Caribbean Journal of Science, Vol. 39, No. 3, 338-347, 2003
Copyright 2003 College of Arts and Sciences
University of Puerto Rico, Mayagüez

Migration Patterns, Densities, and Growth of *Neritina punctulata* Snails in Rio Espiritu Santo and Rio Mameyes, Northeastern Puerto Rico

MARK PYRON[1] AND ALAN P. COVICH[2]

[1]*Department of Biology, Ball State University, Muncie, IN 47306, USA*
[2]*Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523 USA*
Email address for corresponding author: mpyron@bsu.edu

ABSTRACT.—Snail size-frequency distributions in Rios Espiritu Santo and Mameyes, which drain the Luquillo Experimental Forest, Puerto Rico, showed that *Neritina punctulata* with shell lengths greater than 30 mm were the most abundant size class at upstream sites. The highest densities for all size classes were at the downstream sites. Growth rates were 0.015 mm/day for a large cohort (~25 mm shell length) and 0.035 mm/day for a small (~15 mm shell length). Minimum longevity estimates range from 3 to 7 years. Size distribution data suggest that snails migrate upstream. An August mark-recapture study resulted in most snails remaining at the release site, and some moved downstream. The greatest upstream distance reached was 200 m in 12 weeks. In a May mark-recapture study, when snails were observed moving in aggregations, the greatest distance moved was 200 m in 27 days, suggesting seasonality in movements and reproduction. Movement rates of snails in aggregates in May were between 0.08 and 0.17 cm/s. All of the snails marked in May moved upstream, and none were observed downstream from, or at the release site. We suggest that upstream movements can be explained by snails avoiding increased predation in the downstream reaches of these rivers from fishes, crustaceans, and birds.

INTRODUCTION

Distribution patterns (Krieger and Burbanck 1973), life history variables (Miller-Way and Way 1989), and ecosystem functions (Hill 1992; Hill et al. 1992) were described for temperate freshwater snails, but few tropical freshwater snail studies are available for ecological comparison. Additional tropical studies are necessary for comparisons of tropical and temperate streams or faunas. Comparisons of ecological patterns are useful to understand ecosystem functioning (Covich 1988).

Ecological patterns studied in snails include: distributions, migrations, and growth. Movement or migration patterns were observed in temperate marine snails (e.g., Tankersley 1989; Vaughn and Fisher 1992), temperate lotic snails (e.g., Krieger and Burbanck 1973), and tropical lotic snails (e.g., Schneider and Frost 1986; Resh et al. 1992; Brasher 1997; Myers et al. 2000; McIntosh et al. 2002). Schneider and Lyons (1993) observed *Neritina latissima* snails migrating hundreds of meters upstream in a Costa Rican stream over a two week period. Other studies of neritid snails found similar migration patterns using marked individuals (Nishiwaki et al. 1991) and upstream/downstream distribution (Shigemiya and Kato 2001).

Snail growth has been examined in numerous temperate ecosystems including: marine (Frank 1969), inland streams (Miller-Way and Way 1989), and coastal streams (Shigemiya and Kato 2001). These studies resulted in substantial variation between species (Powell and Cummins 1985) and evidence that snails can be long-lived in coastal streams (Shigemiya and Kato 2001) or marine ecosystems (Frank 1969). Similar comparisons are not available for snails in tropical coastal streams.

Puerto Rico has a low diversity of freshwater snails (van der Schalie 1948) that have not been studied, other than brief notes (e.g., Ferguson 1959). Conservation of these and other aquatic organisms is vital. Puerto Rico is similar to other Caribbean islands where there are increasing difficulties to supply freshwater to inhabitants. Rio Espiritu Santo has a major water diversion which prevents above-ground freshwater to reach the estuary (and presumably snail larvae) during extreme low-water conditions (Benstead et al. 1999). Rio Mameyes has a major water diversion, however it does not restrict movement of aquatic organisms. A congener snail in Hawaii (*Neritina granosa*) requires estuarine (or perhaps marine) salinity levels for larval development (Ford 1979), suggesting similar requirements for neritids in Puerto Rican streams.

We examined the distribution, movements, and growth of *Neritina punctulata* snails in two streams that drain the Luquillo Experimental Forest (LEF), Puerto Rico. This study was designed to identify if similar migration and life history patterns occur in Puerto Rican coastal streams as was observed in other coastal streams (Schneider and Lyons 1993; Shigemiya and Kato 2001).

MATERIALS AND METHODS

Study area

We sampled two streams (Rios Espiritu Santo and Mameyes) that drain the LEF (Luquillo Experimental Forest), part of a national forest in eastern Puerto Rico (Fig. 1). These streams have unimpacted drainage areas in the headwaters within the LEF and extremely variable flow that fluctuates with rainfall in the upper watershed. One of them (Espiritu Santo), as most of the rivers in Puerto Rico, has low dams for small water diversions (Benstead et al. 1999). Stream gradients are low in the coastal plain and become steeper at higher elevations. Upstream of the estuaries in these rivers the common snails are *Neritina punctulata* and *Thiara granifera* (March et al. 2002). *Neritina clenchi,* synonymous with *N. virginea* (Cosel 1984; Diaz and Puyana 1994), occurs primarily in the estuary. *Neritina punctulata* and *T. granifera* are dominant grazers on the algal community of the Rio Mameyes (March et al. 2002). Juan F. Blanco (University of Puerto Rico Rio Piedras) verified *N. punctulata* identifications. *Thiara granifera* was introduced from the Orient (Abbott 1952) and reported in Puerto Rico about 1954 (Harry and Aldrich 1958).

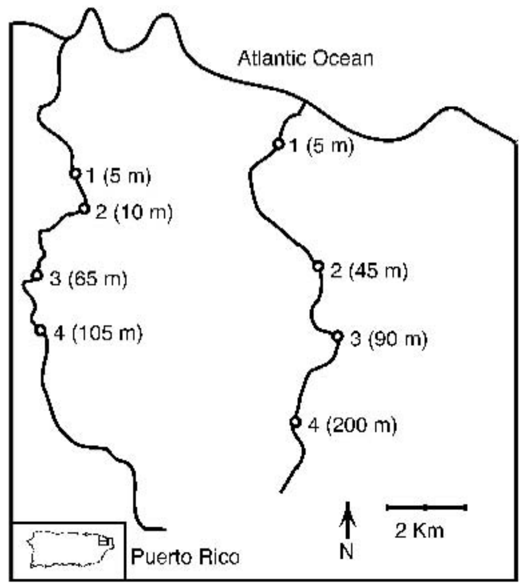

FIG. 1. Location of sites (open circles) sampled for snails. Elevations are in parentheses.

Size and density distribution

We chose four sampling sites per stream based on access, e.g., proximity to bridges or roads, except for the most upstream sites—selected as higher elevation sites that had snail eggs present. For stream elevational segments of 50 m, we calculated the gradients of the two rivers from USGS topographic maps with 10 m contour intervals. In both streams cursory visual surveys were conducted up to the next upstream waterfall above the highest elevation site where snails were located. We collected all sizes of *N. punctulata* that occurred in our quadrats. *Neritina punctulata* snails were collected haphazardly, by hand for at least 30 minutes at each site, and the maximum shell length of each was measured to the nearest 0.1 mm with dial calipers. Collections were made in Rio Espiritu Santo in October 1994 and May 1995, and in Rio Mameyes in December 1994 and May 1995. We estimated densities in May 1995 with three to seventeen, 0.25 m^2 square quadrats per site. Cohorts were visually identified from frequency histograms. Increased quadrat samples were necessary with upstream distance sites to effectively locate snails. Since snails were scattered throughout the substrata at lower elevation sites, we excavated by hand to 5 cm within quadrats to effectively sample all snails. Exact quadrat locations were not resampled. At the lowest site on Rio Espiritu Santo, we sampled snails on the upstream wall of a low-water dam. During the course of the study the stream portion immediately downstream of the dam contained brackish water. *Thiara granifera* were easily separated from *N. punctulata* at all sizes.

Movement of marked individuals

On the Rio Espiritu Santo at site three (elevation = 65 m), we marked 290 *Neritina punctulata* with numbered tags made of plastic flagging (five mm diameter, attached to the shell with cyanoacrylate glue). Within eight hours of capture, marked snails were released at one location within the capture pool on 7 and 10 August 1994. They were observed for 27 days during the following 15 weeks. A single diver located marked snails by underwater observations; starting at the release site and moving upstream and downstream until no marked snails were located in a 50 m interval. The distance from the release site and snail tag number were recorded on a dive slate. We compared sizes of snails (based on original size data) that moved more than 20 m upstream to those that did not move, or moved less than 20 m, with a two-tailed t-test (all snails observed during the study). We calculated correlation coefficients between the distance moved each day and time since release. A 20 m upstream movement at this site required snails to climb a 2-3 m falls.

In May 1995, aggregates of medium-sized snails (~15-25 mm) were observed moving upstream 50 m above site three. We marked 307 of these individuals with tags (different color from the previous experiment) and made observations on three days (3, 9, and 27 days from release). At this same site and on the same day, a group of 20 unmarked snails were observed to move 30 cm on a large boulder in the pool. They moved on established mucus trails. The 20 snails were measured and the relationship between snail size and speed examined with a regression.

During the study period, daily discharge was obtained from a USGS website (http://waterdata.usgs.gov/nwis) based on a gage station on the lower Rio Espiritu Santo. Mean discharge was compared between the two periods with a t-test and discharge patterns were visually examined for relationships with snail movements.

Growth rate

On 9 September at site three of Rio Espiritu Santo, we collected, marked, and released 956 *N. punctulata*. Tags were 5 mm circles from flagging tape, but not individually numbered. On 3 November, 8 December, and 8 February we recaptured and measured maximum shell lengths for as many marked snails found by searching up- and downstream. We identified generations of snails by examining frequency histograms for cohorts of each collection date. Growth rates were estimated as the difference between cohort average shell length in the three recapture dates.

RESULTS

Gradient, snail size and density distribution

At elevations below 150 m the vertical profile of the Rio Mameyes channel is steeper than that of the Rio Espiritu Santo, although the latter is steeper at higher elevations. The gradients of Rio Mameyes and Rio Espiritu Santo above the highest elevation where snails were found were 0.10 and 0.25, respectively.

We found *N. punctulata* adults and egg cases at all sampled sites (Fig. 1). *Thiara granifera* was present at all sites except in the farthest upstream site of both rivers (Fig. 1). Based on visual surveys, *N. punctulata* was absent at elevations greater than 105 m and 200 m in Espiritu Santo and Mameyes rivers, respectively. Absolute densities of *N. punctulata* were not significantly different among sites in the two rivers (Table 1). The highest densities were at the lowest sites and decreased rapidly with upstream distance.

We found a linear increase in mean size of *N. punctulata* with site distance from the ocean (Fig. 2). In the Rio Espiritu Santo, mean sizes of snails ranged from 5.3 mm at site one (five m elevation) to 32.8 mm at site four (105 m elevation; Fig. 3). At least five size classes (cohorts) were distinguished from the size-frequency histograms (assuming longitudinal continuity of the populations), with modes at 4, 11, 17, 22, and 33 mm (Fig. 3). The farthest upstream that *N. punctulata* were found was 15.3 km from the ocean (elevation of 105 m) in Rio Espiritu Santo. In our May 1995 resampling of Rio Espiritu Santo, similar size distributions were found at the two lowest sites, but a smaller mean size of *N. punctulata* was found at upstream sites (Fig. 3).

In Rio Mameyes we observed a similar pattern of mean snail size that increased with river distance upstream (Fig. 4). Five size classes were separated from the size-frequency histograms, although not as distinct as in Rio Espiritu Santo (possibly due to smaller sample sizes). *Neritina punctulata* was present at the most upstream station sampled, 10.7 km from the estuary (elevation of 200 m) in Rio Mameyes. The May 1995 resampling of Rio Mameyes resulted in similar mean size to those from December 1994 (Fig. 4).

Movement of marked individuals

We recaptured 274 of the 290 snails that were marked in August 1994, over the following 15 weeks, for 1140 observations on 27 days. Water clarity allowed observations only between rain events. Thus, there were several weeks in which we could not observe snails. Seventy percent of the marked snails that were observed the first week following tagging remained at the release site during the second week, as did most of the snails (between 40 and 60%) the following weeks. The maximum upstream distance for a recaptured snail was 200 m, in week 12. The mean (± SD) upstream movement for observed snails was 16.1 m (±35.6) over the 15 weeks. A significant correlation was found between mean total distance moved per day from the release site and time since release ($r = 0.40$, $P < 0.04$, $n = 26$ observation days). A negative (downstream) mean movement was recorded on the last observation day (day 104 after release), perhaps due to the low number of observations ($n = 32$). The greatest mean movement rate was 0.81 m/day, on day eight for the August 1994 marking. Several snails were observed to move downstream, but none were found farther than 20 m downstream of the release site. Mean shell size (± SD) of 77 snails, that moved upstream more than 20 m, was not significantly different ($\overline{X} = 25.4 \pm 4.1$ mm) from 198 snails ($\overline{X} = 24.4 \pm 4.2$) that remained at the marking site or moved less than 20 m ($t_{273} = -1.8$, $P < 0.08$).

Snails marked in May 1995 moved more rapidly than those marked in August 1994, reaching 200 m upstream of the marking

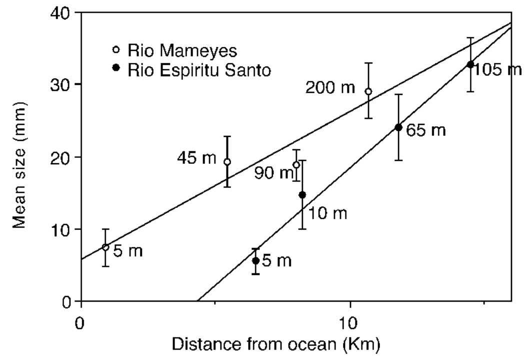

FIG. 2. Regressions of mean snail size against distance from the ocean for sites of Rios Mameyes and Espiritu Santo. Equations are $Y = 5.89 + 2.04X$ ($R^2 = 0.92$) and $Y = -13.9 + 3.24X$ ($R^2 = 0.98$), respectively. Elevations are listed next to each site.

TABLE 1. Mean (±SD) numbers by site of *Neritina* punctulata per 0.25 m^2 quadrat for two Puerto Rico rivers. Comparisons were adjusted for tablewise error rate ($\alpha = 0.0125$).

	Rio Espiritu Santo	Rio Mameyes	t-statistic$_{df}$ (P)
Site 1	116 (18)	82 (74)	1.2_7 (0.35)
Site 2	20 (9.4)	10 (4.9)	1.6_{18} (0.13)
Site 3	9.8 (13)	16 (12)	-1.2_{26} (0.25)
Site 4	0.93 (1.4)	8.7 (2.5)	-2.4_{28} (0.02)

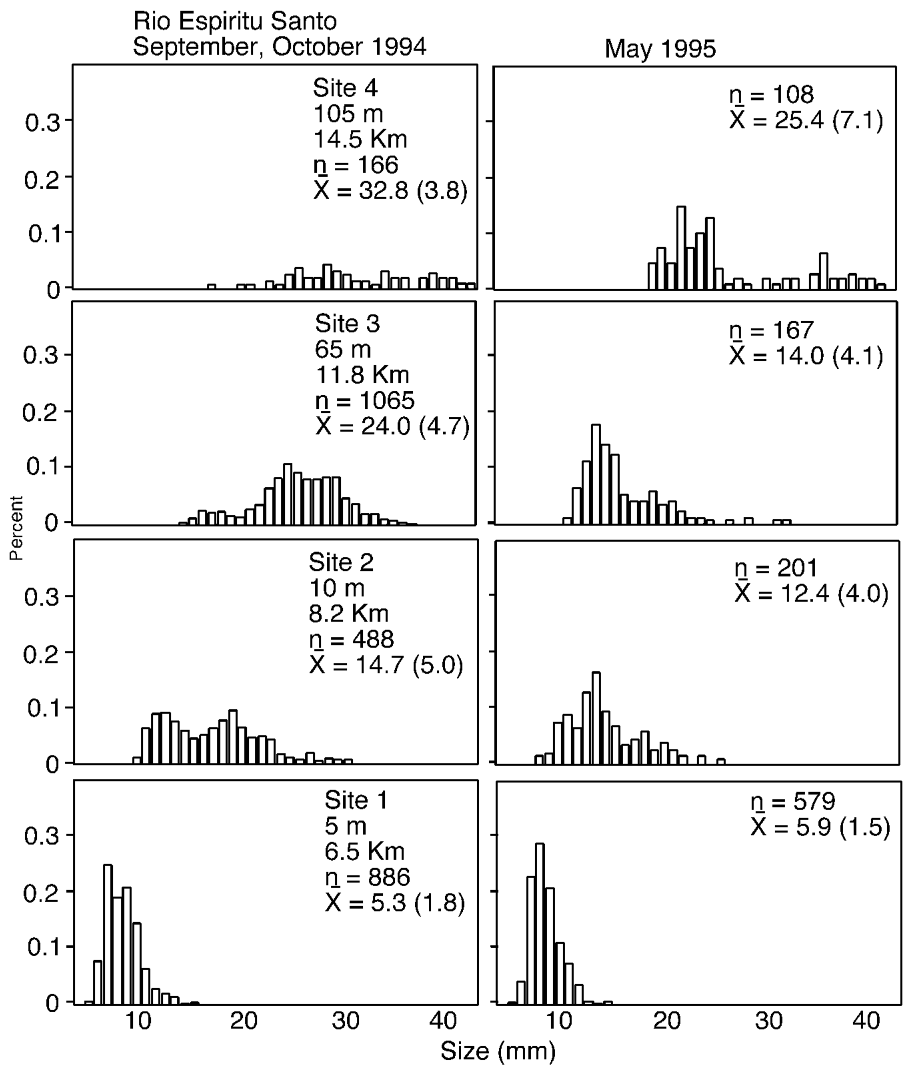

FIG. 3. Length frequency histograms of *Neritina punctulata* from Rio Espiritu Santo for the fall of 1994 and spring of 1995. Elevation, distance from ocean, sample size, and mean size (± SD) are listed for each site.

site within 27 days (Table 2). The greatest mean movement rate was 7.3 m/day, on day nine. None of the marked snails were observed downstream of the release site. Snails marked in 1995 were smaller than those marked in 1994 (12.39 ± 2.9 and 24.0 ± 4.7 mm, respectively). This difference may have resulted from including only snails that were observed moving in aggregates. No aggregated snails were observed in 1994, and all snails captured were marked. Mean daily discharge of Rio Espiritu Santo was not significantly higher in May ($\overline{X}$ = 0.96 ± 1.4 m^3/s) than in the Fall of 1994 ($\overline{X}$ = 0.92 ± 1.6 m^3/s; $t_{139} = 0.14$, $P = 0.89$; Fig. 5).

In May 1995 we observed twenty snails, with an average size [± SD] of 11.8 [± 1.6] mm, move an average of 0.14 cm/s (SD = 0.02); these snails moved in a line. Snail size and speed were negatively correlated ($r = -0.46$, $P < 0.037$). At the range of movement rates we observed (0.08 – 0.17 cm/s) daily movement range is predicted to be 6.9 to 15 m. With continuous upstream movement at constant maximum speed it would take an individual 2.7 years to reach the

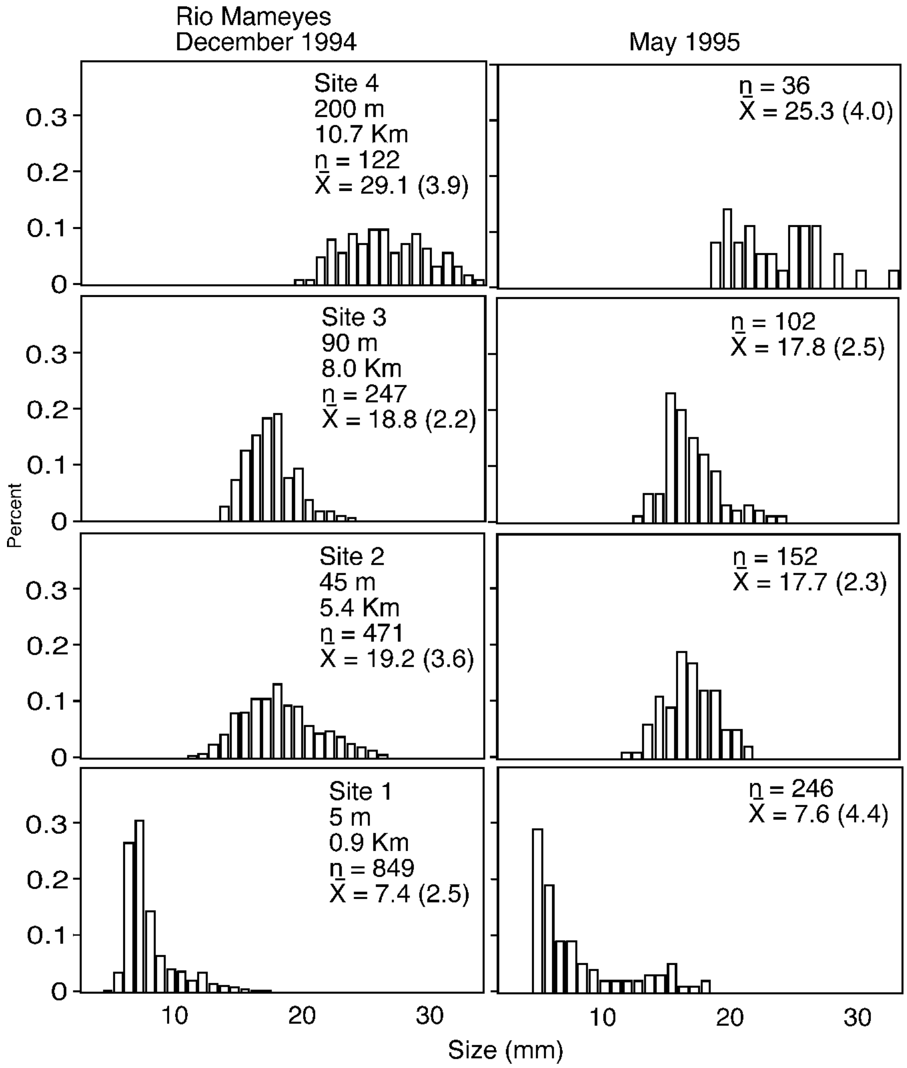

FIG. 4. Length frequency histograms of *Neritina punctulata* from Rio Mameyes for the fall of 1994 and spring of 1995. Elevation, distance from ocean, sample size, and mean size (± SD) are listed for each site.

uppermost sites (areas) where *N. punctulata* are in Rio Espiritu Santo (14.5 km from the estuary).

Growth rate

A histogram of marked individuals, at site three on Rio Espiritu Santo, revealed two distinct cohorts that we separated visually for growth estimates. Average growth rates between September 1994 and February 1995 for *N. punctulata* were 0.035

TABLE 2. Comparison of snail movements experiments between August 1994 and May 1995. The number of days from release, in parentheses, refers to the experiment in all 1995.

Days from release	Mean ± SD (m)		t-statistic, df (one-tailed)	P
	Fall 1995	Spring 1995		
3 (3)	0.3 ± 4.1	12.9 ± 8.1	$^{t}69 = -8.6$	0.0005
9 (10)	8.2 ± 18	65.9 ± 28	$^{t}63 = 7.9$	0.0005
27 (34)	8.5 ± 26	64.0 ± 77	$^{t}91 = -40$	0.0005

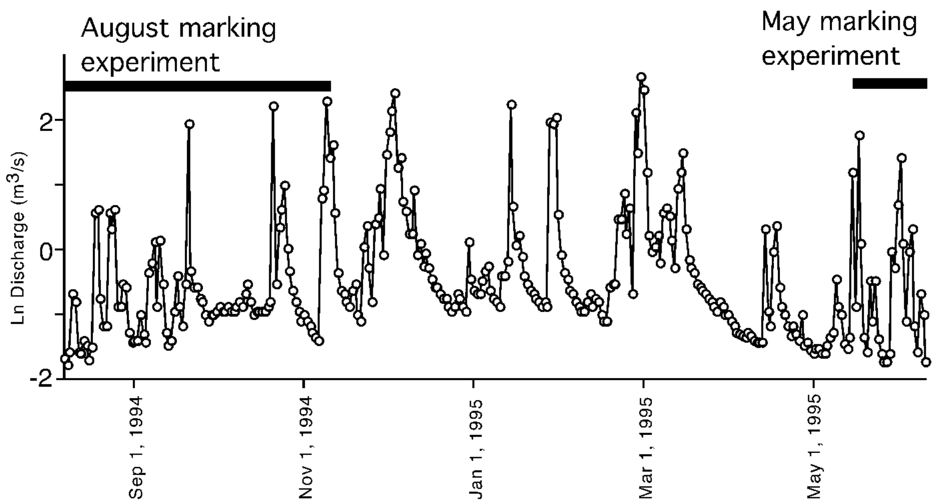

FIG. 5. Daily discharge for Rio Espiritu Santo during the study period. Data obtained from a USGS gage station at Rio Grande.

mm/day and 0.015 mm/day for the 15 and 25 mm length cohorts, respectively. When these growth rates are projected over the entire snail life, longevity is predicted to range from 3.1 to 7.3 years to reach a size of 40 mm. This is a minimum estimate because growth rates decrease with size in most snails (Vermeij 1993). The average shell size of individuals recaptured for growth rate was always larger than the mean shell size of all individuals marked (Fig. 6).

DISCUSSION

Our results indicate a trend for larger snails to occur with increasing upstream distance. This trend is similar to the pattern observed by Schneider and Lyons (1993) for *Neritina latissima* in Costa Rica. Schneider and Lyons (1993) proposed a graphical model to explain the upstream migration of *N. latissima* in Costa Rica, based on a similar size distribution pattern along a stream. The model was driven by changes in predation risk with upstream/downstream position, energetic costs of movement, and size of individuals: large snails occupy a size refuge and thus have a low susceptibility to predation, and are expected to remain in a given location; intermediate-sized snails have a higher susceptibility to predation and a moderate cost of moving upstream and are expected to continually move upstream; small snails achieve a higher fecundity by moving to a midstream location, to lower their predation risk while minimizing energy spent in migration. When the Puerto Rican snails reach a maximal location in the stream—perhaps stopped by waterfall barrier or by a lack of food material—they may be approaching longevity limits for this species.

Neritina punctulata snails were abundant from the estuary to maximum elevations of 200 m in Rio Mameyes and 105 m in Rio Espirito Santo. A strong gradation of sizes from downstream to upstream was similar to *Neritina granosa* from Hawaii (Ford 1979) and *Clithon retropictus* from Japan (Shigemiya and Kato 2001). The largest *N. granosa* that Ford (1979) found were 49 mm, comparable to snails we collected at the upstream site in Rio Espiritu Santo (Fig. 2). However, Ford (1979) found more within site overlap in sizes for *N. granosa* than we found in these rivers. The streams that Ford (1979) sampled were shorter and had steeper gradients than the rivers we sampled in Puerto Rico; perhaps resulting in clustering of snails that were attempting to move upstream.

Our data demonstrated that *N. punctulata* individuals have an upstream migration

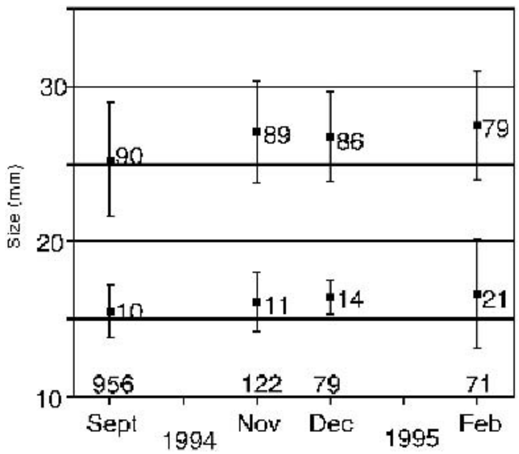

FIG. 6. Mean sizes of two cohorts of *Neritina punctulata* at site three in Rio Espiritu Santo. Error bars are standard deviations. The numbers to the right of squares are the percentages recaptured for that cohort. Numbers above the sampling dates are sample sizes.

pattern with a seasonal component; we never observed aggregated groups of snails moving upstream in the fall 1994 marking experiment. Schneider and Lyons (1993) and Hodges (1992) observed similar aggregation patterns. Intermediate-sized snails appear to migrate more than large snails as in *C. retropictus* (Shigemiya and Kato 2001). This size difference and seasonality pattern is also apparent from comparisons of the size-frequency histograms in Rio Espiritu Santo. There is a bias toward higher frequencies of smaller individuals in the May sample. Snails marked in 1995 were smaller than the snails marked in 1994. There was a difference in movements of individuals marked in May compared with movements of the snails we observed in an aggregation in May. The aggregated snails moved more rapidly. We do not have an explanation for this pattern of rapid movements of individuals in aggregates. Seasonal differences in movements are likely linked to differences in flow—peak flows tend to be in May-June and September-November (Covich et al. 2003).

Upstream movement is apparently interrupted either by a waterfall barrier that cannot be climbed, or perhaps because the river becomes too small to provide a critical habitat requirement (e.g., minimum flow or grazing base). Snails congregated beneath waterfalls in lower reaches of both rivers, as observed in Hawaii for *N. granosa* (Ford 1979). Rios Espiritu Santo and Mameyes have waterfalls higher than 5 m (estimated) upstream of the maximum location where snails were found (MP, pers. obs.). However, there was no evidence that snails were in higher abundance below these upstream waterfalls.

One possible problem with our marking study is that tags might inhibit movements. We did not test this; however we think that tags of 5 mm diameter, with negligible mass are not likely to obstruct movements of even the smallest individuals that we marked. This study did not have the problem of not recovering large numbers of marked individuals (Gowan et al. 1994). We recovered 95% of the marked individuals. An additional problem with our study was our visual approach to estimate the number of cohorts, which may introduce biases in growth estimates.

There are a number of potential predators in the Puerto Rican streams. Freshwater crabs (*Epilobocera sinuatifrons*) were observed carrying *N. punctulata* snails in lower reaches of the Rio Espiritu Santo (MP, pers. obs.). Hamilton (1976) demonstrated that *Callinectes sapidus* crabs are predators of *Littorina irrorata* (Say 1822) snails in an intertidal zone, and Vermeij (1978) and Vermeij and Covich (1978) reviewed many additional examples of crab predation on snails. Shrimp species are also potential predators; *Macrobrachium* spp. prey on *Neritina* snails in Hawaii (A. Brasher, pers. comm.). Freshwater fishes in the Puerto Rican rivers (sleeper, *Gobiomorus dormitor;* and mountain mullet, *Agonostomus monticola;* March et al. 2002) are also potential predators of snails; additional fish predators are present in the estuaries. An eleotrid (sleeper) fish species, *Eleotris pisonis,* prey mainly on neritid snails in estuaries of Brazil (Teixeira 1994). Ford (1979) observed birds foraging on snails in Hawaii streams, although they are present in both upstream and downstream locations (A. Brasher, pers. comm.). In the Puerto Rican streams, birds are the only potential predators present in both upstream and downstream locations. Our study supports the importance of predation at lower elevations suggested by Schneider and Lyons (1993).

Our shell-length growth data for *N. punctulata* showed that small individuals grow at a faster rate than larger individuals as is typical for snails (Vermeij 1993). Average growth rates of our snails (0.015 and 0.035 mm/day) were comparable to temperate snail growth rates of 0.03 mm/day found by Miller-Way and Way (1989) in *Leptoxis dilatata*. Our growth data suggest a minimum longevity between 3 and 7 years, and our size-frequency plots suggest at least 6 years. However, our estimates assume that growth rate at this location is representative of growth at all sites. Further, our growth estimates were based on visual separation of cohorts (individual growth rates could not be estimated because the tags were not individually numbered). This approach assumes that the individuals we recaptured were representative of all marked individuals. If we tended to recapture more large individuals than small individuals our growth results are over estimates. Huryn et al. (1994) found similar longevity ranges for four species of *Elimia* snails in Alabama streams. The longevity estimates we found are not as long-lived as the neritid, *Clithon retropictus*, that inhabits a coastal stream of Japan and with longevity of up to 12 years (Shigemiya and Kato 2001).

In summary we found that the largest individuals of *N. punctulata* in two streams of eastern Puerto Rico are at the most upstream sites. Our data indicate this pattern is the result of seasonal upstream migration of small-medium sized snails. Growth and longevity estimates for *N. punctulata* in Rios Espiritu Santo and Mameyes are in similar ranges as for other snail species. We suggest that future research into likely causes for upstream migration might test: 1) if predation is higher downstream; 2) if productivity varies from downstream to upstream; or for 3) variation among adults and juveniles in tolerance of physical parameters such as salinity or temperature. Assuming that *N. punctulata* in Puerto Rico require estuary connections for larval development, these connections between the estuary and upstream reaches need to be maintained to avoid local extinctions.

Acknowledgements.—We thank Margie Pyron for field assistance and personnel of the El Verde Field station for frequent help. The following persons provided critical reviews of earlier drafts: Juan Felipe Blanco, Anne Brasher, Carlos Santos, Dan Schneider, and Caryn Vaughn. Mark Pyron was supported by the International Institute of Tropical Forestry (Rio Piedras, Puerto Rico) and NSF grant DEB-9306758 to Alan P. Covich.

Literature Cited

Abbott, R. T. 1952. A study of an intermediate snail host (*Thiara granifera*) of the Oriental lung fluke (*Paragonimus*). Proc. U.S. Nat. Mus. 102:71-117.

Benstead, J. P., J. G. March, C. M. Pringle, and F. N. Scatena. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. Ecol. Appl. 9:656-668.

Brasher, A. M. 1997. Life history characteristics of the native Hawaiian stream snail *Neritina granosa* (hihiwai). Cooperative National Park Resources Study Unit, Hawaii. Studies Unit Technical Report 114. 46 pp.

Cosel, R. von. 1984. Moluscos de la región de la Cíenaga Grande de Santa Marta (Costa del Caribe de Colombia) An. Inst. Inv. Mar. Punta de Betín 15-16:79-370.

Covich, A. P. 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. J. N. Am. Benthol. Soc. 7:361-386.

Covich, A. P., T. A. Crowl, and F. N. Scatena. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. Freshwater Biol. 48:1199-1206.

Díaz, J. M., and M. Puyana. 1994. Moluscos del Caríbe colombiano. Un catálogo ilustrado. COLCIENCAS—Fundacíon Natura—Invemar. Santafé de Bogotá. 291 pp.

Ferguson, F. F. 1959. Intraspecific predation in a Puerto Rican neritid snail. Trans. Amer. Micr. Soc. 78:240-242.

Ford, J. I. 1979. Biology of a Hawaiian fluvial gastropod *Neritina granosa* Sowerby (Prosobranchia: Neritidae). MSc thesis, University of Hawaii, Honolulu, Hawaii: 94 pp.

Frank, P. W. 1969. Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia 2:232-250.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: A paradigm lost? Can. J. Fish. Aquat. Sci. 51:2626-2637.

Hamilton, P. V. 1976. Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). Bull. Mar. Sci. 26:403-409.

Harry, H. W., and D. V. Aldrich, 1958. The ecology of *Australorbis glabratus* in Puerto Rico. Bull. World Health Org. 18:819-832.

Hill, W. R. 1992. Food limitation and interspecific competition in snail-dominated streams. Can. J. Fish. Aquat. Sci. 49:1257-1267.

Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit primary productivity. Can. J. Fish. Aquat. Sci. 49:504-512.

Hodges, M. H. 1992. Population biology and genetics of the endemic Hawaiian stream gastropod *Neritina granosa* (Prosobranchia: Neritidae): implications for conservation. Honors Thesis, Wildlife Biology Program, University of Montana. 37 pp.

Huryn, A. D., J. W. Koebel, and A. C. Benke. 1994. Life history and longevity of the pleurocerid snail *Elimia*: a comparative study of eight populations. J. N. Am. Benthol. Soc. 13:540-556.

Krieger, K. A., and W. D. Burbanck. 1973. Distribution and dispersal mechanisms of *Oxytrema (=Goniobasis) suturalis* Haldeman (Gastropoda: Pleuroceridae) in the Yellow River, Georgia, U.S.A. Am. Midl. Nat. 95:49-63.

March, J. G., C. M. Pringle, M. J. Townsend, and A. I. Wilson. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshwat. Biol. 47:377-390.

Miller-Way, C. A., and C. M. Way. 1989. The life history of *Leptoxis dilatata* (Conrad) (Prosobranchia: Pleuroceridae) from the Laurel Fork River, West Virginia. Am. Midl. Nat. 122:193-198.

McIntosh M. D., M. E. Benbow, and A. J. Burky. 2002. Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. River Res. Appl. 18:569-581.

Myers, M. J., C. P. Meyer, and V. H. Resh. 2000. Neritid and thiarid gastropods from French Polynesian streams: How reproduction (sexual, parthenogenetic) and dispersal (active, passive) affect population structure. Freshwat. Biol. 44:535-545.

Nishiwaki, S., T. Hirata, H. Ueda, Y. Tsuchiya, and T. Sato. 1991. Studies on the migratory direction of *Clithon retropictus* (Prosobranchia: Neritidae) by marking-and-recapture method (in Japanese). Venus 50:202-210.

Powell, E. N., and H. Cummins. 1985. Are molluscan maximum life spans determined by long-term cycles in benthic communities? Oecologia 67:177-182.

Resh, V. H., J. R. Barnes, B. Benis-Steger, and D. A. Craig. 1992. Life history features of some macroinvertebrates in a French Polynesian stream. Stud. Neotrop. Fauna Envir. 27:145-153.

Schneider, D. W., and T. M. Frost. 1986. Massive upstream migrations by a tropical freshwater neritid snail. Hydrobiologia 137:153-157.

Schneider, D. W., and J. Lyons. 1993. Dynamics of upstream migration in two species of tropical freshwater snails. J. N. Am. Benthol. Soc. 12:3-16.

Shigemiya, Y. and M. Kato. 2001. Age distribution, growth, and lifetime copulation frequency of a freshwater snail, *Clithon retropictus* (Neritidae). Popul. Ecol. 43:133-140.

Tankersley, R. A. 1989. The effect of trail-following on the locomotion of the marsh periwinkle *Littorina irrorata* (Mesogastropoda: Littorinidae). Mar. Behav. Phys. 15:89-100.

Teixeira, R. L. 1994. Abundance, reproductive period, and feeding habits of eleotrid fishes in estuarine habitats of north-east Brazil. J. Fish. Biol. 45:749-761.

van der Schalie, H. 1948. The Land and Fresh-water Mollusks of Puerto Rico. Misc. Publ. Mus. Zool., Univ. Mich., No. 70.

Vaughn, C. C., and F. M. Fisher. 1992. Dispersion of the salt-marsh periwinkle *Littoraria irrorata*: effects of water level, size, and season. Estuaries 15:246-250.

Vermeij, G. J. 1978. Biogeography and adaptation. Harvard University Press, Cambridge, Massachusetts: 332 pp.

Vermeij, G. J. 1993. A natural history of shells. Princeton University Press, Princeton, New Jersey, 207 pp.

Vermeij, G. J., and A. P. Covich. 1978. Coevolution of freshwater gastropods and their predators. Am. Nat. 112:833-843.