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Hierarchical contribution of river–ocean connectivity, water chemistry, hydraulics, and substrate to the distribution of diadromous snails in Puerto Rican streams

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Abstract. Diadromous faunas dominate most tropical coastal streams and rivers, but the factors controlling their distribution are not well understood. Our study documents abiotic variables controlling the distribution and abundance of the diadromous snail *Neritina virginea* (Gastropoda:Neritidae) in the Caribbean island of Puerto Rico. An intensive survey of *N. virginea* density and shell size, and channel substrate, velocity, and depth was conducted at microhabitat, habitat, and reach scales of a coastal plain reach of the Río Mameyes between August and December 2000. In addition, the inland extent of distribution (stream-network scale) and presence (regional scale) of *N. virginea* were surveyed in 32 coastal rivers around the island during summer 2001 and 2003. At the microhabitat scale, snail density and microhabitat electivity were greater in patches consisting of a mix of boulders and cobbles than in other types of substrate. At the habitat scale, snail density increased with depth. At the reach scale, snail density increased with fast and turbulent flows (riffle > pools > pond), whereas snail size showed the opposite pattern. At the regional scale, populations were present in 13 of 32 streams. Populations of *N. virginea* were not found in rivers that were disconnected from the ocean for most of the year because of channel dewatering, formation of sediment bars at their mouths, and low mean monthly discharge ($Q = 0.69$ m^3/s). In contrast, rivers with *N. virginea* populations had a permanent ($Q = 4.04$ m^3/s) or seasonal ($Q = 2.88$ m^3/s) connection to the ocean over the year. At the regional scale, the inland distribution of populations was not correlated with stream gradient, but was negatively correlated with concentrations of SiO_2, P, and acid neutralizing capacity of the water. Populations colonized montane reaches in only 5 rivers, all of which were forested and protected. Our study highlights the importance of taking a hierarchical approach in managing tropical coastal rivers, and the usefulness of neritid snails as biological indicators of the physical and chemical integrity of rivers.

Key words: freshwater gastropods, tropical streams, spatial hierarchies, landscape filters, downstream–upstream linkages.

Tropical diadromous fauna, including fish, shrimp, and snails, migrate long distances between marine and fresh waters and, therefore, their distributions may be controlled by many factors operating at different spatial scales. These factors are poorly understood in spite of the greater abundance and diversity of diadromous fauna in tropical than temperate streams (Gross et al. 1988). For instance, diadromous fauna represent 60% of noninsect species in temperate streams (McDowall 1998, McDowall and Taylor 2000), but they probably represent 100% of species in streams of the Caribbean (Fièvet et al. 2001a, b), and the Pacific (i.e., Hawaii: Ford and Kinzie 1982; French Polynesia: Resh et al. 1990, 1992). Nonetheless, studies in Puerto Rico and Hawaii reveal that distributions of diadromous fish and shrimp along streams are

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influenced by barriers to migration (e.g., waterfalls and dams), whereas distributions within reaches and habitats are influenced by pool size, water velocity, and depth (Ford and Kinzie 1982, Pringle 1996, Covich et al. 1996, 2006, Scatena and Johnson 2001). Controls on the distribution of benthic diadromous gastropods such as neritids are less known. The aim of our study was to understand the influence of abiotic variables on the distribution and abundance of tropical diadromous fauna by looking at the migratory snail *Neritina virginea* (Linné, 1758) (Gastropoda:Neritidae) at scales from microhabitat to regional in the Caribbean island of Puerto Rico.

We used a hierarchical or multiple-spatial-scale approach because several studies have highlighted the need for observations over several spatiotemporal scales when seeking to understand relationships between stream flow, habitat, and the distributions of organisms (Frissel et al. 1986, Poff 1997, Parsons et al. 2004). In particular, we adapted the "landscape filters" concept (Poff 1997) as a means of explaining differences in community composition across streams. According to this concept, abiotic and biotic variables operating at specific spatial scales act as filters by preventing colonization by some species and facilitating colonization of others in streams, reaches, or habitats. Each species must negotiate filters at higher scales to colonize at lower scales in the landscape hierarchy. The landscape filters concept may be useful for understanding how diadromous fauna move throughout stream networks to complete their life cycles. For instance, to colonize headwater reaches, individuals must be able to negotiate barriers along the stream network and to cross a variety of reaches and habitats that present both biotic and abiotic challenges.

Neritid gastropods generally are distributed in diverse habitats several kilometers inland from the sea in tropical to temperate coastal rivers (Resh et al. 1990, 1992, Schneider and Lyons 1993, Liu and Resh 1997). We tested scale-specific hypotheses derived from the literature to explain the influence of abiotic variables on the distribution and abundance of the diadromous snail *N. virginea* (Table 1). At the microhabitat scale, neritid densities are greater on hard surfaces and, therefore, their distribution is related to *substrate size* (hypothesis 1). This relationship has been observed in other gastropods and insects (e.g., Herrmann et al. 1993, Holomuzki and Biggs 2000). At the habitat scale, neritid distribution is related to *water depth* (hypothesis 2) because neritids are scarce in deep pools or shallow areas dominated by sands and silts. At the reach scale, neritids are more abundant in riffles than pools, and their distribution is related to *habitat hydraulics* (hypothesis 3).

At the stream-network scale, the inland extent of distribution of adult snails varies from tens of meters to tens of kilometers (Table 1), even though individuals migrate long distances in a single day (1–50 m/d; Schneider and Lyons 1993, Pyron and Covich 2003, Blanco 2005). Variable inland extent of distribution suggests that neritid distribution is correlated with *barriers to migration* (hypothesis 4a). Waterfalls (Ford 1979) and road culverts (Resh et al. 1992, Resh 2005) have been identified as barriers to the migration of neritids. Steep-gradient streams have fewer species and shorter inland distributions of diadromous fish than lesser-gradient streams (McDowall 1998, McDowall and Taylor 2000), and these results suggest that *stream gradient* controls inland extent of distribution of neritids (hypothesis 4b).

Information on the regional distribution of neritid gastropods is limited but suggests that snail presence in streams within a region is related to freshwater discharge and, thus, *connectivity with the ocean* (hypothesis 5) and *water chemistry*, particularly hardness and ion concentrations (hypothesis 6) (Table 1). In a recent study in French Polynesia, Myers et al. (2000) suggested that larval dispersal does not limit regional neritid distribution because no population genetic structure was observed at scales ranging from "along-stream" to "among-islands." Nevertheless, neritid distribution is discontinuous at regional and subregional scales. For instance, neritids are broadly distributed in streams around several South Pacific islands, but they are generally absent from streams intermittently disconnected from the ocean (Ford 1979, Haynes 1993). Neritids also are absent from streams draining limestone that have a high concentration of $CaCO_3$ (Haynes 1993, 2000).

Methods

Neritina virginea

Neritina virginea is the dominant freshwater neritid in the Caribbean (Humfrey 1975). In Puerto Rico, *N. virginea* has been observed in large migrating aggregations (>3000 ind/m^2; Pyron and Covich 2003, Blanco and Scatena 2005), and it is found >10 km from some river mouths (Pyron and Covich 2003). In Puerto Rico, as elsewhere, *N. virginea* is amphidromous (a type of diadromy, sensu McDowall 1988). It has both marine and freshwater life stages (Ford 1979), and it undergoes significant growth during upstream migrations. Adults lay egg capsules on hard substrates and are found from estuaries to headwaters. Larvae are released from eggs during

TABLE 1. Patterns of abundance and distribution in neritid gastropods worldwide. Relevant patterns are summarized hierarchically from microhabitats to regions. H1 to H6 refer to hypotheses developed and tested in our study (see text for details).

Scale	Hypotheses and observations	Geographic area	Species	Reference
Microhabitat	*H1: Density increases with substrate size*			
	Hard/stony > muddy/sluggish substrate	Hawaii	*Neritina granosa*	Ford (1979)
	Boulders/large cobbles > small cobbles/granules	Japan	*Clithon retropictus*	Ohara and Tomiyama (2000)
		French Polynesia		Liu and Resh (1997)
Habitat	*H2: Density increases with water depth*			
	Absent from pools >2 m deep and heavy siltation channel areas	Hawaii	*Neritina granosa*	Ford (1979)
	Crowding on thalwegs during upstream migrations	Puerto Rico	*Neritina virginea*	Blanco and Scatena (2005)
Reach	*H3: Density increases with turbulent flow*			
	Riffle > pools	Hawaii	*Neritina granosa*	Ford (1979)
		Costa Rica	*Neritina latissima*	Schneider and Lyons (1993)
		French Polynesia	*Clithon retropictus*	Liu and Resh (1997)
		Japan	*Clithon spinosus*	Ohara and Tomiyama (2000)
	Riffle > run	Puerto Rico	*Neritina virginea*	Blanco and Scatena (2005)
Stream-network	*H4: Inland distribution is blocked by barriers (4a) and reduced by steep stream gradients (4b).*			
	Indirect evidence of migration:			
	Mean size increases upstream, mean density decreases upstream	Hawaii	*Neritina granosa*	Ford (1979)
		French Polynesia	*Clithon spinosus*	Resh et al. (1990, 1992), Resh (2005)
		Japan	*Clithon retropictus*	Nishiwaki et al. (1991), Hirata et al. (1992)
	Direct evidence of migration:			
	Movement in aggregations	Costa Rica	*Neritina latissima*	Schneider and Lyons (1993)
		Puerto Rico	*Neritina virginea*	Pyron and Covich (2003)
	Movements of individuals (mark–recapture)	Hawaii	*Neritina granosa*	Ford (1979)
		Costa Rica	*Neritina latissima*	Schneider and Lyons (1993)
		Japan	*Clithon retropictus*	Nishiwaki et al. (1991)
		Puerto Rico	*Neritina virginea*	Pyron and Covich (2003)
	Upper limit of distribution:			
	114–400 m asl	Hawaii	*Neritina granosa*	Ford (1979)
	0.5–5 km upstream	Japan	*Clithon retropictus*	Nishiwaki et al. (1991), Ohara and Tomiyama (2000), Shigemiya and Kato (2001)
		Vanuatu	>20 species	Haynes (1993, 2000)
	Hundreds of meters to several kilometers	French Polynesia	*Neritina turrita*, *Neritina canalis*, *Septaria porcelana*	Resh et al. (1990, 1992), Resh (2005)
	>200 m asl, >10 km upstream	Puerto Rico	*Neritina virginea*	Pyron and Covich (2003)
	4 km upstream	Costa Rica	*Neritina latissima*	Schneider and Lyons (1993)
	Differences in abundances and distribution related to barriers in 3 streams	French Polynesia	*Clithon spinosus*	Liu and Resh (1997)
			Neritina turrita, *Neritina canalis*, *Septaria porcelana*	Resh et al. (1990, 1992), Resh (2005)
Region	*H5: Population presence is determined by river–ocean connectivity*			
	No genetic structure from within-stream to among-islands	French Polynesia	*Clithon spinosus*	Myers et al. (2000)
	Differences among several streams along the coastline	Japan	*Clithon retropictus*	Nishiwaki et al. (1991), Hirata et al. (1992), Shigemiya and Kato (2001)
	Broad distribution but populations absent in streams without continuous discharge to the ocean	Hawaii	*Neritina granosa*	Ford (1979)
		Vanuatu and Solomon	>20 species	Haynes (1993, 2000)
	H6: Population presence is determined by water hardness			
	Snails absent or having heavy accumulations of $CaCO_3$ on shells in limestone watersheds	Vanuatu and Solomon	>20 species	Haynes (1993, 2000)

floods and flushed to the ocean, where they probably spend several months feeding on plankton (Myers et al. 2000). The pelagic larvae develop into benthic spats or hard-shelled individuals (~2 mm) that migrate upstream to complete their life cycle. Spats are rheophilic and typically have greater density in riffles and fast-flowing areas during migration (Ford 1979, Schneider and Lyons 1993, Resh et al. 1990, 1992, Blanco and Scatena 2005), probably to avoid terrestrial and aquatic predators (Ford 1979, Pyron and Covich 2003, Blanco 2005).

Study area

Puerto Rico is the smallest island (8900 km^2) of the Greater Antilles. Its maritime tropical climate has relatively limited seasonal variations in temperature and rainfall but is influenced by both extratropical cold fronts and tropical depressions (García-Martinó et al. 1996). Minimum air temperature is higher between June and September (>26°C) than between November and January (<25°C). Rainy seasons (>300 mm/mo) occur in April to May and August to December. The island is nearly rectangular and has the highest elevations along the E- to W-trending Central Cordillera (Fig. 1A) that intercepts the northeastern trade winds and generates a southward and westward rainfall shadow. The coastal plain geology is dominated by limestone and alluvial sediments in the northern region, by alluvial and volcanic sediments in the eastern and western regions, and by limestone, alluvial, and volcanic deposits in the southern region (Helmer et al. 2002).

Sampling and data analysis at within-reach scales

Replication.—Within-reach sampling was done in a low-elevation segment of the Río Mameyes (lat 18°22′27″N, long 65°45′50″W; 5 m asl). This river drains the Luquillo Mountains in northeastern Puerto Rico (Fig. 1B) and is the island's only large river without dams. It also is the island's most pristine river. Closed-canopy forests cover the protected montane part of the watershed, whereas pastures, secondary forests, and suburban land use cover the lower elevations (Ramos 2001, Helmer et al. 2002). In contrast, low and mid elevations in most coastal watersheds around the island are extensively covered by urban and agricultural lands (Helmer et al. 2002). Therefore, replicate reach and habitat sites could not be found on different rivers. Likewise, spatial replication along the Río Mameyes, as elsewhere, is limited because snail size increases and snail density decreases with distance from river mouth (Ford 1979, Resh et al. 1990, 1992, Schneider and Lyons 1993, Pyron and Covich 2003, Blanco 2005). However, temporal replication is possible because massive migrations occur every month, and every new cohort of individuals is sorted into the existing habitat template (Pyron and Covich 2003, Blanco 2005). Thus, every cohort may be considered a new trial in a natural experimental setting.

Sampling.—Twelve weekly samplings were conducted at the Route 3 Bridge over the Río Mameyes between September and December 2000 (Fig. 2). *Neritina virginea* individuals were counted within 50 × 50-cm quadrats ($n = 10$–15) placed on the streambed in each habitat. Snails were collected by intensively looking beneath rocks. A random subsample was collected and preserved in ethanol for shell-size measurement. Within each quadrat, water depth was measured and the 3 most dominant substrates (based on areal coverage) were estimated visually (Statzner et al. 1988). Substrates were classified as boulder (b, diameter >256 mm), cobble (c, 256–64 mm), pebble (p, 64–16 mm), and gravel (g, 16–8 mm). Quadrats with ≥⅓ coverage of *Elodea densa* were classified as macrophyte (m). Quadrats with <⅓ *Elodea* cover were classified exclusively according to substrate type because no significant effect of this level of *Elodea* was observed in exploratory analyses (JFB, unpublished data). Sampling was randomly stratified among a riffle, 2 pools (one in a straight and another in a meander of the channel), and a marginal high-flow pond along the 200-m reach (Fig. 2).

Microhabitat availability and electivity.—The microhabitat scale was delimited by the sampling quadrat. Microhabitats were categorized as 1 of 9 readily identified substrate combinations (b, bc, c, cp, bcp, p, g, pg, and m). Microhabitat availability was determined by dividing the number of quadrats having each combination by the total number of quadrats sampled. The distribution of substrate combinations was plotted relative to water depth. Only the data from the 2 pools were used for microhabitat analyses because they showed the greatest variability in substrate combinations and water depth. Moreover, substrate availability and water depth are not correlated with neritid distribution in riffles (Blanco 2005). The distribution of neritids on a substrate may be influenced by substrate availability. Therefore, Ivlev's electivity index (I) (Manly et al. 1993) was computed as:

$$I = (r_i - p_i)/(r_i + p_i)$$

where r_i is the relative snail abundance in the i^{th} substrate combination, and p_i is the relative availability of the i^{th} substrate combination. I ranges from +1 (complete preference) to −1 (complete rejection).

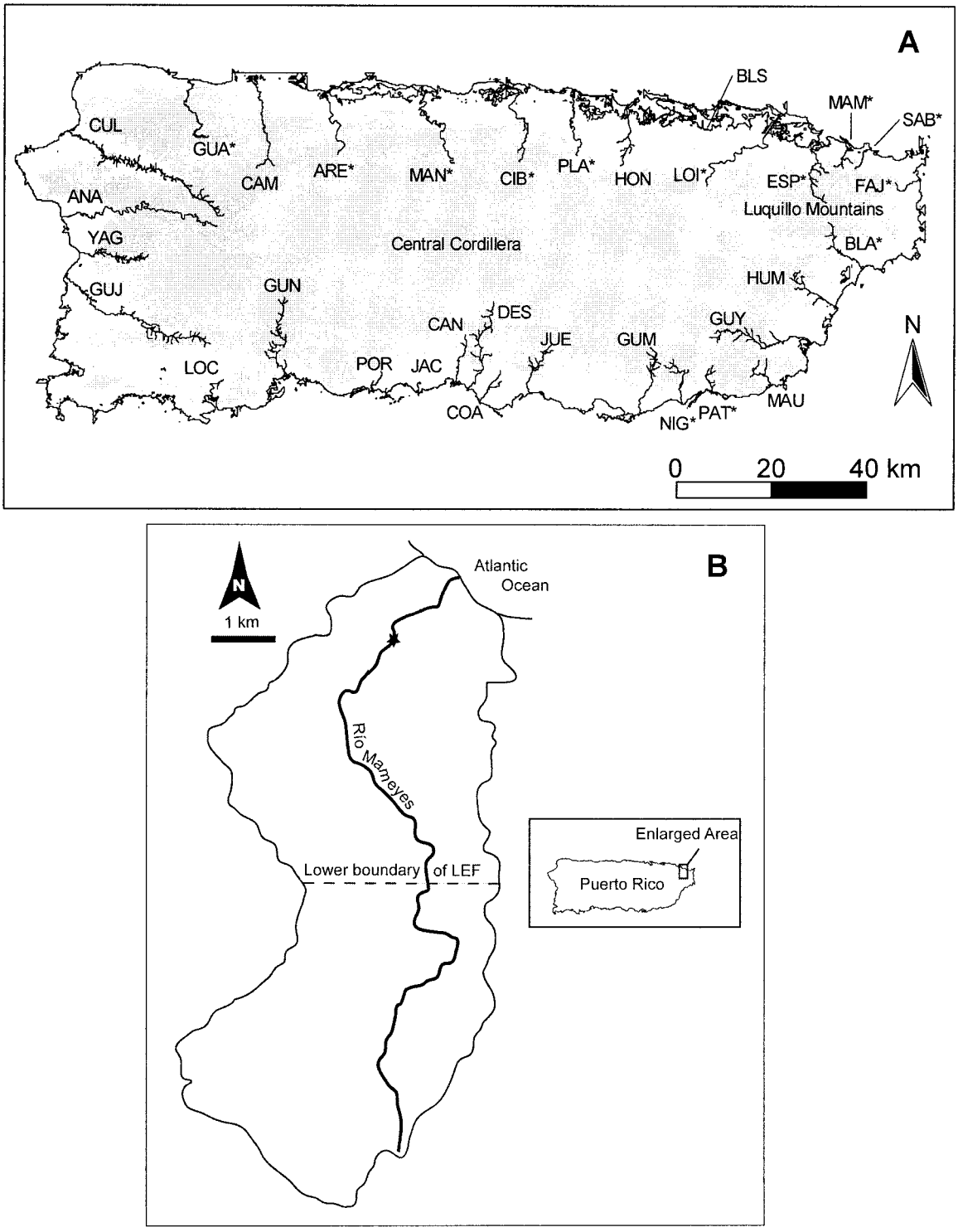

FIG. 1. A.—Coastal streams and rivers in Puerto Rico. Shaded area shows elevations >100 m. GUA = Guajataca, CAM = Camuy, ARE = Grande de Arecibo, MAN = Manatí, CIB = Cibuco, PLA = Grande de La Plata, HON = Hondo or Bayamón, BLS = Blasina, LOI = Grande de Loiza, ESP = Espíritu Santo, MAM = Mameyes, SAB = Sabana, FAJ = Fajardo, BLA = Blanco, HUM = Humacao, GUY = Guayanes, MAU = Maunabo, PAT = Patillas, NIG = Nigua, GUM = Guamaní, JUE = Jueyes, COA = Coamo, DES = Descalabrado, CAN = Cañas, JAC = Jacaguas, POR = Portugués, GUN = Guayanilla, LOC = Loco, GUJ = Guanajibo, YAG = Yaguez, ANA = Añasco, CUL = Culebrinas. * indicates *Neritina virginea* present in stream. B.—Location of the sampling reach at the Route 3 Bridge (asterisk) over Río Mameyes, draining the Luquillo Experimental Forest (LEF).

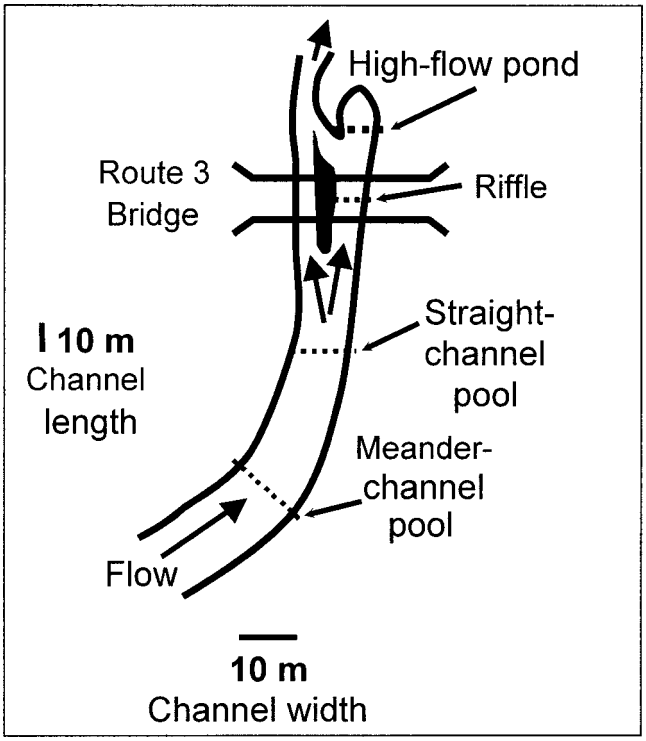

FIG. 2. Habitats sampled at the reach scale in the lower Río Mameyes. Note that the drawing is not to scale (see scale bars indicating channel width and length).

Hydraulic variables.—Habitat hydraulics were characterized by measuring water velocity at 80% and 20% of instantaneous depth and 2.5 cm above the streambed across the section of each habitat channel at rainy-season baseflow (~2 m^3/s) using an electromagnetic current meter (Flo-Mate™, Marsh–McBirney, Frederick, Maryland). Reynolds (Re) and Froude (Fr) numbers were computed to characterize the nearbed flow environment used by the neritids, according to the following equations (Statzner et al. 1988):

$$\mathrm{Re} = \mathrm{UD}/\nu$$
$$\mathrm{Fr} = \mathrm{U}(\mathrm{gD})^{-0.5}$$

where U is the average of repeated measurements of near-bed water velocity at each sampling point, D is measurement depth (2.5 cm), g is acceleration of gravity (9.8 m/s^2), and ν is the kinematic viscosity (1×10^{-6} m^2/s at 20°C). Total water depth, bottom-water velocity, Re, and Fr were compared among habitats using a 1-way analysis of variance (ANOVA).

Tests of hypotheses 1–3.—To test hypothesis 1 (micro-habitat-scale), log-transformed *N. virginea* density was compared among substrate combinations using a 2-way ANOVA (substrate combination × sampling date). To test hypothesis 2 (habitat-scale), analysis of covariance (ANCOVA) was used to test the relationship between log-transformed snail density and water depth in straight and meandering pools. To test hypothesis 3 (reach-scale), nested ANOVA was used to compare snail density and size among the riffle, the 2 pools, and the marginal high-flow pond. Sampling date was nested within habitat because not all habitats were sampled simultaneously on some dates. Mean snail density was plotted against snail size for each sampling date and habitat and fitted to a power model to explore the influence of habitat type on density. All analyses were done using STATISTICA 6 (Statsoft, Tulsa, Oklahoma).

Sampling and data analysis at stream-network to regional scale

Survey.—The distribution of *N. virginea* was studied at the island-wide stream-network scale by surveying 56 sites in 32 coastal streams and rivers (Fig. 1A). Most of the streams visited had US Geological Survey (USGS) gauging stations. The 1st survey was conducted between June and September 2001, and the 2nd between June and September 2003. During each survey, river mouths and upstream areas were visited to determine the presence and inland extent of distribution of *N. virginea*. The river mouth was visited and local inhabitants were interviewed to assess river connectivity to ocean. Rivers were classified as permanently, seasonally, or episodically connected to the ocean (McDowall 1995). Permanently connected rivers ran unimpeded to the sea, whereas sandbars choked the mouths of seasonally connected rivers during prolonged low-flow periods. Yearly flooding reopened the mouths of seasonally connected rivers. Episodically connected rivers had high sand and gravel bars at their mouths, and long lowland reaches usually remained dewatered for most of the year because of dry climate or excessive pumping or regulation. However, these rivers may be sporadically reconnected to the ocean during dam water release or storm flows.

The presence of *N. virginea* was verified by hiking at least 200 m upstream from the river mouth and from sites where bridges crossed each stream or access was easy from roads or trails. When snails were not observed, the next site in an upstream direction was sampled to confirm that populations were absent. The last site where snails were observed was considered the upper limit of the inland extent of distribution and was marked on a topographic map. Based on the surveys, each river was classified as either "snails-present" or "snails-absent". Snails-present rivers were

subdivided into "river mouth populations", "coastal plain populations", and "montane populations" based on the inland extent of snail distribution.

Tests of hypothesis 4a and 4b.—The gradient of each river was obtained using ArcView GIS 3.2 (ESRI, Seattle, Washington) and digital topographic maps provided by the GIS Laboratory of the International Institute for Tropical Forestry (Forest Service, US Department of Agriculture) at San Juan. Only 2 waterfalls and 1 small dam were located in lowland or mid-montane reaches. To test hypothesis 4a, contingency tables and binary logistic regressions were used to compare the presence or absence of *N. virginea* above and below each barrier (Sokal and Rohlf 1995). To test hypothesis 4b, a Kruskal–Wallis test was used to compare river gradient among the snails-present river classifications (river mouth populations: $n = 5$, coastal plain populations: $n = 2$, and montane populations: $n = 6$).

Test of hypothesis 5.—Discharge data for the surveyed rivers was obtained from coastal plain USGS gauges (USGS 2004). Mean annual and monthly discharges were compared among rivers from the 4 climatic regions of Puerto Rico (north, south, west, and east; Daly et al. 2003) using a 1-way ANOVA. A 1-way ANOVA also was used to compare the same variables among rivers that were permanently, seasonally, and episodically connected to the ocean. A χ^2 test was used to compare neritid snail presence among rivers that were permanently, seasonally, and episodically connected to the ocean.

Test of hypothesis 6.—Water chemistry data were obtained from 23 USGS stations (http://nwis.waterdata.usgs.gov/usa/nwis/qwdata) located in lowland and montane sites of 18 rivers to evaluate the importance of river water quality on the regional distribution of *N. virginea*. Only post-1990 data were analyzed because *N. virginea* life span is probably 8 to 10 y (Pyron and Covich 2003, Blanco 2005). Nineteen water-chemistry variables were selected on the basis of the completeness and availability of the historical record and biological relevance. Discriminant Functions Analysis (DFA, Sokal and Rohlf 1995) was used to determine the water-chemistry variables most relevant to snail distribution among and along rivers. Sampling locations with water-chemistry data were grouped into 4 categories: snails absent ($n = 12$), snails present/river mouth ($n = 3$), snails present/coastal plain ($n = 2$), and snails present/montane ($n = 5$). All assumptions of homoscedasticity and normality were tested, and nonnormal data were log-transformed and retested for normality using Kolmogorov–Smirnoff tests. A multivariate analysis of variance (MANOVA) was used to test for differences among these categories considering all water-chemistry variables simultaneously. Multivariate distance among groups was computed as the squared Mahalanobis distance, a multivariate equivalent of Euclidean distance. The DFA was done using only those water-chemistry variables that differed significantly among categories and were least redundant (i.e., low correlation with other variables). A multiple-regression-like model (Fisher's Linear Discriminant Analysis) based on these variables was fitted for each group and used to classify backwards the original river stations into the inland extent of snail distribution groups. The % match between observed and computed classification of rivers was calculated for each group.

Results

Physical features of microhabitats and habitats

At the microhabitat scale in lower Río Mameyes, dominant substrates were cp (26% of all quadrats), c (16%), b (15%), and bc (16%) ($\chi^2 = 20.57$, df = 8, $p < 0.01$; Fig. 3A). Finer substrates such as p, g, and pg were less frequent (<7%). The mixture bcg was scarce (4%). Macrophyte patches were present in intermediate frequency (6%). Substrate type varied with depth (Kruskal–Wallis test, $n = 139$, df = 8, $H = 67.43$, $p < 0.0001$). In general, coarse substrates (b, bc, and bcg) and m were more common in deep (50–100 cm) areas, whereas fine substrates (p and pg) were more common in pool bars. Intermediate-size substrates (c and cp) were found at mid depths (~50 cm).

Mean near-bed water velocity ranged between 0 and 115 cm/s in the riffle, between 0 and 20 cm/s in the pools, and between 0 and 7 cm/s in the marginal high-flow pond (Table 2). Velocity was more variable in time and space in the riffle than in other habitats. Near-bed flow was more turbulent in the riffle ($Re < 10^8$) than in the pools and the pond (Re: $0–10^6$). Near-bed flows were subcritical or nonerosive ($Fr << 1$) in all 4 habitats. However, some areas in the riffle had sustained supercritical flows ($Fr > 1$).

Microhabitat scale

Neritina virginea density was related to substrate type (hypothesis 1; 1-way ANOVA, $F_{8,140} = 2.26$, $p < 0.05$). Mean density was highest (>50 ind/m^2) in b, bc, c, and bcg substrates (Fig. 3B). In contrast, low densities (<50 ind/m^2) were observed more frequently in the finest substrates (cp, pg, g, and p). When density was corrected by substrate abundance (i.e., electivity index), well-mixed substrates (bcg) were preferred over more-uniform substrates (g, m, p, or b; Fig. 3C). Avoidance or negative electivity was observed for the

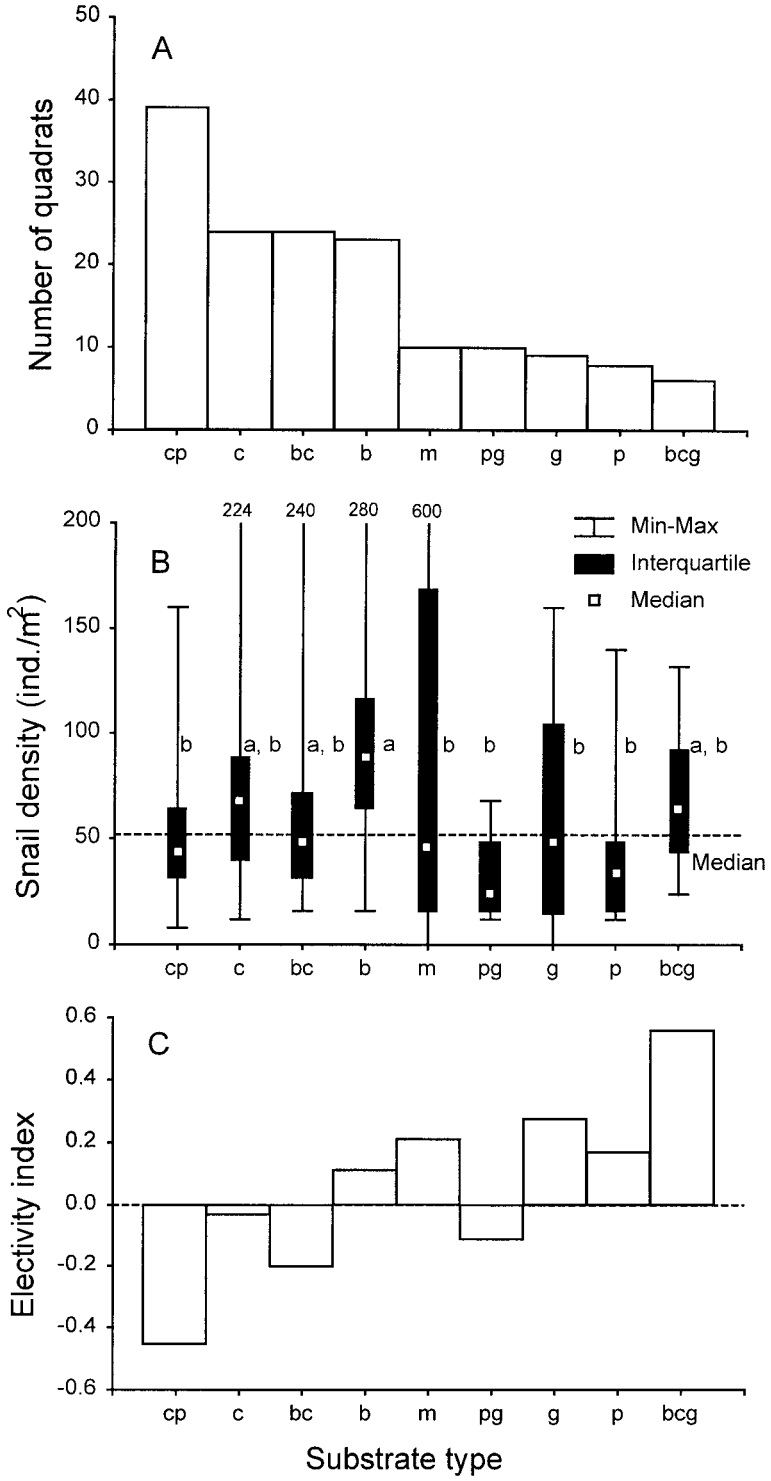

FIG. 3. Number of quadrats with each streambed substrate type (A), *Neritina virginea* density in each substrate type (B), and *N. virginea* electivity for each substrate type (C) at the Route 3 Bridge sampling reach in Rio Mameyes. The horizontal line in B indicates the median density across all substrate types. In B, bars with the same letters are not significantly different. The horizontal line in C indicates no electivity. b = boulder, c = cobble, p = pebble, g = gravel, and m = macrophyte (*Elodea*). Min = minimum, max = maximum.

TABLE 2. Selected physical characteristics (median and range) of 4 habitats in a lower reach in the Río Mameyes. Medians with the same superscript are not significantly different.

Variable	Habitat				Test statistic
	Riffle	Straight pool	Meander pool	Marginal high-flow pond	
Water depth (cm)	30^{c} (14–42)	84^{a} (17–110)	73^{b} (14–105)	58^{b} (22–97)	$F_{3,651} = 75.42$ $p < 0.01$
Near-bed water velocity (cm/s)	8^{a} (0–115)	3^{b} (0–12)	7^{b} (0–20)	2^{b} (0–7)	$H_{3,327} = 83.74$ $p < 0.01$
Near-bed Reynolds number	$1.8 \times 10^{6\ a}$ ($0–1.9 \times 10^{8}$)	$8.3 \times 10^{5\ b}$ ($0–8.2 \times 10^{6}$)	$7.2 \times 10^{5\ b}$ ($0–3.1 \times 10^{6}$)	$6.9 \times 10^{5\ b}$ ($0–6.7 \times 10^{6}$)	$F_{3,323} = 27.02$ $p < 0.01$
Near-bed Froude number	0.08^{a} (0–1.36)	0.02^{b} (0–0.18)	0.02^{b} (0–0.25)	0.02^{b} (0–0.16)	$F_{3,323} = 26.65$ $p < 0.01$

most available substrates (cp, c, bc, and pg). Snails were commonly observed buried in the gravel and pebbles, among macrophyte stems, and on tops of cobbles and boulders.

Habitat scale

Neritina virginea density increased linearly with depth in both pool habitats (hypothesis 2; ANCOVA, $F_{1,132} = 5.81$, $p < 0.05$). However, the regression for the meander pool had the larger correlation index and steeper slope (meander pool: $y = 23.80 + 0.82x$, $r^2 = 0.28$; straight pool: $y = 22.02 + 0.34x$, $r^2 = 0.13$; Fig. 4). Correlations were greatest in both pools during massive migrations (migration period: $r = 0.62–0.93$, nonmigration period: $r = 0.04–0.46$), but an in-depth description of the migration results is beyond the purpose of this paper. The stronger relationship between density and depth in the meander pool apparently was related to an increase in near-bed water velocity with depth ($r = 0.50$, $F_{1,77} = 25.13$, $p < 0.001$) that was not observed in the straight pool ($r = 0.10$, $F_{1,100} = 1.08$, $p > 0.05$).

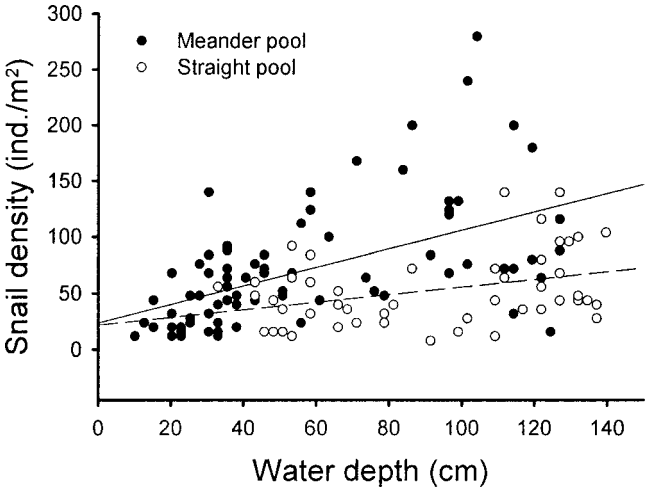

FIG. 4. Variation in *Neritina virginea* density relative to water depth in 2 pool types.

Reach scale

Neritina virginea was observed in areas with laminar to turbulent near-bed flows ($Re = 10^{1}–10^{6}$) and subcritical to supercritical flows ($Fr = 0–1.36$). Large snails preferred habitats with low Re and Fr numbers, whereas small snails preferred more turbulent and erosive habitats. Therefore, snail density was greater in the riffle than in the pools and marginal high-flow pond (hypothesis 3; nested ANOVA, habitat: $F_{20,215} = 2.47$, $p < 0.001$, time × habitat: $F_{3,20} = 12.71$, $p < 0.0001$; median densities = 88, 56, 50, and 20 ind./m^2 in the riffle, 2 pools, and marginal high-flow pond, respectively). Median shell size showed the opposite pattern and was smallest in the riffle, intermediate in the pools, and largest in the marginal high-flow pond (nested ANOVA, habitat: $F_{24,1867} = 4.70$, $p < 0.001$, time within habitat: $F_{3,1867} = 77.23$, $p < 0.0001$; median sizes: 5.8, 9.3, 10.0, and 14.0 mm in the riffle, 2 pools, and marginal high-flow pond, respectively). A power model indicated that snail density and size were tightly related ($y = 4927.5x^{-2}$, $r^2 = 0.62$, $F_{1,28} = 24.8$, $p < 0.001$; Fig. 5), suggesting that the relationship between habitat hydraulics and density is size-dependent.

Stream-network scale

Neritina virginea was present in only 13 of the 32 rivers, and its distribution was similar in the 2001 and 2003 surveys. The inland extent of distribution differed among the 13 snails-present rivers. Populations were restricted to a few tens of meters within the river mouths in 6 rivers. Populations were restricted to coastal plain segments <10 m asl in 2 rivers, to low montane reaches (20–50 m asl) in 3 rivers, and to mid-montane reaches (>50 m asl) in 2 rivers (Fig. 6). Further inland distribution was blocked by high waterfalls in 2 rivers, Sabana (Las Pailas) and Espíritu

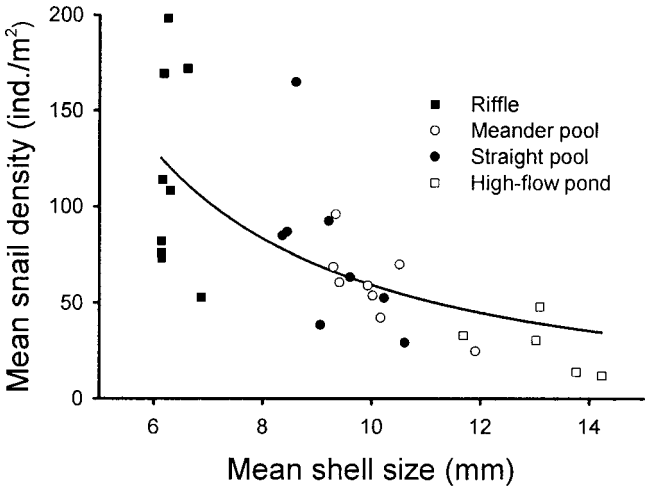

FIG. 5. Relationship between snail density and snail size 4 habitats in the sampling reach.

Santo (Quebrada Sonadora) (concordance = 100%, Kendall's Tau = 1.00), but was not blocked by a low-head dam (<3 m) in lower Espíritu Santo (hypothesis 4a). Inland extent of distribution tended to be greater in rivers with narrow coastal plains and steep montane reaches (i.e., Sabana, Patillas, Guajataca, Espíritu Santo, and Mameyes), but statistical differences were not observed because of high variability of river gradient within categories (hypothesis 4b; Kruskal–Wallis test, $n = 13$, df = 2, $H = 2.60$, $p = 0.27$).

Regional scale

River discharge varied among Puerto Rico's climatic regions (Table 3). Monthly discharge was greater in the west and north compared to the east and south (2-way ANOVA, $F_{3,296} = 77.23$, $p < 0.0001$). Variance in mean monthly discharge was greater in the north, west, and east than in the south (Levene's homogeneity of variance test, $F_{3,296} = 33.61$, $p < 0.0001$). Mean annual discharge had the same pattern as monthly discharge, but annual variability was greater than monthly variability in the south and the north ($CV_{annual} = 220$ and 172%, respectively).

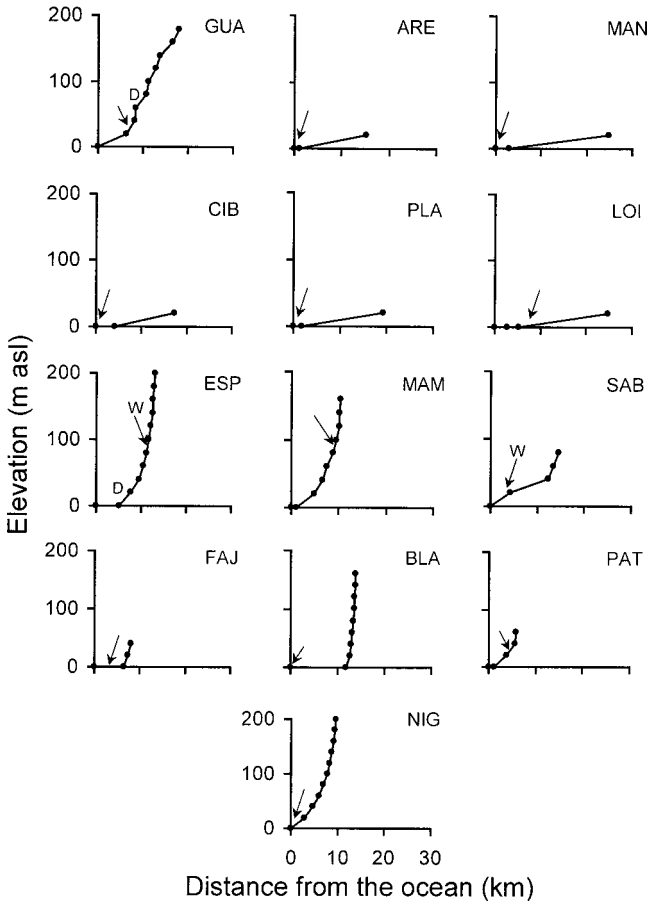

FIG. 6. Inland distribution of *Neritina virginea* relative to stream gradient in different watersheds. Arrows indicate the inland extent of distribution (uppermost distance and elevation at which individuals were recorded). The upper limit of populations coincides with high waterfalls in Sabana and Espiritu Santo. See Fig. 1 for river name codes. Locations of dams and waterfalls are indicated with letters (D and W, respectively).

Discharge also changed with river–ocean connectivity (2-way ANOVA, connectivity: $F_{3,264} = 12.66$, $p <$

TABLE 3. Comparison of mean (range) monthly and annual discharge (m^3/s) among rivers in 3 categories defined by temporal variation in river–ocean connectivity and 4 geographic regions in Puerto Rico. Means with different superscripts are significantly different ($p < 0.05$). – = river connectivity category not found in climatic region.

River–ocean connectivity	Climatic region				Island mean
	North	East	South	West	
Annual discharge (among streams)	5.50^{b} (1.30–14.37)	2.26^{c} (1.97–2.73)	2.29^{c} (1.43–4.20)	9.34^{a} (6.89–11.14)	4.67 (1.27–11.14)
Monthly discharge (within streams)	3.85^{b} (0.08–22.54)	1.78^{bc} (0.27–8.07)	0.90^{c} (0.06–4.01)	7.51^{a} (1.31–19.23)	3.21 (0.06–22.54)
Permanently connected rivers	3.85 (0.39–22.54)	0.63 (0.27–1.12)	1.43 (0.29–4.01)	7.51 (1.31–19.22)	4.04^{a} (0.27–22.54)
Seasonally connected rivers	3.83 (0.08–20.26)	2.36 (0.47–8.07)	0.67 (0.18–1.74)	–	2.88^{a} (0.08–20.26)
Episodically connected rivers	–	–	0.69 (0.06–3.51)	–	0.69^{b} (0.06–3.51)

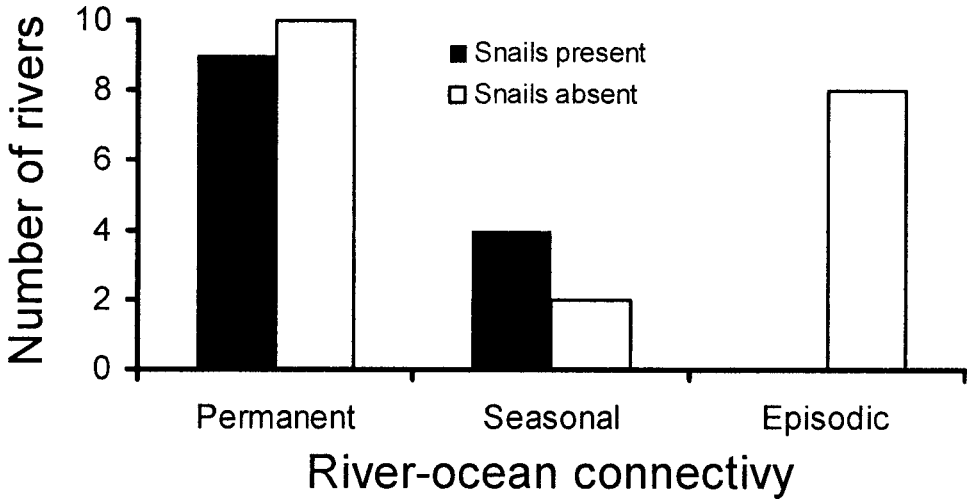

FIG. 7. Presence of populations of *Neritina virginea* in 32 rivers in 3 river categories defined by temporal variation in river–ocean connectivity. Permanent = permanently connected river, seasonal = seasonally connected river, episodic = episodically connected river.

0.0001, month: $F_{11,264} = 1.69$, $p = 0.08$; Table 3). Mean monthly discharge was greater and more variable throughout the year in permanently connected rivers than in episodically connected rivers (Table 3). Mean annual discharge showed greater variation among episodically connected rivers (245%) than among permanently or seasonally connected rivers (151 and 165%, respectively). In the north and east, rivers were permanently or seasonally connected to the ocean. In the west, all rivers were permanently connected to the ocean, but in the south, most of rivers were episodically connected. Nine of the 13 snails-present rivers were permanently connected to the ocean, whereas 4 were seasonally connected (Fig. 7). Snails were absent

TABLE 4. Mean (±1 SD) values for selected water-chemistry variables (data obtained from 23 USGS stations [http://nwis.waterdata.usgs.gov/usa/nwis/qwdata]) in coastal rivers in Puerto Rico. Multiple analysis of variance (MANOVA) *F*-test (df 1,17) results refer to comparisons of snails-present and snails-absent rivers. Some stations were excluded from the MANOVA test because of missing data. MS (marginally significant) = $0.05 < p < 0.20$, NS = $p > 0.20$.

Variable	All rivers ($n = 23$)		Snails-absent rivers ($n = 11$)	Snails-present rivers ($n = 8$)	MANOVA test (p)
	Mean ± SD	Range	Mean ± SD	Mean ± SD	
Temperature (°C)	26.5 ± 1.6	24.1–31.1	26.5 ± 1.9	26.4 ± 1.2	NS
Discharge (m^3/s)	2.6 ± 2.8	0.3–26.6	113.4 ± 123.6	152.8 ± 77.0	NS
Turbidity (NTU)	26.8 ± 25.4	1.9–88.9	36.0 ± 29.3	14.1 ± 10.4	MS
Conductivity (μS/cm)	324.1 ± 144.4	9.8–8541	341.3 ± 138.1	300.4 ± 159.0	NS
Dissolved O_2 (mg/L)	7.3 ± 1.7	3.2–12.4	7.7 ± 2.0	6.6 ± 0.9	MS
Dissolved O_2 saturation (%)	80.3 ± 10.2	34.7–94.2	80.6 ± 11.4	79.8 ± 9.2	NS
pH	7.5 ± 0.3	7.0–7.9	7.6 ± 0.3	7.4 ± 0.2	MS
Acid neutralizing capacity (mg $CaCO_3$/L)	122.4 ± 55.6	32.8–215.9	132.4 ± 49.6	108.7 ± 63.8	MS
Total suspended solids (mg/L)	42.9 ± 42.8	4.6–167.8	57.7 ± 49.9	22.4 ± 18.4	<0.05
NH_4 (mg/L)	0.4 ± 1.0	<0.1–4.4	0.2 ± 0.2	0.6 ± 1.5	NS
$NO_2 + NO_3$ (mg/L)	0.9 ± 0.7	<0.2–2.7	1.0 ± 0.5	0.9 ± 0.9	NS
Total P (mg/L)	0.3 ± 0.5	<0.1–2.16	0.2 ± 0.2	0.3 ± 0.7	NS
Ca (mg/L)	33.00 ± 17.8	7.2–66.8	33.6 ± 12.8	32.1 ± 24.1	NS
Mg (mg/L)	9.5 ± 7.7	3.5–106.4	11.6 ± 9.5	6.7 ± 2.8	MS
Na (mg/L)	17.3 ± 8.7	5.5–732.9	17.2 ± 8.2	17.4 ± 10.0	NS
K (mg/L)	2.4 ± 1.0	<1.0–28.4	2.4 ± 0.6	2.4 ± 1.5	NS
Cl (mg/L)	20.1 ± 10.7	7.6–1591.2	18.6 ± 10.9	22.2 ± 10.7	NS
SO_4 (mg/L)	12.9 ± 8.4	<4.0–233.6	14.6 ± 9.2	10.5 ± 7.0	MS
SiO_2 (mg/L)	24.6 ± 6.8	5.6–35.8	28.4 ± 4.6	19.4 ± 6.0	<0.05

TABLE 5. Mean (±1 SE) values of water-chemistry variables used for forward stepwise Discriminant Function Analysis of rivers with different inland distributions of *Neritina virginea*. Additional variables showing significant or marginal differences among river categories are reported but were not included in the model because of intolerance. *F*-values in bold font are statistically significant ($p < 0.05$). ANC = acid neutralizing capacity, P = total P, TSS = total suspended solids.

Variable	Inland distribution of *N. virginea*				Wilks' lambda	*F*-value (df = 3,13)
	Absent	River mouth	Coastal plain	Mountains		
% of rivers correctly classified by the model	100	100	100	80		
Included in model:						
SiO_2 (mg/L)	28.4 ± 4.6	18.4 ± 0.8	23.3 ± 1.4	17.8 ± 10.2	0.55	**41.1**
ANC (mg $CaCO_3$/L)	132.4 ± 49.6	152.2 ± 30.5	42.4 ± 7.1	109.3 ± 77.8	0.31	**21.3**
P (mg/L)	0.18 ± 0.18	0.16 ± 0.07	0.03 ± 0.01	0.03 ± 0.01	0.26	**17.0**
Not included in model:						
Discharge (m^3/s)	113.4 ± 123.6	130.4 ± 109.2	50.8 ± 4.8	28.2 ± 20.2	0.02	**4.9**
Turbidity (NTU)	36.0 ± 29.3	21.8 ± 14.5	8.8 ± 0.1	9.8 ± 5.1	0.02	**6.8**
Conductivity (μS/cm)	341.3 ± 138.0	382.7 ± 88.9	135.6 ± 19.6	328.0 ± 204.7	0.03	**4.0**
TSS (mg/L)	57.7 ± 49.9	35.3 ± 24.9	14.0 ± 7.4	15.3 ± 11.8	0.02	**9.6**
NH_4 (mg/L)	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.03	3.3
Na (mg/L)	17.2 ± 8.2	16.5 ± 5.8	12.0 ± 1.3	21.9 ± 16.0	0.03	**4.2**
SO_4 (mg/L)	14.6 ± 9.2	13.9 ± 4.6	4.1 ± 0.7	11.2 ± 9.7	0.03	2.7

from all episodically connected rivers (hypothesis 5). Half (10) of the rivers permanently connected to the ocean lacked populations of *N. virginea* (Fig. 7).

The presence of snails in a river was related to hardness and ion concentrations (hypothesis 6). Snails-absent rivers had greater total suspended solids and SiO_2 concentrations than snails-present rivers (Table 4). In addition, water turbidity, dissolved O_2, pH, water acid neutralizing capacity (ANC), Mg, and SO_4 were marginally greater in snails-absent rivers than in snails-present rivers. When these 8 water chemistry variables were considered together, snails-absent and snails-present rivers were marginally different (MANOVA, Wilks' Lambda = 0.33, $F_{8,11} = 2.82$, $p < 0.057$), but after excluding dissolved O_2 and pH, the significance of the model increased (MANOVA, Wilks' Lambda = 0.37, $F_{6,13} = 3.74$, $p < 0.022$).

TABLE 6. Squared Mahalanobis distances between categories of rivers relative to inland distribution of *Neritina virginea*. Distances were computed using water-chemistry variables included in the discriminant function model (Table 5). Values in parentheses are *F*-values associated with differences in water-chemistry values between categories. Bold font indicates significant differences ($p < 0.05$).

	Inland extent of distribution of *N. virginea*		
	River mouth	Coastal plain	Montane
Absent	21.0 (**10.1**)	23.3 (**6.1**)	72.8 (**35.1**)
River mouth		10.3 (2.0)	17.3 (**5.0**)
Coastal plain			23.8 (**4.6**)

The best discriminant function for predicting inland extent of distribution included SiO_2, ANC, and P (Wilks' Lambda = 0.052, $F_{9,31} = 8.33$, $p < 0.0001$; Table 5). The squared Mahalanobis distance computed using these 3 variables showed that water chemistry was significantly different among most of the categories of inland extent of distribution of *N. virginea* (Table 6). SiO_2, ANC, and P were significantly lower in snails-present rivers with montane populations than in snails-present rivers with river mouth or coastal plain populations. Backwards classification of rivers into inland extent of distribution categories using the discriminant function was 95.4% accurate. Although not included in the discriminant function, river discharge, water turbidity, and concentration of total suspended solids were significantly lower in montane reaches colonized by *N. virginea* (Table 5). NH_4 was marginally higher in snails-absent rivers.

Discussion

Scale-specific controls

At the within-reach scale, our results agreed with the existing literature on abiotic controls of invertebrate distributions. At the microhabitat scale, hypothesis 1 was supported: neritids preferred large substrates. Similar results have been obtained in laboratory experiments on French Polynesian neritids (Liu and Resh 1997) and on other lotic species (Moore 1964, Crowl and Schnell 1990, Herrmann et al. 1993, Holomuzki and Biggs 2000). In addition, the greater

preferences of *N. virginea* for heterogeneous patches agree with existing theory regarding the role of microhabitat complexity as flow refugia (Lake 2000).

At the habitat scale, hypothesis 2 was supported: *N. virginea* density increased with water depth. A similar relationship has been reported for freshwater snails in irrigation channels in southern England (Watson and Ormerod 2004) and for fish and shrimp in neotropical streams (Power 1984, Pringle 1996). This pattern seems to be linked to avoidance of shallow areas where terrestrial predators are present (Power 1984, Pringle 1996). Direct evidence is lacking, but predator avoidance also may be also responsible for the presence of adults and the absence of juveniles of *N. virginea* in shallow margins in our study pools (JFB, personal observations).

At the reach scale, hypothesis 3 was supported: habitat hydraulics controlled the distribution of *N. virginea*. This type of control on density and size of diverse snails and insects has been documented extensively (e.g., Holomuzki and Messier 1993, Johnson and Brown 1997), and it is apparently related to predators and competitors (Hart and Finelli 1999), food availability (e.g., Johnson and Brown 1997), and drag force (e.g., Statzner and Holm 1989). Uncovering the mechanism explaining the spatial arrangement of *N. virginea* at the different habitats was not the aim of our study, but the mechanism seems to be mediated by individual size.

At the stream-network scale, hypothesis 4a was partially supported: physical barriers blocked snail movement depending on barrier height. Physical barriers are undoubtedly important for diadromous fauna worldwide, but only 2 waterfalls and 1 low-head dam blocked the upriver migration of *N. virginea* in the rivers we surveyed. Waterfalls and dams in Puerto Rico and elsewhere are more common in montane reaches and apparently have greater influence in blocking the upstream migrations of long-distance swimmers such as fish and shrimp (Pringle 1997). Studies in the Caribbean have documented reductions of large-bodied diadromous fish and shrimp in unaltered headwaters above dams (Puerto Rico: Holmquist et al. 1998, Guadeloupe: Fièvet et al. 2001b). Hypothesis 4b was not supported: *N. virginea* was found in montane reaches of the steepest streams. Other studies have shown that the abundances of diadromous fauna decline upstream because of steep gradients and barriers (Ford 1979, Liu and Resh 1997, McDowall 1998, Joy and Death 2001, Resh 2005).

At the regional and stream-network scales, water quantity and quality were the best predictors of the extent of inland distribution of *N. virginea*. At the regional scale, hypothesis 5 was supported: snails were absent from episodically connected rivers. This absence may be related to both natural and anthropogenic causes. Several rivers from dry southern Puerto Rico have low discharge and become naturally disconnected from the ocean during the dry season. However, many of those rivers also are dammed for agricultural irrigation, and their coastal-plain reaches are permanently dewatered and disconnected from the ocean supply of *N. virginea* larvae. McDowall (1995) recently warned that diadromous fauna such as New Zealand fishes may eventually be extirpated from rivers if the timing of river-mouth closure coincides with periods of larval upstream migration.

At the regional scale, hypothesis 6 was supported: water chemistry had a larger influence than stream gradient (hypothesis 4b) on *N. virginea* distribution. *Neritina virginea* was limited to the river mouth (estuary) or the coastal plain in all urban, lesser-gradient rivers in the northern region of the island, even though those rivers were permanently connected to the ocean. However, *N. virginea* was present in montane reaches of adjacent streams that drained forested and protected areas. A similar situation occurs in Guadeloupe, where the upstream distribution and composition of diadromous assemblages were controlled by land use in the estuaries and the watershed (Fièvet et al. 2001a). Accelerated downstream degradation of water quality is common in the tropics because landuse change is typically greater in the lowland reaches of tropical streams (Ometo et al. 2000, Santos-Román et al. 2003, Soldner et al. 2004). In Puerto Rico, urbanization increases conductivity, P, and Na concentrations in streams (Santos-Román et al. 2003), and deforestation increases fine sediments and decreases leaf litter and dissolved O_2 (Heartstill-Scalley and Aide 2003). Similar effects have been observed in Madagascar (Benstead et al. 2003), Borneo (Iwata et al. 2003), and New Zealand (Townsend et al. 1997, 2003). In addition, high turbidity and high nutrient loads induced by deforestation and urbanization may further accelerate extirpation of *N. virginea* by reducing food resources such as periphyton and biofilm (March and Pringle 2003) and promoting invasion by alien snails, as has been observed in southern Australia (Schreiber et al. 2003). Last, *N. virginea* was naturally absent from limestone watersheds in dry southern Puerto Rico, probably because of the elevated conductivity and high concentrations of dissolved ions (Na, Cl, K, Mg, and SO_4) in water draining limestone. Absence of snails from limestone watersheds has been also reported for neritids from several Southern Pacific islands (Haynes 1993, 2000). Our results at the regional and stream-network scales provide support for the idea that disturbances in

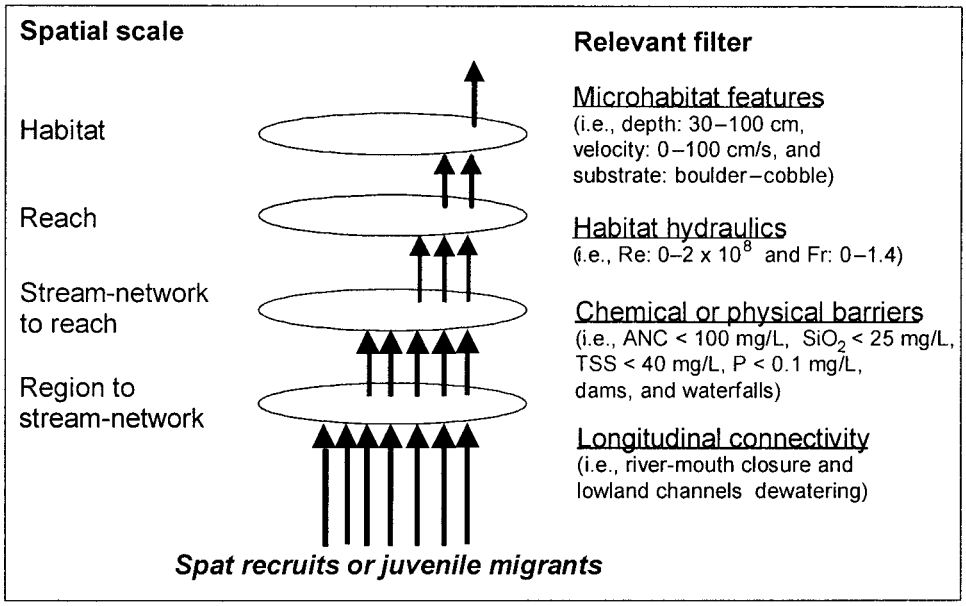

FIG. 8. Relevant landscape filters (sensu Poff 1997) controlling the distribution of *Neritina virginea* at particular spatial scales in Puerto Rican streams. Disks represent filters at specific spatial scales and arrows represent individuals moving across the landscape. Reduction in arrow number indicates exclusion or mortality of individuals because of filters relevant to each scale. Spatial scales are listed from bottom to top in descending order of size. Re = Reynolds number, Fr = Froude number, ANC = acid neutralizing capacity, TSS = total suspended solids.

lowland reaches may propagate upstream by preventing diadromous fauna from colonizing pristine headwater reaches (sensu Pringle 1997).

Hierarchical approach for the management and conservation of diadromous fauna

The analyses presented here indicate that the distribution of *N. virginea* in coastal rivers of Puerto Rico can be explained by a combination of abiotic variables that operate in a descending hierarchical fashion from the regional to the microhabitat scales (Fig. 8). At the regional scale, upriver migration is affected by the river's connectivity with the ocean. Once juveniles enter a particular river that has sufficient connectivity, they must negotiate physical and chemical barriers within the stream network. At the scales of reaches, habitats, and microhabitats within stream networks, hydraulics, water depth, and substrate heterogeneity provide additional influences on their spatial arrangement. At these scales, the abiotic variables controlling neritid snail distribution appear to be environmental clues to other correlated biotic and abiotic factors that deserve further investigation. We are unaware of studies similar to ours that have been done with other benthic organisms, but our hierarchical-scale model based on environmental filters (Fig. 8) presumably is applicable to other diadromous species and geographic locations and can be used to assess and to manage the overall biotic integrity of coastal rivers. Stream managers should consider using *N. virginea* and other freshwater neritids as bioindicators of river connectivity and water quality in lowland reaches because these snails are probably the diadromous fauna most sensitive to physical and chemical landscape filters.

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