

THE SPATIAL ARRANGEMENT OF *NERITINA VIRGINEA* (GASTROPODA: NERITIDAE) DURING UPSTREAM MIGRATION IN A SPLIT-CHANNEL REACH[†]

JUAN F. BLANCO^{a,b,*} and FREDERICK N. SCATENA^{b,c}

^a *Department of Biology, University of Puerto Rico, Rio Piedras, San Juan, PR 00931-3360, USA*

^b *International Institute of Tropical Forestry, USDA Forest Service, San Juan, PR 00926-1119, USA*

^c *Department of Earth and Environmental Sciences, University of Pennsylvania, Philadelphia, PA 19104-6313, USA*

ABSTRACT

This paper relates differences in flow hydraulics between a main channel (MC) and a side channel (SC) of a river to patterns of upstream migration by *Neritina virginea* (Neritidae: Gastropoda), a dominant diadromous snail in streams of Puerto Rico (Greater Antilles). Near-bed water velocity, snail density and shell size were measured on a weekly basis between August and December 2000 along cross-sections in a main channel (MC) and an adjacent channel (SC) under a bridge crossing of the Río Mameyes of Northeastern Puerto Rico. Near-bed velocity and water depth were used to compute Reynolds (Re) and Froude (Fr) numbers, and to classify flows within each channel. During base flow conditions ($<2\text{ m}^3\text{ s}^{-1}$), flow was chaotic and supercritical ($Fr > 1$) in the MC, and non-chaotic and subcritical ($Fr < 1$) in the SC. Higher mean densities ($>100\text{ ind m}^{-2}$) of relatively small snails (mean \pm s.d., $6.3 \pm 2.8\text{ mm}$) were consistently recorded in the MC. Conversely, the SC had lower mean densities ($<20\text{ ind m}^{-2}$) and significantly larger snails ($7.6 \pm 2.4\text{ mm}$). Within the MC, migratory groups preferred near-bed velocities $> 0.8\text{ m s}^{-1}$. Within the SC, they preferred the channel thalweg and depths $> 30\text{ cm}$. The spatial arrangement that was observed between and within the channels may be related to food resources, predation pressure or biomechanics. Characteristics of preferred upstream migration pathways of *N. virginea* must be accounted when building road crossings in coastal streams with diadromous fauna. Published in 2007 by John Wiley & Sons, Ltd.

KEY WORDS: diadromous fauna; neritid snails; hydraulic ecology; habitat selection; tropical streams; Puerto Rico

Received 3 August 2006; Accepted 9 August 2006

INTRODUCTION

Diadromous fauna migrate between marine and stream waters to complete their life cycles and are dominant in number and biomass in tropical islands (Gross *et al.*, 1988). Both catadromous and amphidromous fish, shrimp and gastropods migrate upstream in large aggregations as juveniles or postlarvae (Ford and Kinzie, 1982). Upstream migrations are known in at least 10 gastropod families (Huryn and Denny, 1997). Worldwide, the largest migrations ($>5000\text{ ind m}^{-2}$) have been documented for neritids (Hawaii: Ford, 1979; Costa Rica: Schneider and Frost, 1986; Schneider and Lyons, 1993; Japan: Nishiwaki *et al.*, 1991; Hirata *et al.*, 1992; French Polynesia: Resh *et al.*, 1990, 1992; Liu and Resh, 1997; Puerto Rico: Pyron and Covich, 2003; Blanco and Scatena, 2005). These migrations typically occur within 5 days after a flood and end after nearly a week of continuous upstream movement (Schneider and Frost, 1986; Pyron and Covich, 2003; Blanco and Scatena, 2005). During the migrations, the snails occur in either clusters of migrating individuals or in long trail-like aggregations.

Habitat preferences of resident individuals have been studied in a few species of atyid shrimps and neritid snails (i.e. Johnson and Covich, 2000; Scatena and Johnson, 2001; Blanco and Scatena, 2005, 2006), but their preferred pathways during upstream migrations remain poorly understood. Neritid snails are often referred to as rheophilic due to their preferences for fast-flowing water habitats (Huryn and Denny, 1997). Greater densities of neritids occur in stream riffles than pools in Hawaii (*Neritina granosa*: Ford, 1979; Way *et al.*, 1993), Japan (*Clithon spinosus*:

*Correspondence to: Juan F. Blanco, Instituto de Biología, Facultad de Ciencias Naturales y Exactas, Universidad de Antioquia, Medellín, Colombia. E-mails: jblanco@LTERnet.edu; blanco@exactas.udea.edu.co

[†]This article is a U.S. Government work and is public domain in the U.S.A.

Ohara and Tomiyama, 2000), French Polynesia (*C. retropictus*: Resh *et al.*, 1990, 1992; Liu and Resh, 1997), Salomon and Vanuatu Islands (Haynes, 1993, 2000), Costa Rica (*N. latissima*: Schneider and Lyons, 1993) and Puerto Rico (*N. virginea*: Blanco and Scatena, 2005, 2006). Resident neritid snails also prefer boulders and cobbles over gravel and sand (*N. granosa*: Ford, 1979; *C. spinosus* and *C. retropictus*: Liu and Resh, 1997; Ohara and Tomiyama, 2000; *N. virginea*: Blanco and Scatena, 2006).

This paper studies the distribution of the diadromous snail *Neritina virginea* (Neritidae: Gastropoda) in a split-channel beneath a road crossing to identify the influence of between- and within-channel scale hydraulics on migration. In particular, we compared how mean body size and density of *N. virginea* changed between and within channels during migratory and non-migratory events.

MATERIALS AND METHODS

Study area

This study was conducted in a lower segment of Río Mameyes, which drains the Luquillo Mountains in Northeastern Puerto Rico (Figure 1a). The Río Mameyes is the most pristine, and the only undammed large river on the island. The upper part of the watershed is protected and managed by the US Forest Service (Caribbean National Forest) and is covered by mature cloud and rain forests. The lower elevations of the watershed are covered by pastures and secondary forests. The highest discharges in the year are typically observed during the two rainy seasons of the year (April–May and August–December) and are associated with northern cold fronts, and tropical depressions, respectively. The study area was described in detail in Blanco and Scatena (2005, 2006).

The study site is located at Bridge 1771 of PR Route 3 (18° 22' 27" N, 65° 45' 50" W, elevation: 5 m a.s.l.). This reach is located approximately 1 km upstream from the uppermost limit of brackish water intrusion. During most flows, the study reach is split into two channels by an elevated and stabilized island that formed after the bridge was constructed in 1982 (Figure 1b). Most of the flow is conveyed through the fast and turbulent flows of the main channel (MC). This channel has the general morphology of a riffle and is formed by mid-sized boulders (diameter: <50 cm) and cobbles. This MC is 11 m wide and ~40 cm deep, and has a sloped concrete embankment along its entire right margin under the bridge. The second, or side channel (SC) has the morphology of a straight run and is 3 m wide, and has an average depth of ~30 cm. Flow through this channel is slower and smoother than in the MC. Unlike the relatively uniform geometry of the MC, the SC has a skewed geometry. The deepest part of this channel consists of cobbles, while the shallow part is gravel. The two channels form a uniform reach about 40 m downstream of the bridge (Figure 1b). At this point, snails moving upstream may choose between the two channels. Previous observations indicated that snail density was homogeneous where the study channel is a single thread, and therefore, did not bias upstream habitat selection of migrating individuals (Blanco, 2005).

Sampling and data analysis

The study channels were visited weekly between 15 August and 12 December 2000. Near-bed water velocity was measured at 2 cm above the streambed using a Marsh-McBirney flowmeter. Each velocity measurement was averaged over 30 s and three to five measurements were made at each point. Ten points every 1 m were sampled across the MC. Paired sampling points were measured in five cross sections along SC (Figure 1b). Near-bed velocity and depth were used to compute Reynolds (Re) and Froude (Fr) numbers to characterize flows in both channels (Statzner *et al.*, 1988):

$$Re = U D \nu^{-1} \quad (1)$$

$$Fr = U(g D)^{-0.5} \quad (2)$$

where U is the average of repeated measurements of near-bed velocity at each sampling point, D is the depth of near-bed velocity measurement (2 cm), g is gravity acceleration (9.8 m s^{-2}) and ν is the kinematic viscosity ($1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ at 20°C). Near-bed flows are classified as laminar ($Re < 500$), transitional ($500 < Re < 2000$) or turbulent ($Re > 2000$) and as subcritical ($Fr < 1$) or supercritical ($Fr > 1$). A Two-way Analysis of Variance (ANOVA) was used to compare near-bed velocity, Re and Fr between channels and sampling dates.

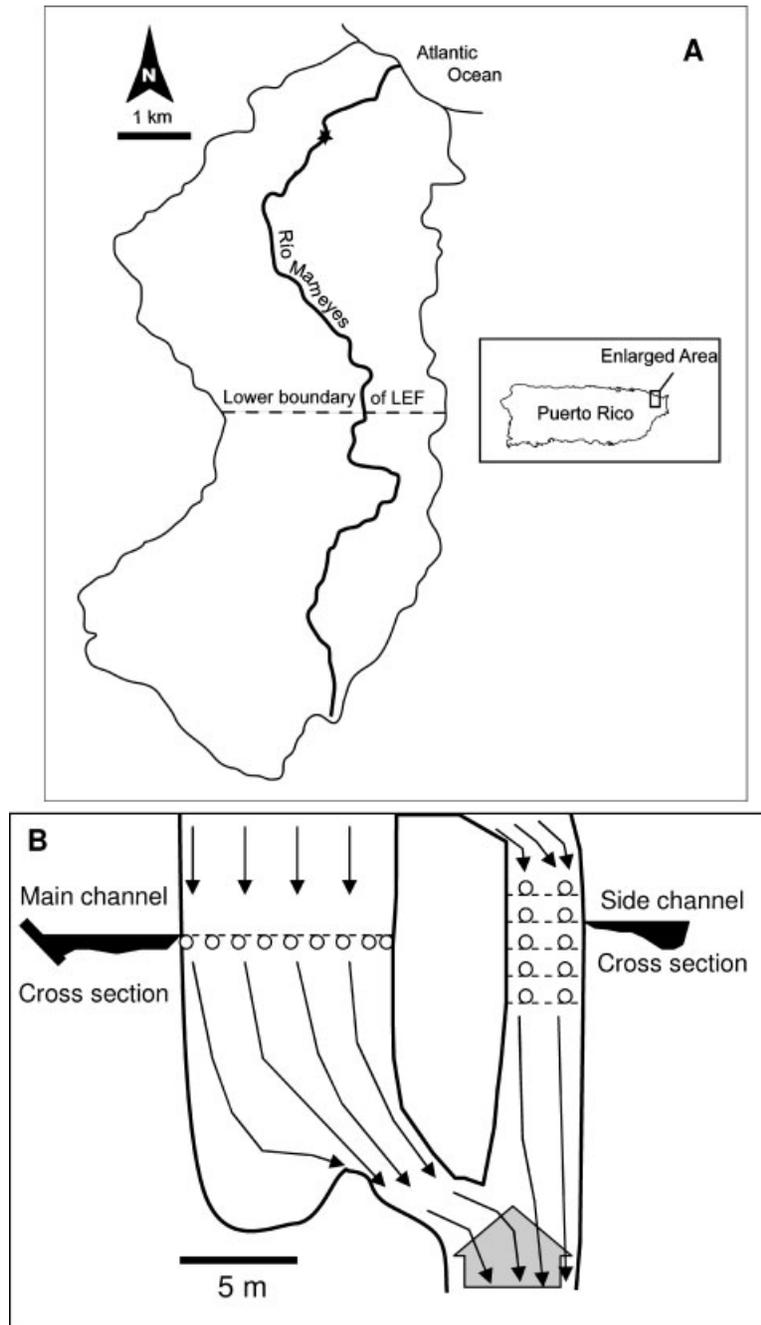


Figure 1. (A) Location of Route 3 bridge at Río Mameyes (star). LEF = Luquillo Experimental Forest. (B) Sampling design. Circles indicate location of sampling plots and velocity measurements in cross sections (broken lines) at main and side channels. Arrows show proximate flow direction. Upstream migrations of snails move against direction of flow (see bottom arrow). Channel length not at scale

Detailed snail sampling was limited to 10 dates when water level was low and visibility was high (see Blanco and Scatena, 2005). On these sampling days, snails on and under rocks were counted within 0.5×0.5 m quadrats ($n = 10$) placed on the streambed. Sampling quadrats were placed ~ 1 m apart across the MC, and in five pairs along the SC (Figure 1b). At the SC, one quadrat of each pair was placed on the thalweg and another on the shallow part.

In addition, a random sample of individuals was collected from each quadrat to measure shell size (see Blanco and Scatena, 2005).

Each sampling date was classified as either a migration or non-migration event. Migratory events were readily identified because small individuals were abundant and aggregated into dense clusters or long trails that persistently moved upstream (Blanco and Scatena, 2005). All massive migrations appeared a few days after spates ($>2 \text{ m}^3 \text{ s}^{-1}$) and increased snail density 2–10 times ($200\text{--}800 \text{ ind m}^{-2}$) over values observed during non-migration periods ($20\text{--}100 \text{ ind m}^{-2}$). During non-migratory sampling periods, the snails were dispersed and rarely forming groups of more than five individuals. Over the study period, there were two migration periods that were related to large channel scouring floods. The first migratory period occurred between 5 September and 3 October 2000. The second period occurred during November 2000. Non-migration periods were scattered between October and December. Detailed temporal patterns and hydrologic correlates of upstream migration events are described in Blanco and Scatena (2005).

To study habitat selection between the two channels, both size and density were log-transformed to reduce variance effect on the mean and meet homocedasticity assumptions of tests. A Two-Way ANOVA was used to test differences of size and density between channels, and between migration and non-migration events (Zar, 1999). A two-way design was preferred over a repeated measures design because (a) sampling quadrats (sampling units) were never placed in the exact same position, (b) sampling quadrats were pooled according to migration and non-migration events and (c) every migration event can be considered as an independent trial where individuals selected upstream pathways in a natural channel-split setting. Homogeneity of variance of untransformed data was tested between channels and migration events using Levene's test.

The spatial arrangement of the snails was studied separately within each channel. Within the MC, microhabitat selection relative to near-bed water velocity was tested. Frequency distribution of near-bed water velocity was used to determine modes (Labonne *et al.*, 2003), and thus microhabitat availability for *N. virginea*. Modes from the first to the fourth interquartile were calculated. Outliers were considered as a fifth category. Snail densities were grouped into the five near-bed velocity categories within each sampling date. The Ivlev's electivity index (Manly *et al.*, 1993) was computed to test microhabitat preferences in *N. virginea*, as follows:

$$I = \frac{r_i - p_i}{r_i + p_i} \quad (3)$$

where r_i is snail density and p_i is availability of near-bed velocity in i -th category. I ranges from +1 (complete preference) to -1 (complete rejection). Homogeneity of density distribution and electivity indices throughout velocity categories was tested using Chi-square tests within each study period.

Within the SC, microhabitat selection was tested relative to both near-bed water velocity and depth. Sampling dates were pooled as migratory or non-migratory events. Although some storm-related streambed scour also occurred in the SC, its geometry remained similar throughout the study. This allowed a comparison of snail density between the thalweg and shallower microhabitats of the channel relative to migratory and non-migratory events. Near-bed velocity and snail density were compared between SC microhabitats and migration events using a Two-way ANOVA.

RESULTS

Hydraulics of the study channels

The two study channels differed in their nearbed hydraulics (Table I). Instantaneous near-bed velocity was more variable in the MC than in the SC, and had a dominance of unsteady and heterogeneous flows (Levene's test: $F_{1, 489} = 11.48$, $p < 0.001$). However, mean near-bed velocity was not significantly different between the channels (mean \pm s.d., MC: $0.30 \pm 0.30 \text{ m s}^{-1}$, SC: $0.27 \pm 0.20 \text{ m s}^{-1}$; $F_{1, 489} = 1.04$, $p = 0.31$). Mean near-bed velocity did change significantly among sampling dates in both channels (Two-way ANOVA: $F_{6, 411} = 768.00$, $p < 0.0001$) and the SC had a larger variation between moderate (Q_{75} , $> 2 \text{ m}^3 \text{ s}^{-1}$, Table I) and low ($< Q_{50}$, $1 \text{ m}^3 \text{ s}^{-1}$) discharges (Two-way ANOVA: channel \times time interaction, $F_{6, 411} = 3.46$, $p < 0.01$). Near-bed flow at both channels was

Table I. Characteristics of the study channels in lower Río Mameyes

Variable	Main channel	Side channel
Bankfull width (m)	11	3
Base flow depth (cm)	30 (10–50)	20 (5–30)
Dominant substrates	Boulder, cobble	Cobble, pebble, gravel
Near-bed water velocity (m s^{-1})	0.15 (0.00–1.00)	0.20 (0.00–0.50)
Reynolds number	3000 (0–20 000)	4000 (0–10 000)
Froude number	0.21 (0–1.14)	0.14 (0–0.86)

Means and ranges are reported for baseflow ($1\text{--}2\text{ m}^3\text{ s}^{-1}$) conditions.

turbulent ($Re > 2000$) at both discharge levels. In contrast, flow at low discharge was subcritical ($Fr < 1$) in the SC and supercritical ($Fr > 1$) in parts of the MC, particularly over the concrete embankment.

Within the MC, the frequency distribution of near-bed water velocity was skewed toward values lower than 0.50 m s^{-1} . Fifty percent of the sampling quadrats exhibited velocities ranging between 0.10 and 0.40 m s^{-1} . Modes from the first to fourth quartiles were 0.05 , 0.15 , 0.30 and 0.60 m s^{-1} , respectively. Outliers were greater than 0.8 m s^{-1} and were most frequently observed on the concrete embankment. Within the SC, near-bed velocity was normally distributed, but significantly greater in the thalweg than at the shallow area of the channel ($F_{1, 14} = 6.97$, $p < 0.05$).

Snail density and size patterns between channels

Significant differences in both shell size and snail density of *N. virginea* were observed between the MC and the SC (Figure 2). Mean snail size was smaller in the MC than in the SC (mean \pm s.d., MC: $6.3 \pm 2.8\text{ mm}$, $n = 940$, SC: $7.6 \pm 2.4\text{ mm}$, $n = 299$; Two-way ANOVA: $F_{1, 1235} = 101.96$, $p < 0.0001$). Moreover, the smallest individuals ($< 3\text{ mm}$) were always observed at the MC, while the largest individuals ($> 10\text{ mm}$) were predominantly observed in the SC (Figure 2a). Mean shell size was significantly smaller during migration events in both channels ($F_{9, 1235} = 40.54$, $p < 0.0001$). However, the greatest change in shell size relative to migration events occurred in the SC (interaction factor: $F_{1, 1235} = 40.81$, $p < 0.0001$). Dispersion around the mean shell size was significantly narrower in the MC than in the SC, particularly during upstream migration events (Levene's test: $F_{1, 1235} = 76.13$, $p < 0.001$).

Mean snail density was 6.5 times higher in the MC than in the SC (mean \pm s.d., MC: $115.7 \pm 118.4\text{ ind m}^{-2}$, $n = 86$, SC: $17.8 \pm 33.8\text{ ind m}^{-2}$, $n = 78$; Two-way ANOVA: $F_{1, 159} = 161.14$, $p < 0.0001$). In addition, mean snail density changed significantly between migratory and non-migratory events ($F_{8, 159} = 6.29$, $p < 0.05$). During migration events, snail density was 2–10 times greater than during non-migratory periods (200–800 and 20–100 ind m^{-2} , respectively). The interaction factor was significant ($F_{1, 159} = 0.35$, $p < 0.05$).

Snail density patterns within channels

Within the MC, the snails were not homogeneously distributed and more snails were consistently observed in specific areas of the cross section (Figure 3a). During the first migration period, the greatest densities were observed in areas on the concrete embankment or areas in the centre of the channel where near-bed velocities exceeded 0.60 m s^{-1} ($\chi^2 = 61$, $n = 5$, $p < 0.001$). During the second migration period, greater density was also observed on the concrete embankment, but a large migratory aggregation was also observed in the centre of the channel where velocities were 0.15 m s^{-1} ($\chi^2 = 84$, $n = 4$, $p < 0.001$). During non-migration events, density was nearly similar across the entire MC, though very few snails were observed at 0.60 m s^{-1} ($\chi^2 = 65$, $n = 5$, $p < 0.001$). When the availability of microhabitats based on near-bed velocity categories was considered, greater electivity was observed for areas with velocities $> 0.80\text{ m s}^{-1}$, regardless if there were migratory (both periods pooled: $\chi^2 = 40.9$, $n = 5$, $p < 0.001$) or non-migratory ($\chi^2 = 38.5$, $n = 5$, $p < 0.001$) periods (Figure 3b). Near-bed velocities within the interquartile range ($0.10\text{--}0.40\text{ m s}^{-1}$) were either slightly selected or rejected ($I \pm 0.3$). Electivity for $> 0.8\text{ m s}^{-1}$

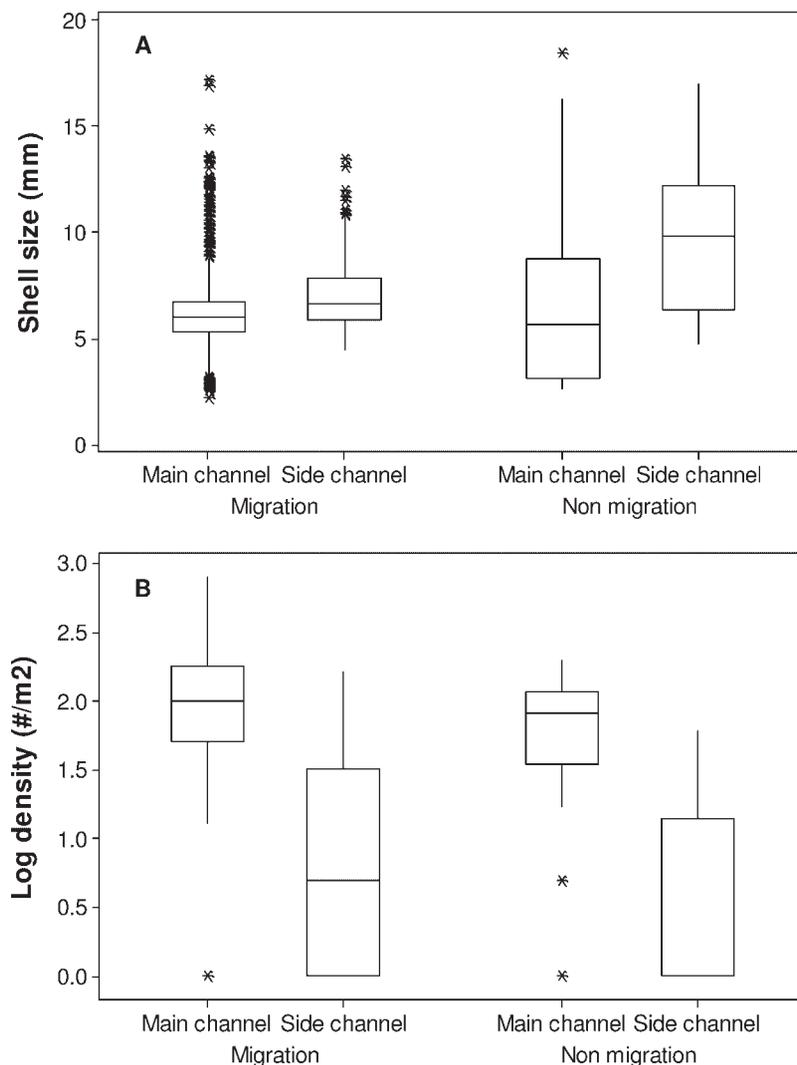


Figure 2. Box plots comparing shell size (A) and snail density (B) between channels and migration events

was slightly reduced during non-migration events because large clusters or long trails did not occur on the concrete embankment and preference for velocities around 0.60 m s^{-1} was increased.

Snail density in the SC dropped to nearly zero during non-migration dates ($F_{2, 98} = 34.75$, $p < 0.001$). When snails did migrate through the SC, they were nine times more abundant in the thalweg than in the shallow areas (Figure 4; $F_{1, 98} = 19.88$, $p < 0.001$). Near-bed velocity was consistently slower in the thalweg ($0.17 \pm 0.10 \text{ m s}^{-1}$) compared to shallow areas ($0.31 \pm 0.10 \text{ m s}^{-1}$) (Figure 4).

DISCUSSION

In general, small ($< 8 \text{ mm}$) *N. virginea* migrated through fast and turbulent flows in the MC. Larger individuals ($> 7 \text{ mm}$) migrated through the slower velocity, smoother flows in the thalweg of the SC (Figure 5). It is worth noting that the sloping concrete embankment of the MC seemed to facilitate migration by allowing the formation of long

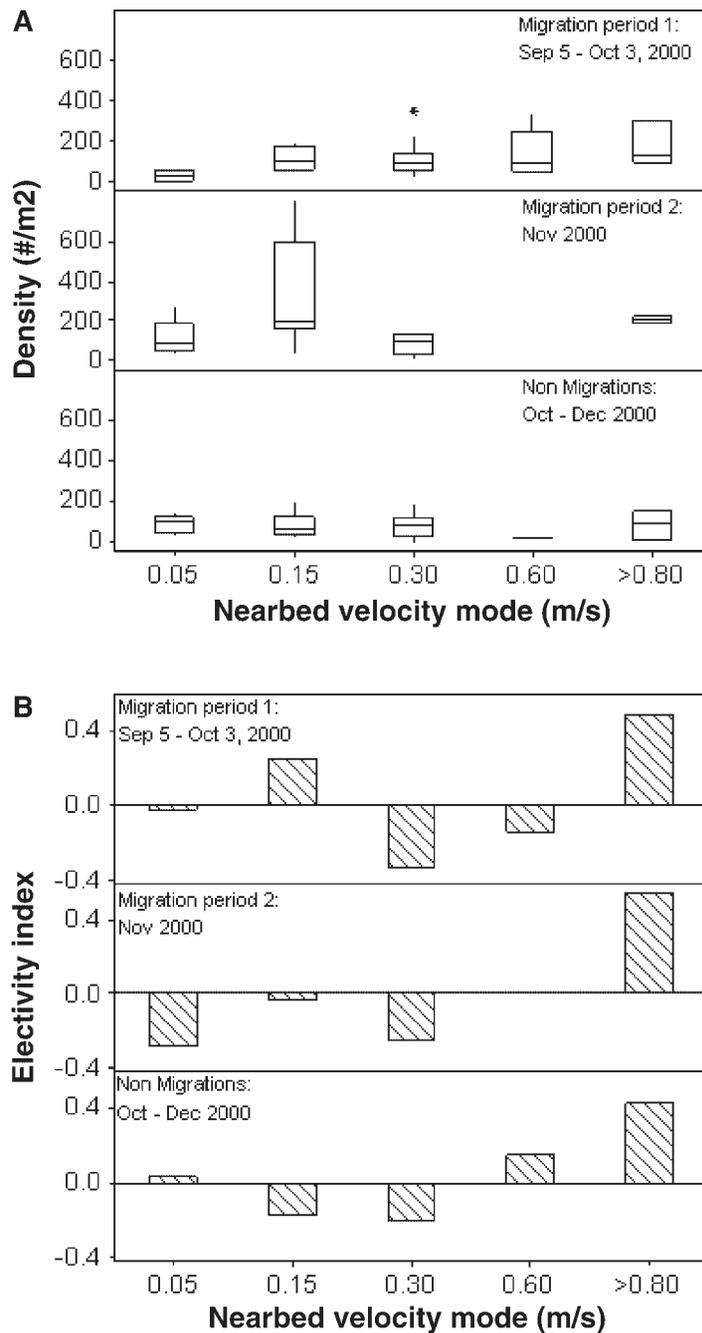


Figure 3. Density distribution (A) and electivity (B) relative to various near-bed velocity categories within main study channel. Data are shown to migration and non-migration events

trails of snails. Similar trails of migrating postlarval shrimp also occurred along the embankment (J. F. Blanco, *personal observations*) and are probably facilitated by snail trails (T. Crowl and D. Kikkert, Utah State University, *personal communication*). These results confirm that rheotactic behaviour in neritid snails occurs in migrating individuals as well as resident individuals (Blanco and Scatena, 2006). However, they also demonstrate that rheotactic behaviour is better expressed in juveniles than adults.

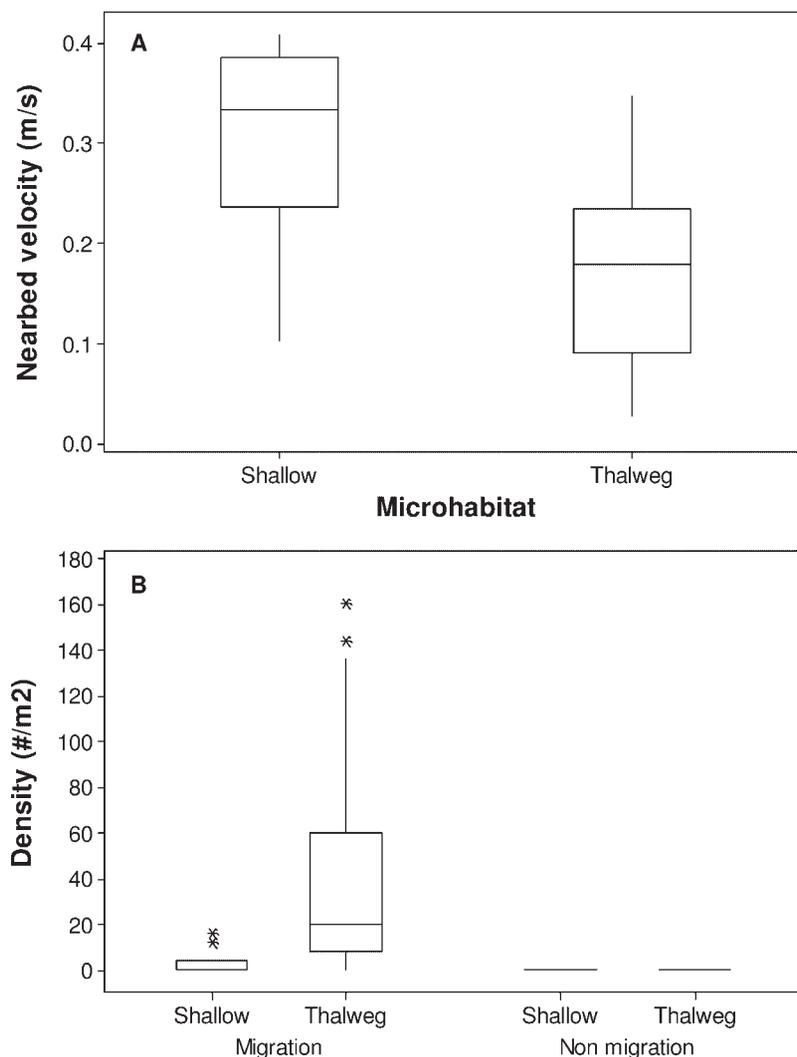


Figure 4. Near-bed velocity (A) and snail density (B) relative to shallow and thalweg microhabitats within side study channel

Mechanisms explaining the observed patterns of between- and within-channel spatial arrangement of migrating individuals were not directly studied but may include the availability and type of food, predation risk and biomechanical factors. Primary production and the content of nutritious compounds in periphyton are usually greater in riffles than slow-flow habitats (Lane, 1991; Johnson and Brown, 1997). Algal biomass and turnover for grazing neritid snails may be greater in the MC because the fast and turbulent flows reduce sedimentation. Predation risk can also be a factor in causing the selection of faster flowing areas because eleotrid fishes, well-documented predators of neritid snails (Corujo-Flores, 1980; Alpirez *et al.*, 1984; Teixeira, 1994; Resh *et al.*, 1999), are usually more abundant in slow-flowing reaches of the Río Mameyes (Nieves, 1998). In addition, terrestrial and visual aquatic predators such as birds, freshwater crabs and palaemonid shrimps may also be less effective in riffles. Ford (1979) reported that some birds foraged upon *N. granosa* in Hawaiian streams, and suggested that individuals in slow-running waters might avoid shallow areas where terrestrial predators are more likely to forage. Similarly, in headwater stream pools in Puerto Rico, atyid shrimps are reported to avoid shallow areas due to the presence of various terrestrial predators (Pringle, 1996).

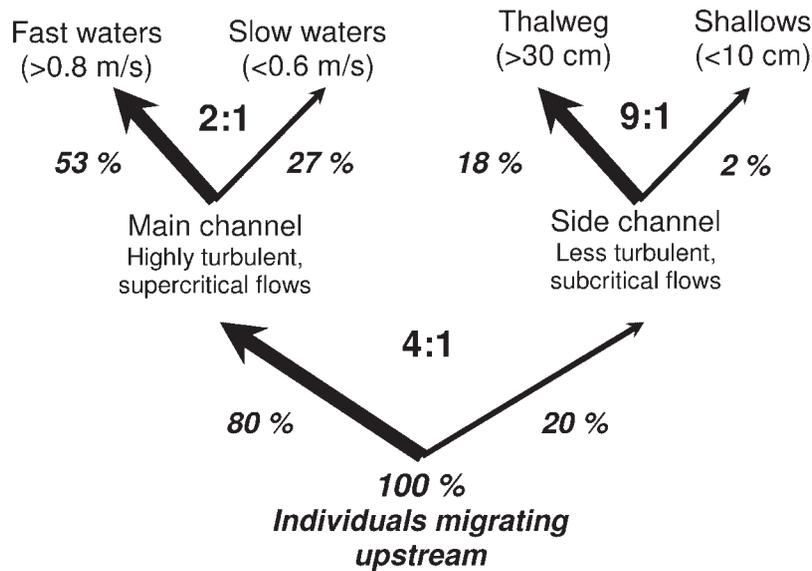


Figure 5. Hypothesized decision tree for *N. virginea* during upstream migrations. Ratios are proportional to mean densities. Percentages represent the proportion of individuals choosing specific conditions

Stream hydraulics can also exert additional influences on *N. virginea*, particularly upon large individuals. It is known that micro-scale forces experienced by benthic invertebrates under fast flows influence their distribution and directional movement (Huryn and Denny, 1997; Hart and Finelli, 1999). Large snails (>8 mm) were more abundant on slow and subcritical flows in the SC suggesting that they may experience greater drag and lift under supercritical flows in the MC. Narrower size range of individuals migrating through the MC, particularly close to the water mark on the concrete embankment provides further evidence that supercritical and turbulent flows impose biomechanical constraints to upstream movements in large individuals. Scaling of drag and lift with body size has been experimentally demonstrated in gastropods and insects (Statzner, 1988; Statzner and Holm, 1989). Measurements of microvelocities around lotic snails demonstrate that individuals inevitably enter into turbulent flow layers and experience greater drag force as they grow, regardless of streamlining (Statzner, 1988; Statzner and Holm, 1989; Way *et al.*, 1993). Future study on the biomechanics of snail migration movement relative to sizes and flow would be valuable as shown for Hawaiian neritids (Way *et al.*, 1993) and other stream gastropods (Statzner, 1988; Statzner and Holm, 1989; Huryn and Denny, 1997).

CONCLUSIONS

Neritid snails such as *N. virginea* show marked habitat and microhabitat preferences as both migrating and resident individuals. These preferences are proximately related to hydraulic characteristics. Therefore, human and natural alterations of channel morphology or hydraulics can influence the spatial arrangement of migrating snails between and within channels. These influences need to be considered in the design of instream structures associated with roads. In this particular study, a concrete embankment facilitated the migration of small individuals in long trails, but might impose constraints to larger individuals. This study also demonstrated that migrating individuals of *N. virginea* naturally preferred near-bed velocities greater than 0.8 m s^{-1} , Fr numbers greater than 1 and Re numbers between 10^3 and 10^4 . Designs with vertical embankments, shallow, rectangular or sand filled channels will not provide suitable microhabitats and will be greater barriers or filters to migration. Ecologically sound designs should avoid these extremes and offer greater habitat and microhabitat diversity.

ACKNOWLEDGEMENTS

This research was funded by Cooperative Agreement 00-CA-11120101-004 between the International Institute of Tropical Forestry (USDA-Forest Service) and the University of Puerto Rico, Río Piedras, and was designed to support the Long-Term Ecological Research Program at Luquillo Experimental Forest, Puerto Rico. NSF Biocomplexity Project 'Modeling complex interactions of overlapping river and road networks in a changing landscape' provided postdoctoral funding for Juan F. Blanco while writing this paper. Andres García, Samuel Moya and Brynne Brian kindly provided transportation to the field site. Alonso Ramírez, Eric Benbow, Vincent Resh and Brick Fevold reviewed early drafts. Discussions with Dan Schneider, Alan Covich and Alberto Sabat helped to expand some of the ideas presented in the manuscript. Reviews from James Gore, Jim Layzer and two anonymous referees are greatly acknowledged.

REFERENCES

- Alpirez O, Ureña JM, Brenes R. 1984. Hallazgo de un depredador de *Neritina latissima* (Gastropoda: Neritidae) en el río Punta Mala, Costa Rica. *Revista de Biología Tropical* **32**: 159–160.
- Blanco JF. 2005. Physical habitat, disturbances, and the population ecology of the migratory snail *Neritina virginea* (Gastropoda: Neritidae) in Puerto Rico streams. PhD Dissertation, University of Puerto Rico, Río Piedras, Puerto Rico.
- Blanco JF, Scatena FN. 2005. Floods, habitat hydraulics and upstream migration of *Neritina virginea* (Gastropoda: Neritidae) in Northeastern Puerto Rico. *Caribbean Journal of Science* **41**: 55–74.
- Blanco JF, Scatena FN. 2006. Hierarchical contribution of river-ocean connectivity, water chemistry, hydraulics, and substrate to the distribution of diadromous snails in Puerto Rico streams. *Journal of the North American Benthological Society* **25**: 82–98.
- Corujo-Flores IN. 1980. A study of fish populations in Espíritu Santo River estuary. MSc thesis, University of Puerto Rico, Río Piedras, Puerto Rico.
- Ford JI. 1979. Biology of a Hawaiian fluvial gastropod *Neritina granosa* Sowerby (Prosobranchia: Neritidae). MSc thesis, University of Hawaii, Honolulu, Hawaii.
- Ford JI, Kinzie RA. 1982. Life crawls upstream. *Natural History* **91**: 60–67.
- Gross MR, Coleman RM, McDowall RM. 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**: 1291–1293.
- Hart DD, Finelli CM. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* **30**: 363–395.
- Haynes A. 1993. The gastropods in the streams and rivers of four islands (Guadalcanal, Makira, Malaita, and New Georgia) in the Solomon Islands. *The Veliger* **36**: 285–290.
- Haynes A. 2000. The distribution of freshwater gastropods on four Vanuatu Islands: Espíritu Santo, Pentecost, Efate and Tanna (South Pacific). *Annals du Limnologie* **36**: 101–111.
- Hirata T, Nishiwaki S, Ueda H, Tsuchiya Y, Sato T. 1992. Seasonal changes in moving activity of *Clithon retropictus* (Prosobranchia: Neritidae). *Venus* **51**: 57–66.
- Hurn AD, Denny MW. 1997. A biomechanical hypothesis explaining upstream movements by the freshwater snail *Elimia*. *Functional Ecology* **11**: 472–483.
- Johnson PD, Brown KM. 1997. The role of current and light in explaining the habitat distribution of the lotic snail *Elimia semicarinata* (Say). *Journal of the North American Benthological Society* **16**: 545–561.
- Johnson SL, Covich AP. 2000. Day and night differences in freshwater shrimp foraging activity as related to instream flow. *Regulated Rivers: Research and Management* **16**: 91–99.
- Labonne J, Allouche S, Gaudin P. 2003. Use of a generalized linear model to test habitat preferences: the example of *Zingel asper*, an endemic endangered percid of the River Rhône. *Freshwater Biology* **48**: 687–697.
- Lane JM. 1991. The effect of variation in quality and quantity of periphyton on feeding rate and absorption efficiencies of the snail *Neritina reclinata* (Say). *Journal of Experimental Marine Biology and Ecology* **150**: 117–129.
- Liu HTT, Resh VH. 1997. Abundance and microdistribution of freshwater gastropods in three streams of Moorea, French Polynesia. *Annals du Limnologie* **33**: 235–244.
- Manly BFJ, McDonald LL, Thomas D. 1993. *Resource selection by animals. Statistical design and analysis for field studies*. Chapman and Hall: New York.
- Nieves LO. 1998. Ecological study of the freshwater stream fishes of the upper Mameyes River (Bisley) in the Luquillo Mountains of Puerto Rico. PhD Dissertation. George Mason University, Virginia.
- Nishiwaki S, Hirata T, Hueda H, Tsuchiya Y, Sato T. 1991. Studies in the migratory direction of *Clithon retropictus* (Prosobranchia: Neritidae) by marking-recapture method. *Venus* **50**: 202–210.
- Ohara T, Tomiyama K. 2000. Niche segregation of two coexisting freshwater snail species, *Semisulcospira libertina* (Gould) (Prosobranchia: Pleuroceridae) and *Clithon retropictus* (Martens) (Prosobranchia: Neritidae). *Venus* **59**: 135–147.
- Pringle CM. 1996. Atyid shrimps (Decapoda: Atyidae) influence spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. *Freshwater Biology* **35**: 125–140.

- Pyron M, Covich AP. 2003. Migration patterns, densities and growth of *Neritina punctulata* snails in Río Espíritu Santo and Río Mameyes, Northeastern Puerto Rico. *Caribbean Journal of Science* **39**: 338–347.
- Resh VH, Barnes JR, Craig DA. 1990. Distribution and ecology of benthic invertebrates in the Opunohu river catchment, Moorea, French Polynesia. *Annals du Limnologie* **26**: 195–214.
- Resh VH, Barnes JR, Benis-Steger B, Craig DA. 1992. Life-history features of some invertebrates in a French Polynesian stream. *Studies on Neotropical Fauna and the Environment* **27**: 145–153.
- Resh VH, Moser M, Poole M. 1999. Feeding habits of some freshwater fishes in streams of Moorea, French Polynesia. *Annals du Limnologie* **35**: 205–210.
- Scatena FN, Johnson SL. 2001. Instream-flow analysis for the Luquillo Experimental Forest, Puerto Rico: Methods and analysis. IITF General Technical Report 11. Río Piedras, Puerto Rico. Forest Service-USDA.
- Schneider DW, Frost TM. 1986. Massive upstream migrations by a tropical freshwater neritid snail. *Hydrobiologia* **137**: 153–157.
- Schneider DW, Lyons J. 1993. Dynamics of upstream migration in two species of tropical freshwater snails. *Journal of the North American Benthological Society* **12**: 3–16.
- Statzner B. 1988. Growth and Reynolds number of lotic macroinvertebrates: a problem for adaptation of shape to drag. *Oikos* **51**: 84–87.
- Statzner B, Holm TF. 1989. Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. *Oecologia* **78**: 145–157.
- Statzner B, Gore JA, Resh VH. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* **7**: 307–360.
- Teixeira R. 1994. Abundance, reproductive period and feeding habits of eleotrid fishes in estuarine habitats of northeast Brazil. *Journal of Fish Biology* **45**: 749–761.
- Way CM, Burky AJ, Lee MT. 1993. The relationship between shell morphology and microhabitat flow in the endemic Hawaiian stream limpet (Hihiwai), *Neritina granosa* (Prosobranchia: Neritidae). *Pacific Science* **47**: 263–275.
- Zar JH. 1999. *Biostatistical Analysis*. Prentice Hall, Inc.: New Jersey.