINCEQ36), number of days since a storm flow (DAYSSINCEQ18), and number of days since a flashflood (DAYSSINCEQ3.5). $N = 9$ sampling dates.

Dependent variable	Main reach	Side reach
Mean density (#/m ²)	$F_{3,6} = 12.31, P > 0.01, R^2 = 0.79$ Intercept = 131.60 SE Error = 23.19 #Q>36/WK (-1.40*) #Q>18/WK (1.48*) DAYSSINCEQ36 (-0.56*)	$F_{4,5} = 56.17, P < 0.001, R^2 = 0.96$ Intercept = -15.20 SE Error = 3.39 QINST (1.22*) #Q>36/WK (-0.53*) #Q>18/WK (1.09*) #Q>3.5/WK (-0.75*)
CV of density	$F_{3,6} = 14.75, P < 0.001, R^2 = 0.82$ Intercept = -1.38 SE Error = 14.01 #Q>36/WK (-0.66*) #Q>3.5/WK (1.45*) DAYSSINCEQ3.5 (0.91*)	$F_{6,3} = 18.55, P < 0.05, R^2 = 0.92$ Intercept = 90.85 SE Error = 5.45 QMED24 (-0.68*) #Q>36/WK (1.30*) #Q>18/WK (-1.10*) DAYSSINCEQ36 (2.10*) DAYSSINCEQ18 (-4.00*) DAYSSINCEQ3.5 (1.72*)
Mean size (mm)	No significant model	$F_{1,8} = 6.96, P < 0.05, R^2 = 0.40$ Intercept = 11.20 SE Error = 2.13 #Q>3.5/WK (-0.68*)
% Spats	$F_{3,6} = 8.51, P < 0.05, R^2 = 0.71$ Intercept = 1.05 SE Error = 0.10 QINST (-0.73) #Q>3.5/WK (-1.30*) DAYSSINCEQ3.5 (-1.40*)	Spats not found
% Early juveniles	$F_{3,6} = 20.71, P < 0.01, R^2 = 0.87$ Intercept = 0.82 SE Error = 0.07 QINST (0.82*) #Q>3.5/WK (1.41*) DAYSSINCEQ3.5 (1.65*) DAYSSINCEQ3.5 (1.65*)	$F_{4,5} = 19.45, P < 0.01, R^2 = 0.89$ Intercept = -0.27 SE Error = 0.04 QINST (0.96*) #Q>3.5/WK (0.70*) DAYSSINCEQ36 (0.48*) DAYSSINCEQ3.5 (0.50)
% Late juveniles	$F_{2,7} = 4.88, P < 0.05, R^2 = 0.46$ Intercept = 0.19 SE Error = 0.08 #Q>36/WK (-0.64) #Q>18/WK (1.16*)	$F_{3,6} = 4.83, P < 0.05, R^2 = 0.56$ Intercept = -0.65 SE Error = 0.15 QINST (0.77) #Q>3.5/WK (-1.21*) DAYSSINCEQ3.5 (1.45*)
% Adults	$F_{1,8} = 11.34, P < 0.01, R^2 = 0.53$ Intercept = 0.29 SE Error = 0.06 #Q>3.5/WK (-0.77*)	$F_{4,5} = 6.67, P < 0.05, R^2 = 0.72$ Intercept = 2.01 SE Error = 0.17 QINST (-1.00*) #Q>3.5/WK (-1.20*) DAYSSINCEQ18 (-0.97) DAYSSINCEQ3.5 (-0.56)

both Re and Re^* increased more rapidly in the SR than in the MR, and therefore the streambed is probably more prone to scour because greater shear stress and lack of flow separation (Davis and Barmuta 1989; Hart and Finelli 1999). Recent field experiments in a New Zealand stream (Matthaei et al. 1999a, b) provide evidence on stone movement relative to both high flows and habitat hydraulics. These experiments demonstrated less stone movement in riffles than in runs, but warned on the importance of upstream elements forcing the flows (i.e., bends, high banks and bedrock outcrops) in reducing stone stability. Forced flows by an upstream bend and an elevated bank may have contributed to a habitat instability at the SR.

Gastropod density and size differences between reaches were related to hydraulics, and seemly scour patterns. Greater densities were continuously observed at the MR while densities dropped to zero at the SR during non-migration dates. Therefore, the SR may be considered a non-permanent habitat and a transient passage. During upstream migrations, *N. virginea* mean size and its variance decreased in both habitats, however spats and juveniles primarily used the MR while the adults used the SR. Nonetheless, the percent of adults was more constant at the MR than at the SR, probably due to the greater streambed scour during storm flows. Recently, Holomuzki and Biggs (2000) conducted flume-tank experiments to study behavioral responses of lotic gastropods and insects to high flows, and observed that mortality in *Potamopyrgus* gastropods was negligible in streambeds consisting of stable, large stones because snails moved underneath of large rocks to avoid dislodgment during high flows. In contrast, when the gastropods and insects were placed in unstable, gravel substrate, high mortality occurred during high flows.

Many studies have demonstrated that hydraulic conditions influence habitat stability and aquatic refugia (e.g., Lancaster and Hildrew 1993; Townsend et al. 1997; Townsend and Scarsbrook 1997; Gjerløv et al. 2003). In our study, substrates large enough to separate flow and create dead

spaces may function as instream refugia during high flows (sensu Lancaster and Hildrew 1993) and helped explain the observed habitat preferences of *N. virginea*. Habitat dependent response to disturbances was documented in temperate streams under distinct climatic regimes (e.g., Grimm and Fisher 1989; Palmer et al. 1995; Robertson et al. 1995), but examples for the tropics are scarce (see Flecker and Feifarek 1994). According to some models for temperate streams in England (Lancaster and Hildrew 1993; Robertson et al. 1995; Lancaster and Belyea 1997), the spatial distribution of lotic organisms change as a function of flow variability, while low patchiness is observed at baseflows marked patchiness arises due to concentration of individuals in refugia at high flow. In our study, the populations of *N. virginea* might be incompletely affected by high flows (incomplete catastrophe) and frequent recruitment could be possible at habitat scale within riffles and runs. Stable habitats can also provide more refugia than less stable habitats at the reach scale (riffle vs. run) and help secure population persistence in larger scales.

Discharge regime and upstream migration

Different disturbance parameters explained the dynamics of *N. virginea* variables in our study. An increase in mean density due to migratory aggregations was related to intermediate storm events ($Q > 18 \text{ m}^3/\text{s}$) in both reaches. Nevertheless, such high densities were recorded at the SR only during high discharges and the patchiness of snail density increased with the number of flashfloods in the MR. Similar patterns were observed at the SR, but additional interacting factors were also involved. Such increase in both mean density and patchiness is promoted by strong habitat selection by migrating individuals. Blanco and Scatena (unpublished data) found that *N. virginea* used specific areas of the channels during upstream migrations thus increasing patchiness. These areas (i.e., fast flowing or deep waters) may function not only as migratory pathways, but also as flow refugia.

Although mean snail size was poorly explained by disturbance regime, floods significantly explained the proportion of individuals in different cohorts. The percent of spats increased with instantaneous high discharge but rapidly decreased as water level receded. Similarly, the percent of early juveniles (50% in migratory aggregations) increased with high instantaneous discharge after several flashfloods ($\#Q > 3.5/\text{WK}$) and with time after last flashflood in both reaches (R^2 : MR = .87, SR = .89). At the SR, the percent of early juveniles also increased after large storms ($>36 \text{ m}^3/\text{s}$). Unlike young juveniles, percent of late juveniles varied more, regardless of disturbance regime, suggesting that other factors may be more important. Finally, the percent of adults was reduced by successive flashfloods at the MR. In contrast, they appeared right after floods and then quickly disappeared in the SR. This may be due to dislodgment and streambed scour at an upstream plane-bed reach during floods, followed by upstream compensatory movement. The greater refugia availability at the MR may also have reduced effect of flashfloods on adult populations. Our results supported previous studies that report that reliability of disturbance variables is both species and habitat specific (Grimm and Fisher 1989; Death and Winterbourn 1994; Biggs and Smith 2002; Townsend and Scarsbrook 1997; Doisy and Rabeni 2001), but we also provided evidence that they are size-dependent.

Finally, our findings contrasted with the observance of frequent crashes in macroinvertebrate abundance relative to storm flows in tropical streams (Flecker and Feifarek 1994; Ramirez and Pringle 1998) and desert streams of North America (Grimm and Fisher 1989). Population crashes in neritid gastropods are exclusively caused by large, infrequent storm flows ($>36 \text{ m}^3/\text{s}$) responsible for streambed scour even in stable habitats (i.e., riffles and deep pools). Smaller events, in contrast, increase population density by stimulating upstream migration presumably due to reduction of periphyton. Therefore, neritid gastropods are resistant to small disturbances in stable habitats and highly resilient in unstable

habitats. This study supported previous works (Grimm and Fisher 1989; Flecker and Feifarek 1994) reporting species-specific responses to flood disturbances. In our study, *N. virginea* displayed a pulse response (sensu Lake 2000) characterized by a density reduction dependent on both disturbance magnitude and habitat stability, followed by a massive upstream migration.

CONCLUSIONS

Aggregations of large numbers of juveniles of *N. virginea* that migrate upstream occur during rainy periods in Puerto Rico. Both long- and the short-term studies indicate that upstream migrations are relatively frequent (once every 15 days), promoted by floods, and are strongly influenced by reach-level habitat stability. In a stable riffle reach, the density varied less compared to an unstable plane-bed reach and peaked nearly 5 days after flashfloods, dropping to previous levels afterwards. Conversely, in an unstable habitat, density was lower, increasing 1 day after floods, then decreasing exponentially to zero in some instances. *N. virginea* was more resistant to flashfloods (instantaneous discharge $>3.5 \text{ m}^3/\text{s}$) and intermediate storm flows (instantaneous discharge $>18 \text{ m}^3/\text{s}$) in the stable habitat providing flow refugia (riffle), but it was resilient in the unstable habitat (fine-substrate run). Lastly, since stable habitats are preferred as both residence areas and passages during upstream migrations, they should be protected to preserve populations of *N. virginea* and other migratory fauna.

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Appendix. Hydraulic variables and equations

<i>D</i> :	Water depth	<i>Re</i> _r :	Roughness Reynolds number (<5 hydraulically smooth, >70 hydraulically rough)
<i>k</i> :	Substratum roughness	<i>Fr</i> :	Froude number (<1 subcritical, =1 critical, >1 supercritical)
<i>U</i> _* :	Shear velocity measured 2 cm above the streambed	<i>g</i> :	Gravity acceleration (9.8 m/s ²)
<i>Re</i> :	Mean Reynolds number (<500 laminar, 500-2000 transitional, >2000 turbulent)	<i>ν</i> :	Kinematic viscosity (1 × 10 ⁻⁶ m ² /s at 20°C)
		<i>Re</i>	= $U_* D \nu^{-1}$
		<i>Re</i> _r	= $U_* k \nu^{-1}$
		<i>Fr</i>	= $U_* (g D)^{-0.5}$
