



Upstream migration and altitudinal distribution patterns of *Nereina punctulata* (Gastropoda: Neritidae) in Dominica, West Indies

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Abstract The snail *Nereina punctulata* has been observed performing amphidromous migrations (salt to freshwater migration, post-larval settlement) in the Caribbean, with small- and medium-sized snails achieving maximum fitness at the mid- and high altitudes, but they may be restricted by energy stores. Large snails show no difference in fitness across altitude, but their previous migration history dictates their high-altitude placement in watersheds. The factors determining the rate of migration have not yet been studied. In this study, we sought to understand how migration rate changes with shell size and altitude. We used mark–recapture to track individual snails across seven sites of varying altitude in a single watershed on Dominica and measured the shell length

of randomly collected snails at sites. Volunteers were assisted with data collection in both cases. Shell length was positively correlated with distance from river mouth, although smaller snails were more frequently found at high altitude, high flow sites. Snails closer to the river mouth had faster upstream migration rates than those at mid-altitude. While we found large snails at higher altitude sites, there was no significant relationship between migration rate and shell size. Our findings suggest that large snails do not migrate at maximal rates allowed by energy stores. We also observed erosion of the outer shell periostracum and calcium carbonate underneath, which was seen significantly more often on larger shells. We hypothesise that this erosion is a product of exposure of the structural calcium carbonate to low alkalinity in Dominican streams, following an initial chipping of the periostracum.

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Introduction

Migration of freshwater animals at different life stages is common, with benefits for an organism's reproduction, feeding and refuge-seeking (Lucas et al. 2001).

Amphidromy is a type of diadromy in which an organism's adult life and spawning take place in freshwater, and larval development takes place in saltwater. Upstream seasonal migration is a component of amphidromy, at first to reach freshwater once adult physiology loses osmoregulatory tolerance to saline water, but migration also allows amphidromous organisms to reach food sources, avoid predation and avoid intraspecific competition (Pyron and Covich 2003; McDowall 2010; Zydlewski and Wilkie 2013). Schneider and Frost (1986) also suggest that downstream drift of an organism (e.g. in snails, due to dislodgement) can be remediated through upstream migration, particularly if upstream habitats are more optimal than downstream habitats in later life stages. Amphidromous organisms are most often found in tropical and subtropical zones, with a high prevalence on oceanic or geologically young islands (McDowall 2010). With high rates of gene flow as amphidromous larvae drift in the ocean to different watersheds, amphidromous organisms are common colonisers of new and isolated environments (Hodges and Allendorf 1998; Crandall et al. 2010; McDowall 2010).

The genera *Nereina*, *Neritina* and *Clypeolum* in the family Neritidae are composed of several pan-tropical species of freshwater snails that often exhibit amphidromy (Crandall et al. 2010; Gorbach et al. 2012). *Neritina granosa* of the Hawaiian archipelago, *Nereina punctulata*¹ of the tropical West Atlantic and *Clypeolum latissimum*¹ also of the tropical West Atlantic are some of the most studied amphidromous nerites. All three species have been observed undergoing mass migrations upstream, with seasonal floods (spates) or yearly seasonality based on the return of the rainy season thought to be possible triggers (Brasher 1993; Schneider and Lyons 1993). *N. punctulata* has been observed undergoing rapid migrations, migrating an average of 16.1 m over 5 weeks (Pyron and Covich 2003). Indeed, large upstream distances have been observed to have been covered by some individuals, up to 200 m in 12 weeks and a single observed rate of 7.3 m/day (Pyron and Covich 2003).

Drivers of upstream migration of nerites likely relate to the maintenance of optimal habitat conditions and not simply fecundity, owing to their ability to

spawn at any altitude in freshwater (Schneider and Lyons 1993; Pyron and Covich 2003). Studies by Schneider and Lyons (1993) and Gorbach et al. (2012) suggest that nerite grazing sites may be more abundant upstream and that these sites may have lower grazer biomass, and therefore lower competition. Nerite snails may also exhibit predator avoidance by moving upstream of cascades, similar to the avoidance of predatory fish (e.g. *Agonostomus monticola*) demonstrated by Caribbean decapod communities (March et al. 2002). Further, Schneider and Frost (1986) contend that migration could counteract downstream drift and maintenance of ideal habitat selection. However, the rate of travel may be influenced by shell size, drag and the associated energy expenditure. Smaller snails may be subject to less drag but possess less energy reserves to crawl long distances quickly or survive when food is limited. Though larger snails may be subject to increased drag, they receive the benefits of a larger foot surface for attachment and increased energy stores (Schneider and Lyons 1993; Trussell et al. 1993). Schneider and Lyons (1993) put forward a series of models determining optimal upstream migration distance of *C. latissimum*. Small snails have higher drives to migrate upstream to avoid predation and dislodgement into the ocean, while large snails have lower migration drives as their size deters predation and dislodgement. Movement throughout a watershed across sizes is likely to be a function of maximising exposure to ideal grazing habitat patches while also avoiding predation or extreme downstream dispersal.

To date, the influence of environmental factors such as flow rate, distance from the river mouth or shell size upon migration speed in *Nereina* has received little attention. In the present study, we characterise *N. punctulata* migration rate on Dominica, West Indies, to understand how migration rate varies across environmental and physiological gradients. We used mark–recapture to track snail movement on a weekly basis at two altitudinal sites and measured snails at multiple sites to record existing size distributions across an altitudinal range. We expected to observe migration rate negatively correlated with altitude as snails migrate away from low-altitude sites to avoid the expected higher intensity of predation at these sites, to avoid competition and to find mates. We also expected to see older, larger snails farther upstream,

¹ *Nereina punctulata* and *Clypeolum latissimum* are the current accepted names for *Neritina punctulata* and *Neritina latissima*, respectively (MolluscaBase 2018a, b).

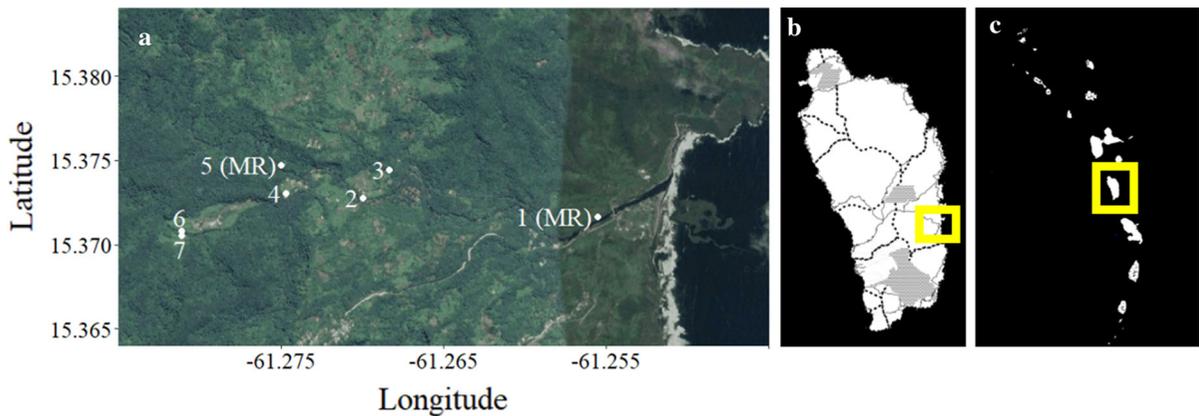


Fig. 1 **a** Location of Rosalie River study sites on Dominica, with *Nereina punctulata* collection and mark–recapture (M–R) sites indicated (also see Table 1). **b** Location of Rosalie River within Dominica. **c** Location of Dominica within the West Indies.

Imagery captured from Google Earth Pro v.7 on 15–10–2018. Map created in R using the ggmap package (Kahle and Wickham 2013)

per Schneider and Lyons (1993) models, due to their upstream migration during younger life stages.

Methods

We collected data on snail size and movement by using two mark–recapture sites and seven intensive-search measurement sites. The purpose of the mark–recapture sites was to track individual snails in the watershed and record movement speeds in situ. The purpose of the intensive-search measurement sites was to characterise size distributions of snails across altitudinal and river flow rates. All data were collected during June and July of 2017.

Volunteers were involved throughout the data collection process. The following mark–recapture and measurement data methods were performed by 6–8 volunteers with the supervision of the lead scientist. Methods training before each field collection was standardised at 45 min.

Mark–recapture

Mark–recapture was undertaken at a mid- and low-altitude site relative to *Nereina* distribution. This was established after an intensive search at a candidate site with altitude 300 m resulted in a single individual, and no individuals were recorded upstream within Rosalie River headwaters (800–1000 m). Thus, an upper vertical limit in *Nereina* distribution was assumed at 300 m.

Mermaid Pool, Brown’s River (Site 5, Fig. 1) is a mid-altitude site (85 m above sea level, ASL) and 3 km from the river mouth. Brown’s River is a tributary to the Rosalie River and is typical for upland Dominican rivers; narrow, boulder-choked and comprised of pools interspersed with steep drops. Rosalie Bay, Rosalie River (Site 1, Fig. 1) is a low-altitude site (14 m ASL), 540 m from the Rosalie River mouth, upstream of the Imperial Road bridge. This site is wider, with a river bottom composed of cobble and with smaller drops between pools (Fig. 2). The mark–recapture study took place across five consecutive weeks in June 23 and July 28, 2017.

One hundred snails were collected from each site (a total of 200 snails). Each snail was numbered by writing in pencil on 1.0 cm × 0.5 cm waterproof paper affixed onto shells using cyanoacrylate glue. Shell sizes and erosion notes were recorded (see intensive-search measurement study details, below). At each collection site, all marked snails were released at a single reintroduction point (± 0.5 m). Markers were placed every 5 m upstream of the reintroduction point, for a total of 60 m and 120 m upstream for Rosalie Bay (site 1) and Mermaid Pool (site 5), respectively, and 10 m downstream of the reintroduction point. The transect length was shorter at Rosalie Bay (site 1) due to impassibility further upstream to researchers and volunteers.

The two study sites were searched for marked snails each week for five consecutive weeks. Search effort was standardised at 16 person-hours of searching



Fig. 2 Mark–recapture sites for *Nereina punctulata*. **a** Mermaid Pool (Browns River), Site 5 (mid-altitude), **b** Rosalie River mouth (Rosalie River), Site 1 (low altitude)

(snorkelling) upstream and downstream of the release areas, covering all mesohabitats. Three student volunteers and the primary researcher constituted each week's search team. The distance of each recaptured snail from the reintroduction point was measured. A reel of tape measure was held at the reintroduction point and the snorkeller held the other end. Where it was not feasible to use a measuring tape (due to obstructions in the river) we measured distance by measuring perpendicular distance of the snail from a line drawn from the nearest 5 m marker. We recorded the distance moved upstream (not including lateral movements across the width of the stream).

Intensive-search measurement

Seven sites were sampled within the Rosalie River watershed, Dominica, West Indies (15°22'23"N; 61°16'29"W), that included a variety of stream types and distance from river mouth (Fig. 1, Table 1). A site was classed as either pool or riffle, and the boundaries of the site were set at a 20 m stretch. *N. punctulata* were collected from each site, and shell sizes recorded using digital callipers in the field. Minimum sample size was 54 snails at site 7, maximum was 100 at sites 1, 2, 3 and 5. The following metrics were measured: shell width, height, length, operculum width and operculum length.

We also noted whether a shell was eroded. Snails were returned to collection points. All site altitudes and coordinates in this study were recorded with a Garmin eTrex Vista GPS unit (Garmin Ltd., Olathe, KS, USA); altitude was measured as above sea level (ASL).

Environmental factors

API test kits (Mars Fishcare, Chalfont, PA, USA) were used to take in situ measurements of pH and KH (carbonate hardness). API test kits measure seven values of pH from 6.0 to 7.6 using bromothymol blue indicator solution. Values greater than 7.6 were assigned a value of 7.8. KH was measured at 12 intervals from 17.9 to 214.8 KH using a dKH test solution. River flow was measured in cubic metres per second at each collection site by timing a float over a known distance and depth of river. The flow measurements were recorded at multiple points (at least three) over the width of the river to account for channelisation. We used the formula below to estimate flow rate in cubic metres per second (m^3s^{-1}):

$$\text{Total flow rate } (\text{m}^3\text{s}^{-1}) = \frac{w_1 d_1 f_1 C}{t_1} + \frac{w_2 d_2 f_2 C}{t_2} + \dots + \frac{w_z d_z f_z C}{t_z}$$

Table 1 Site metadata for mark–recapture and opportunistic collection sites on Dominica

Site	Name	Longitude	Latitude	Altitude (m)	Distance from river mouth (km)	River velocity (m ³ s ⁻¹)	pH	kH	Mark–recapture	Number of snails collected
1	Rosalie Bay	– 61.275	15.37472	14	0.53	3.62	7.8	35.8	Yes	100
2	Second Bridge	– 61.27472	15.37306	57	2.48	5.12	–	–	–	100
3	Ford	– 61.27	15.37278	68	2.24	0.12	7.8	53.7	–	100
4	Lunar Pool	– 61.25556	15.37167	76	3.18	2.09	7.7	–	–	97
5	Mermaid Pool	– 61.28111	15.37083	85	3.12	1.59	7.5	35.8	Yes	100
6	Banana Lama	– 61.28111	15.37056	123	3.97	4.4	7.8	35.8	–	81
7	B-L Tributary	– 61.226833	15.37444	123	4.01	0.095	–	–	–	54

where f is the float distance, t is the time for the float, w is the channel width, d is the average channel depth and C is the correction coefficient for rough stream bottoms (here 0.8, Michaud and Warienga 2005).

Path measurement tools in Google Earth (Google LLC, Mountain View, CA, USA) were used to determine distance of sampling sites from river mouth.

Data analysis

Data analysis was performed in Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA, USA) and in R (R Foundation for Statistical Computing, Vienna, Austria). We first used a two-way ANOVA with post hoc Bonferroni correction to test for the significance between shell length and altitude, distance from river mouth and river flow. We then used linear regression models to test for direction and magnitude of association between altitude, river flow, distance from river mouth and net river displacement (hereafter ‘displacement’) with shell length. Linear regression models were used to compare the influences of site, altitude, river flow and distance from river mouth on shell length. Distance from mouth and altitude, distance from mouth and site, site and altitude were all highly multicollinear (a priori cutoff Pearson’s > 0.5 , multicollinear models all had Pearson’s > 0.9), and so were not included together in our linear models. We used a second-order Akaike information criterion (AICc) to test between alternative hypotheses and to choose the model providing the best fit. The unpaired Student’s t -test was used to test for differences in displacement between the two mark–recapture sites, and to test for a difference in shell size between eroded and non-eroded shells. We used shell length as the primary morphology measurement because pair plotting shell morphometrics showed little significant difference in line slope; thus, we chose shell length for simplicity. For each snail, we calculated the average displacement distance per week as:

$$\Delta d = d_2 - d_1$$

$$\bar{x} = \frac{1}{n} \sum_{i=1}^n \Delta d_n$$

where d is the distance moved (displacement) from the release point, n is the number of weekly samples and \bar{x} is the average weekly displacement along the river. Average displacement and shell lengths are presented

with standard deviation ($\bar{x} \pm SD$). We calculated the distance per week because some snails were only recaptured once, after one week.

Results

Mark–recapture

Of the 200 marked snails, 90 were unique recaptures at Mermaid Pool, and 59 from Rosalie Bay, across the five sampling periods. We observed average weekly migration rate over 5 weeks to be significantly higher at the low-altitude, Rosalie Bay (28.0 ± 19.8 m/week [SD]) than the mid-altitude site, Mermaid Pool (9.2 ± 10.0 m/week, Student's *t*-test, $p < 0.0001$, $n = 149$). Shell length was significantly larger at the mid-altitude (21.4 ± 3.3 mm [SD]) compared to the low-altitude site (19.2 ± 3.1 mm [SD], unpaired *t*-test, $p < 0.0001$, $n = 149$). A linear regression for mark–recapture snails revealed no significant association between shell length and migration rate (Fig. 3, mid-altitude site: $p = 0.63$, $R^2 = 0.26$, $n = 90$; low-altitude site: $p = 0.11$, $R^2 = 0.044$, $n = 59$). The fastest migration rate was 36 m over 1 week at the low-altitude site. One individual at the mid-altitude site moved 89.7 m upstream in 4 weeks but was an outlier.

Individuals were occasionally found downstream of their previously observed location. The proportions of snails in the mark–recapture experiment moving downstream were 13.3% at the low-altitude and 32.8% at the mid-altitude site. Snails at low-altitude site were found farther downstream of previous locations (mean = 10.3 ± 11.1 m [SD]) than at the mid-altitude site (mean = 5.6 ± 7.8 m [SD]), though the significance was marginal (Student's *t*-test, $p = 0.049$, $n = 10$ [low altitude], $n = 76$ [mid-altitude]). River flow rate at the low-altitude site was 3.62 ± 0.94 m³s⁻¹, significantly higher than at the mid-altitude site was 1.59 ± 0.59 m³s⁻¹ (median \pm SD, unpaired Student's *t*-test, $n = 12$, $p < 0.0001$).

Intensive-search measurement

A total of 432 snails were collected from seven sites, in addition to the 200 sampled for mark–recapture. We tested for significant differences in shell length

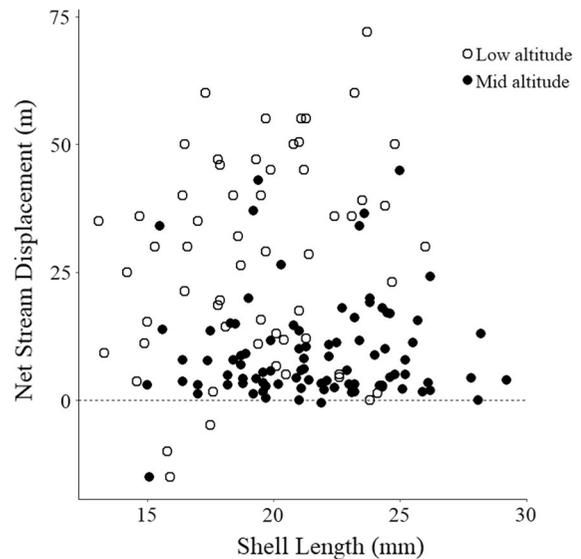


Fig. 3 No linear relationship between shell length and net river displacement (m) of *Nereina punctulata* at both the low-altitude site 1 (Rosalie, 14 m ASL, $p = 0.11$) and mid-altitude site 5 (Mermaid Pool, 85 m ASL, $p = 0.63$). Each point is the average distance moved over the course of the study for each marked individual. Data collected June–July 2017

between sites that were associated with a range of altitudes, distances from river mouth and flow rates (Fig. 4). A two-way ANOVA indicated that shell length was significantly impacted by water flow ($p < 0.0001$) and distance from mouth ($p < 0.0001$) and the interaction of distance from mouth and flow ($p = 0.0004$). Using a linear model determined from AICc, we found that shell length significantly increased with distance from river mouth, altitude and the interaction of distance and altitude, but significantly decreased with flow (all $p < 0.0001$, Table 2). We conducted multiple comparisons of shell length between sites after using Bonferroni's correction and found that all but five sites had means that were significantly different from one another ($p < 0.05$, Table 3).

Other measurements

Apparent erosion was observed on some snail shells (e.g. Fig. 5). The length of shells that had been eroded averaged 24.3 ± 3.7 mm (mean \pm 1 SD), these eroded shells were significantly larger than non-eroded shells at 19.7 ± 3.3 mm (unpaired Student's *t*-test, $p < 0.0001$, $n = 632$). Erosion consumed the

Fig. 4 Box and whisker-plots of *Nereina punctulata* shell length at each sampling site, over **a** altitude, **b** river flow and **c** distance from river mouth. All linear regression slopes are significant from no slope ($p < 0.0001$, $p < 0.0001$ and $p = 0.0004$, respectively) The central line in the boxplot is the median, the bottom and top of the boxes are the first and third quartiles, confidence interval about the linear model is the grey shading around the fitted model, and the vertical lines indicate the range in shell length. Data collected June–July 2017

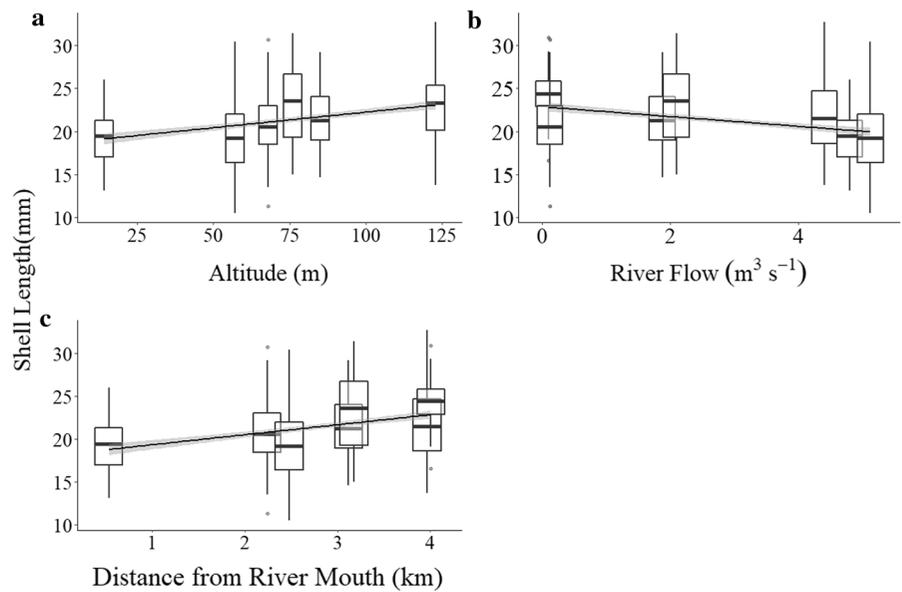


Table 2 Linear model statistics of shell length to environmental variables

Model	Component	Regression coefficient	F	df	p	R ²	n
Shell length–Distance from river mouth*Flow rate	Distance	2.09	36.5	3	< 0.0001	0.15	632
	Flow	0.42	36.5	3	< 0.0001	0.15	632
	Distance*Flow	– 0.32	36.5	3	< 0.0001	0.15	632
Shell length–Altitude	Altitude	0.036	64.6	1	< 0.0001	0.093	632
Shell length–Flow rate	Flow	– 0.57	51.6	1	< 0.0001	0.075	632
Shell length–Distance from river mouth	Distance	1.16	69.9	1	< 0.0001	0.098	632

Table 3 Significance associated with the unpaired *t*-test multiple comparisons of mean shell length between sampling sites after Bonferroni corrections

	Shell length, mean ± SD (mm)	1 Rosalie M-R	2 Second Bridge	3 Ford	4 Lunar Pool	5 Mermaid Pool M-R	6 Banana Lama	7 B-L Tributary
1 Rosalie M-R	19.1 ± 3.10	–	*	***	***	***	***	***
2 Second Bridge	19.3 ± 3.94		–	*	***	**	***	**
3 Ford	21.0 ± 3.61			–	***	–	***	–
4 Lunar Pool	23.6 ± 4.50				–	**	–	*
5 Mermaid Pool M-R	21.4 ± 3.33					–	***	–
6 Banana Lama	21.7 ± 3.85						–	**
7 B-L Tributary	24.4 ± 2.81							–

Significance codes: < 0.0001 = ‘***’, < 0.001 = ‘**’, < 0.05 = ‘*’, > 0.05 ‘–’. Alpha set at 0.05. Mark–recapture sites denoted with M-R



Fig. 5 *Nereina punctulata* shell erosion. Dark outer periostracum has been eroded away to reveal green structural calcium carbonate

underlying calcium carbonate where the periostracum had been chipped away. Water pH varied between 7.4 and 7.8 between sites, and alkalinity (KH) varied between 35.8 and 53.7 mg/L (Table 1).

Discussion

Several species of the family Neritidae, including *N. punctulata*, exhibit upstream migration behaviour. However, previous research has not considered how snail size, altitude and water flow rate impact migration patterns of *N. punctulata*. Using mark–recapture techniques to track *N. punctulata* snails in Dominica, West Indies, we predicted migration speed to be faster lower in the watershed, as juveniles and adults may move upstream to avoid predation (McDowall 2010), to move towards denser algal beds (March et al. 2002) or to lessen the impacts of potential downstream drift (Schneider and Frost 1986). Crawl speeds were faster at the low-altitude and high river flow site than compared to the mid-altitude site with low-river flow site. These results are similar to those obtained by Gorbach et al. (2012), who found that *N. granosa* on Maui, Hawai’i, migrated at faster rates in ‘normal’ flow ($0.92 \pm 0.31 \text{ m}^3\text{s}^{-1}$) with high snail density and a ‘normal’ flow ($1.09 \pm 0.06 \text{ m}^3\text{s}^{-1}$) at low snail density, compared to a ‘restricted’ ($0.03 \pm 0.02 \text{ m}^3\text{s}^{-1}$) flow (mean \pm SE; migration rates of 8.12 m day^{-1} , 4.62 m day^{-1} and 1.75 m day^{-1} , respectively). *N. punctulata* in this study had a higher

migration rate than *N. granosa* in the Gorbach et al. (2012) study, with our recorded migration rate of $28.0 \pm 19.8 \text{ m}$ at low-altitude and high flow site (14 m , $3.62 \text{ m}^3\text{s}^{-1}$) and a rate of $9.2 \pm 10.0 \text{ m}$ (mean \pm SD) at mid-altitude and low flow site (85 m , $1.59 \text{ m}^3\text{s}^{-1}$). More rapid migration rates at faster river velocities (as observed in our low-altitude site and in the two normal flow regimes from Gorbach et al. (2012)) fits the hypothesis put forth by Schneider and Frost (1986) that upstream migration serves in part to prevent downstream drift into undesirable habitat area (i.e. ocean, high-predator density in low-altitude areas). Snails are hypothesised to ‘escape’ high flow areas where dislodgement is likely through quick upstream migration and can reach low flow areas, where migration rates are lessened.

In agreement with Schneider and Lyons (1993), we found no significant relationship between snail size and displacement, suggesting that even with increases in foot size, and energy stores with shell size, large snails do not crawl at the maximal rates allowed. Smaller snails ($< 20 \text{ mm}$) at the low-altitude site showed a weak positive correlation with positive displacement, but this effect was not statistically significant. The overall lack of effect of size on displacement lends more support to our findings that location within watershed has more impact on crawl rate than size does.

Downstream displacement was recorded at both sites, with greater frequency at the mid-altitude, low flow site but with greater average distance at the low-altitude high flow site. Gorbach et al. (2012) found higher rates of downstream migration at low flow sites (43% compared to $\sim 5\%$ for normal flow). We observed the same effect: downstream displacement occurred more often at a low river flows (mid-altitude site). Thus, our data suggest that altitude and water flow rate influence migration speed and decreased water flow rate, and more downstream displacement is likely to occur in higher watershed altitude. Upstream migration rates likely decrease as feeding and mating opportunities are prioritised by *N. punctulata*. Downstream displacement could also be a function of seeking out ideal grazing grounds on a local scale; at the low flow site 5, a pool and resulting sparser tree canopy immediately downstream of the introduction site likely allowed for more light to reach river bottom and thus could drive higher densities of microalgae. Overall, however, canopy cover was sparser at site 1

than site 5. Further research on canopy cover, microalgal density and snail movement is necessary to understand how riverine microhabitats affect displacement rates.

Fewer snails were recovered at the low-altitude site during the mark–recapture experiment than at the mid-altitude site. This could be for several reasons: (1) riverbed topography and increased river flow may complicate snail recovery while snorkelling, (2) increased flow at the low-altitude site could wash snails beyond the downstream survey extent, and (3) given the maximum observed snail migration speed (36 m in 1 week), snails may have crawled upstream and beyond the transect within the first week. Snails were also frequently recaptured downstream of their previous location at the low-altitude site, supportive of the second hypothesis. This may be due to dislodgement by spates which occurred several times during our study period, which would explain slower and even negative migration rates, but may also be the result of a weaker upstream drive as ideal habitat is reached and a dislodgement event less likely in low flow and at higher altitudes in the watershed (Gorbach et al. 2012).

Models of snail fitness (Schneider and Lyons 1993) indicate location within watershed is a function of size-dependent survival and fecundity. Small snails experience a maximum fitness at intermediate distances from river mouth, due to smaller energy stores, but have steep survival curves that drive upstream movement in response to predation and dislodgement. Intermediate-sized snails have energy stores that allow them to travel upstream and achieve higher survival rates than smaller snails. Large snails have relatively even survival curves across the watershed, due to their larger size functioning as a predation deterrent. These larger snails should experience fitness maxima low in the watershed because of high dislodgement and predation resistance, but low upstream mobility. However, their previous migration history as juveniles results in them maintaining a high-altitude position in situ as adults (Schneider and Lyons 1993).

With these models, we predicted that smaller snails were likely to be more abundant near the river mouth, where they have just entered the river after settling as benthic juveniles in the Atlantic Ocean. Our data support this prediction, with larger shells tending to be found higher in the watershed. The slope gradient coefficient of shell size over altitude (in our study

$m = 0.036$) is not as strong as snails observed by Pyron and Covich (2003), who studied the larger and less steep watersheds of the Rio Mameyes ($m = 2.04$) and Espiritu Santo ($m = 3.24$) in Puerto Rico. Due to the larger altitude gradient of our studied watershed, we expected to see a stronger regression coefficient between shell size and altitude in our study. However, alternate models suggest that watershed length may be important. For example, the Rosalie River reaches an altitude of 123 m within 4 km of the ocean, while the Rio Mameyes reaches less than 40 m in that same distance (Pyron and Covich 2003). The altitude of the Pyron and Covich (2003) study sites is, however, comparable to those in the present study (85 m and 14 m); the Rio Espiritu Santo sites are at altitudes of 5, 10, 65 and 105 m, while the Rio Mameyes are at 5, 45, 90 and 200 m. While altitudinal barriers such as waterfalls associated with steep gradients such as in Dominica certainly impact *N. punctulata* distribution, our data show that location within watershed dictates shell size; larger shells were found farther from the river mouth. More large snails were found at high watershed altitudes as an artefact from their previous migration history. However, our linear model shows river flow to have a negative correlation with shell length as distance from mouth increases. According to this model, larger snails could also be seeking out low flow sites at close distance to the ocean; however, the absence of large snails at low altitudes generally indicates that the small snails at high flow and far distance are what drives the negative correlation with shell length and distance from ocean. Smaller snails, therefore, are seeking out high flow stretches at high altitudes; this finding aligns with those of Blanco and Scatena (2007), who found smaller snails migrated through a wide high flow channel while larger snails migrated through a low flow channel at the same altitude. They conclude that small snails experience less turbulence in high flow environments and may avoid predators who prefer low river flow (Blanco and Scatena 2007). While it appears that smaller snails were able to resist high water flows, ‘hitchhiking’ behaviour was observed with snails of all sizes. We note that this behaviour may explain the presence of smaller snails at high flow sites far from the river mouth. Kano (2009) posits that such hitchhiking behaviour may assist juveniles to complete more rapid and less energetically expensive migrations

upstream and could provide a mechanism for some smaller snails to reach upstream sites.

We observed high rates of shell erosion in the periostracum and underlying calcium carbonate in large *N. punctulata* individuals. These observations are consistent with those reported by Maciolek (1978) in Hawaiian nerite snails and by Blanco-Libreros and Arroyave-Rincó (2009) in *Neritina virginea* in Puerto Rico. We hypothesise that the process begins when the periostracum is chipped through predation, conspecific rasping and/or tumbling against boulders, revealing calcium carbonate beneath. Blanco-Libreros and Arroyave-Rincó (2009) found birds and decapods responsible for predated chipped shells, while damage to shells containing live snails was caused by conspecific grazing (Craig 1967). Conspecific hitchhiking behaviour as observed by Kano (2009) may also provide a mechanism for shell removal; Amortegui-Torres et al. (2013) hypothesise conspecifics climb atop and rasp shells to gain calcium carbonate in a carbonate-limited environment. Euendolith (boring) microorganisms such as cyanobacteria may also be responsible for removal of periostracum and calcium carbonate, allowing for water ingress into shell matrix (Golubic et al. 1981; Cockell and Herrera 2008). Based on our observation of downstream movement, possibly caused by dislodgement, we add tumbling as a potential cause of shell erosion. Damage to live snails could therefore be caused by unsuccessful predation events by birds (*Butorides virescens* observed during surveys), decapods (many species observed during surveys), cyanobacterium boring or tumbling.

However, erosion of the shell is inconsistent with these events in isolation. The periostracum, as an organic layer composed of proteins resilient to low water pH, protects the vulnerable calcium carbonate from dissolution (Taylor and Kennedy 1969; Rodolpho-Metalpa et al. 2011). Older snails are larger and have had more time to erode than younger snails. It is likely that *N. punctulata* does not possess the physiological mechanisms to buffer low pH freshwater, relying on the periostracum to protect the calcium carbonate shell structure from senescence these environments. Water pH and alkalinity measurements at sampling sites indicate neutral pH and a good buffering capacity; however, calcium carbonate mass loss can occur at 7.9 pH and calcite saturation states of 2.19 with oysters in marine environments (Waldbusser et al. 2011). Dominica is predominantly composed of

rock of volcanic origin, containing little calcium (Smith et al. 2013). However, given that *N. punctulata* clearly can deposit calcium carbonate to grow to large sizes high in the watershed, acidic erosion of sub-periostracum calcium carbonate is most likely. A direction for future research could investigate these fitness impacts within the context of *N. punctulata* migration behaviour, as well as grazer-exclusion studies to understand the role of conspecific rasping on shell erosion.

Limitations

This study relied on a single season of *N. punctulata* observations from June to July (Dominica's rainy season lasting from June to October). Mark-recapture undertaken during different parts of the year would enable seasonal variations in migration to be characterised. Further, a third 'high' altitude, comparative mark-recapture site would have provided opportunities to explore the movements. However, the ruggedness of the watershed and associated issues with access prevented this. We used volunteers to assist with weekly mark-recapture data collection with a lead scientist present, and therefore accuracy and sampling effort may have slightly differed week to week. Distance was measured with tape measures, and we estimate error of migration distances to be on the order of ± 0.5 m. We used time-float methodology for river flow; it is likely that the use of flowmeter would be more accurate.

Conclusion

Upstream migrations of amphidromous organisms fulfil a critical ecological role in island montane streams by transporting nutrients of marine origin high into nutrient-poor headwaters (Engman et al. 2018). Understanding how high-biomass amphidromous organisms such as *N. punctulata* migrate throughout a watershed sheds light on the mechanics of this major nutrient transport system, we found displacement rate of *N. punctulata* to be a function of river flow and the effects of altitude and distance from ocean. This migration system is ripe for additional research to answer questions on: movement to microhabitat patches in comparison with overall riverine displacement, energy budgeting in varying river flows, and

mechanics and fitness impacts of shell erosion in gastropods.

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