DIADROMOUS NERITID GASTROPODS: EXAMINING HOW WATER VELOCITY, DISTANCE FROM OCEAN, AND LOCATION ON SUBSTRATE SHAPE STREAM COMMUNITIES

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Abstract. The species composition, size distribution and abundance of diadromous neritid gastropods were studied in two coastal streams on Mo'orea French Polynesia, from October to November 2010. Five species of the family Neritidae were examined: *Neritina auriculata* Lamarck, *Neritina canalis* Lamarck, *Neritina turrita* Gmelin, *Clithon spinosa* Budgin, and *Septaria porcellana* Linnaeus. Sampling occurred at increasing distances from the ocean. Water velocity, depth, and shell height was measured, location on substrate was recorded for each species, and comprehensive site surveys were conducted. Species composition changed at increasing distances from the ocean, with percentages of *Neritina canalis* increasing when moving upstream in the Amehiti River and percentages of *Neritina auriculata* decreasing when moving upstream in the Uufau River. Average shell heights were larger in upstream reaches and smaller in downstream reaches. Abundances of neritids decreased at water velocities greater than 0-2 m/s. *Neritina auriculata* and *Neritina canalis* were both found on the sides and bottoms of substrate.

Key words: gastropods; Neritidae; species composition; Mo'orea, French Polynesia; diadromous; coastal streams; water velocity; shell height; substrate; water depth; migration

INTRODUCTION

River and stream ecosystems are different from terrestrial ecosystems in that most physical and biological processes within these habitats are the result of movement of water within the system. For example, moving water initially creates these aquatic ecosystems and later determines the spatial and temporal distributions of the organisms that live within them. Flow regimes have a daily impact on the biological processes in which stream fauna engage, such as larval dispersal, habitat utilization, competition with other organisms, escape and avoidance of predators, and resource acquisition (Hart and Finelli 1999). In addition, water movement manipulates and shapes stream community composition through the occurrence of disturbances created by large and unpredictable changes in flow regimes (Poff et al. 1997, Lake 2000). These "flow-generated disturbances" are typically responsible for increasing habitat patchiness and diversity, which leads to increases in species diversity (Lake 2000).

Oceanic islands are created as the Pacific Plate passes over one or more regions of volcanic activity, known as hotspots. Islands begin as volcanoes growing out of the ocean, but rainfall shapes their geologic features. Weather that is created once an island reaches a large enough size and rain erodes soil and forms channels that eventually become rivers and streams (Craig 2003). Rivers and streams present on tropical oceanic islands are considered to be complex and diverse with regard to their associated habitats and organisms (Smith et al. 2003). This complexity and diversity of tropical oceanic rivers and streams is the result of rain and weather patterns on the islands. In some regions of the tropics, rivers and streams are subjected to predictable seasonal rainfall, and the changes in water level are large and gradual. In other regions, the rainfall is unpredictable, and changes in water level are large and flashy. In either case, the organisms living within island streams have evolved and adapted to deal with the natural disturbances associated with these ecosystems (Wantzen et al. 2006).

In many rivers and streams of tropical islands, organisms occurring in these freshwater habitats are linked to ancestors that lived in the surrounding oceans (Smith et al. 2003). In accordance with their marine ancestry, many of these organisms are diadromous in that part of their life is spent in freshwater lakes or streams and the other part is spent in the ocean. Amphidromy, a

specific type of diadromy that involves migration between land and sea for purposes other than breeding, occurs mainly on islands in both temperate and tropical latitudes (McDowall 2008). Scientists studying patterns of migrations in fish have recognized amphidromy as different from other types of diadromy in that amphidromous migrations are focused around moving to new areas for feeding as opposed to moving to new areas for spawning. Newly hatched larvae migrate to the ocean where they feed and develop before returning to their freshwater habitat as juveniles to finish out their life cycle. Some argue amphidromy is beneficial to organisms living in streams of oceanic islands because it allows them to leave these habitats during stressful disturbances, like dramatic changes in flow regimes, and return to these habitats during more stable times (McDowall 2007). The dominance of amphidromous species occupying oceanic island streams highlights the instability of these rare island habitats (Crandall et al. 2010).

In addition to the many species of fish that exhibit amphidromy on tropical oceanic islands, other organisms have been known to lead amphidromous life styles as well (McDowall 2007). The family Neritidae, which occurs in streams on many oceanic islands in the Pacific, is amphidromous. The larvae of these gastropods are initially planktonic before hatching in freshwater and being carried downstream to the ocean where they require marine salinity levels to correctly develop into juveniles (Liu and Resh 1997, Crandall et al. 2010). The juveniles then migrate back upstream to carry out the rest of their life cycle (Liu and Resh 1997). For example, Schneider and Frost (1986) studied the migrational behavior of *Neritina latissima* in a coastal stream in Costa Rica. They found smaller individuals are more easily washed downstream and have adapted to migrating back upstream against river currents (Schneider and Frost 1986). In addition, populations of the neritid snail *Neritina virginea* in coastal streams of Puerto Rico also are known to engage in large upstream migrations of mainly young juveniles (Blanco and Scatena 2005).

Neritid gastropods typically have streamlined shells, which allow them to inhabit streams with fast moving water; however, shell morphology can vary significantly within a species. In addition to hydrodynamic shells, they have strong muscles that aid in the attachment of individuals to rocks in high current velocities (Haynes 1988). A number of studies have looked at the distribution and composition of neritid gastropods with respect to hydrology and substrate (Blanco and Scatena 2006, Liu and Resh 1997, Blanco and Scatena 2005, Resh et al. 1990). On the island of Puerto Rico, the density of *Neritina virginea* was greater in areas of the rivers that had larger substrate, which allowed individuals access to the underside of rocks where they could take refuge during high flow events (Blanco and Scatena 2005, Blanco and Scatena 2006). *Neritina virginea* was also found at higher densities at greater depths possibly using these deeper waters as another type of refugia during upstream migrations (Blanco and Scatena 2005, Blanco and Scatena 2006). These behavioral adaptations have possibly allowed this species to colonize steep streams in montane reaches that have proven difficult for other diadromous species to colonize (Blanco and Scatena 2006).

On the island of Mo'orea, French Polynesia, different aspects of the biology and ecology of neritid snails have been examined. Factors affecting the distribution and microdistribution of neritid snails have been studied in Uufau River, Afareaitu River, Vaioro River, Urufara River and rivers in the Opunohu Valley of Mo'orea (Liu and Resh 1997, Liu 1995, Morton 2004, Resh et al. 1990). Liu (1995) found that the important abiotic factors affecting abundances and distributions of neritid gastropods were flow, depth, and composition of substrate. The author found that neritids exhibited higher species richness in riffles areas and unique habitat preferences for the tops, sides and bottoms of substrate (Liu 1995). Just as suitable habitat varies within a stream, so does the distribution of species within that stream. Within the Opunohu Valley, Resh *et al.* (1990) found that different species of Neritidae have different sized ranges, with *Neritina turrita* and *Clithon spinosa*, having the smallest distribution range and *Neritina canalis* having the largest. Populations of *Neritina auriculata* are restricted to locations near the river mouth where salinity can be as high as 33 ppt, but suitable depths and substrate protect this species from both biotic and abiotic stresses (Morton 2004).
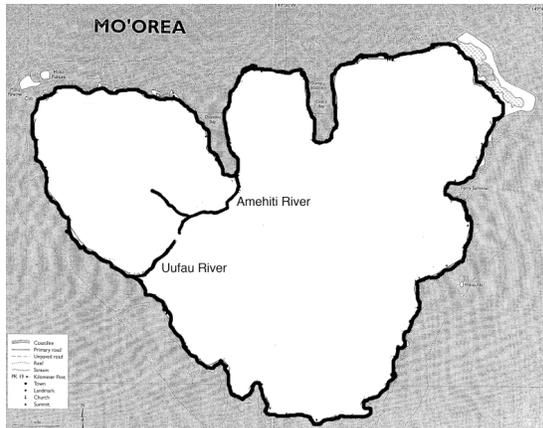
FIG. 1. Map of study streams Mo'orea, French Polynesia. The Amehiti River and Uufau River are coastal streams.

The objectives of this study were to determine: 1) how the neritid species composition changes with increasing distance from the ocean; 2) how different sized individuals are distributed between upstream and downstream reaches; and 3) whether there are differences in the abundances of neritids found in certain water velocities and locations on substrate. These objectives have important implications for understanding the distribution patterns of neritid snails on the island of Mo'orea and potentially on other Pacific Islands where these snails also exist.

METHODS

Study streams

The study focused on two coastal streams on the island of Mo'orea, French Polynesia. Five study sites were located in the Amehiti River in the 'Opunohu Valley on the north side of the island, and another five study sites were located in the Uufau River on the west coast of the island (Table 1). Sampling occurred in the morning and early afternoon during October and November 2010.

Study organism

The organisms included in this study are all diadromous gastropods from the family Neritidae (Resh et al. 1990). Neritid species were identified using an identification key from Boyer (1998). All gastropods were easily distinguished by

examining the external morphology of each specimen in the field. Previous studies on have identified species according to differences in shell structure and operculum color (Resh et al. 1990; Morton 2004). *Neritina turrita* Gmelin has a distinctive shell that spirals to a point, but often part of the shell was chipped or missing. *Neritina canalis* Lamarck has a canal along one side, which was visible by turning the gastropod over and looking underneath. *Clithon spinosa* Budgin has thin, long spines on the top of its shell. *Septaria porcellana* Linnaeus has a limpet-like shell. *Neritina auriculata* Lamarck also has a limpet-like shell with flared wings.

Stream sampling

Beginning at the downstream-most region of each site and progressing upstream, sampling was conducted until data on 100 snails were collected. First, a small region of the streambed was surveyed for snails obviously located on the tops or sides of substrate. If no snails were found this way, then rocks were randomly turned over in search for snails located on the bottom. Once a snail was observed, water velocity and depth were measured at its location. A Flow Wand Backpack Flow Meter was used to measure the water velocity over each snail. Next, species name, shell height, intermediate axis, and location on substrate were recorded. Clumping of snails was noted as well when multiple snails were found on the same rock.

Stream site survey

Once data for 100 snails had been collected, data on the physical parameters of each site were recorded. Using a transect tape, the total length and average width of the area sampled was recorded. Next, the discharge at each site was calculated by stretching a transect tape along a cross-section of the stream and recording water velocity and depth at several points from one stream bank to the opposite stream bank. To calculate the discharge, water velocity and depth measurements were averaged separately. The averaged values were then multiplied by each other and multiplied by the total width of the stream at that location. Using a Multi-Parameter PCSTestr 35, water temperature, salinity and pH at three locations in each site were

TABLE 1. Physical characteristics of study sites in Amehiti River and Uufau River, Mo'orea, French Polynesia.

Physical variable	Amehiti River					Uufau River				
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10
salinity (ppt)	0	0	0	0	0	32	0	10	1	0
pH	7.4	7.3	7.4	6.8	7.3	8.2	8.1	8	7.5	7.5
water temperature (°C)	23	24.8	23.2	23.5	-	25.1	24.3	24.3	-	-
channel width (m)	10	14	4.7	7.3	2.3	9.5	8.2	8.6	8.1	8.2
average depth (m)	0.16	0.07	0.13	0.06	0.08	0.26	0.11	0.33	0.15	0.09
average water velocity (m/s)	0.73	2.49	0.54	2.79	2.15	2.49	3.15	0.09	0.11	0.26
discharge (m^3/s)	0.115	0.234	0.128	0.245	0.182	6.079	0.331	0.119	0.009	0.007
shading	low	med	med	high	med-high	high	low	high	low	none
elevation (m)	1.7	3.5	7.9	3.9	1.2	2.44	3.33	3.03	3.77	2.75
slope (degrees)	1.15	1.76	0.29	1.29	2.58	1.43	0.38	1.43	0.57	0.19
distance from ocean (m)	593	981	1360	1151	757	62	106	86	128	150

recorded and averaged. The shading and channel width were recorded for each site.

Lastly, elevation and slope data for all sites in the two streams was determined using a tape measure, 2-meter wooden stick, and level. Beginning at the most upstream site, the change in height for each 2-meter segment was determined by holding the wooden stick level at waist height. Waist height had been previously measured and recorded. A tape measure was held vertical two meters downstream for the starting location, and the wooden stick was used to locate a second height. This process was repeated until the ocean was reached. The difference between waist height and the second height was calculated for all two-meter intervals and then added up to determine the total change in elevation from each site to sea level. Slope for each site was calculated by dividing the change in height across each site by length of the sampled area. It should be noted that the wooden stick did bow, but this error was corrected for during calculations.

Statistical analysis

Chi-Squared tests were performed to determine any differences in species composition at increasing distances from the ocean, differences in abundances of neritids at increasing water velocities, and differences abundances of neritids on varying locations of substrate. An ANOVA tests was used to determine if there were any differences in average shell heights between neritid communities in the Amehiti River and neritid communities in the Uufau River. A linear regression test was used to determine if average shell heights of neritids increased as distances from the ocean increased in the Uufau River.

RESULTS

Species composition

In the Amehiti River, the percentage of each species within neritid communities varied with increasing distance from the river mouth (Fig. 2). A Chi-squared test
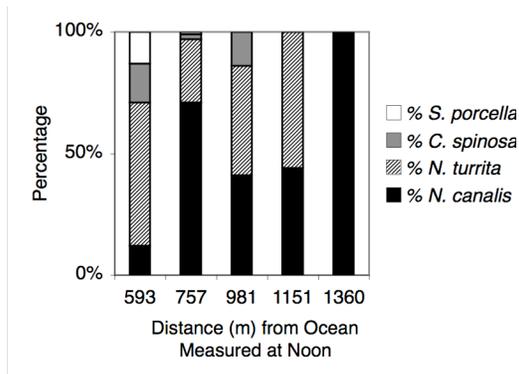
FIG. 2. This figure shows the percentages of each species of Neritidae at five distances upstream from the river mouth of the Amehiti River. A Chi-squared test showed percentages of each species differed significantly between upstream and down stream locations (Likelihood Ratio X^2=276, df=12, p<0.0001).

FIG. 3. This figure shows the percentages of each species of Neritidae at five distances upstream from the river mouth of the Uufau River. A Chi-squared test showed percentages of each species differed significantly between upstream and downstream locations (Likelihood Ratio X^2=382, df=16, p<0.0001).

showed this pattern was statistically significant (Likelihood Ratio X^2=276, df=12, p<0.0001). *Neritina canalis* represented 12% of the neritid community at 593 meters upstream and increased to 100% of the neritid community at the 1360 meters upstream. *Clithon spinosa* and *Septaria porcellana* represented the smallest percentage of neritids at distances less than 1000 meters from the ocean. *Septaria porcellana* was not found farther than 757 meters upstream, and *Clithon spinosa* was not found farther than 981 meters upstream. However, when present at distances less than 1360 m the percentage of *Neritina*
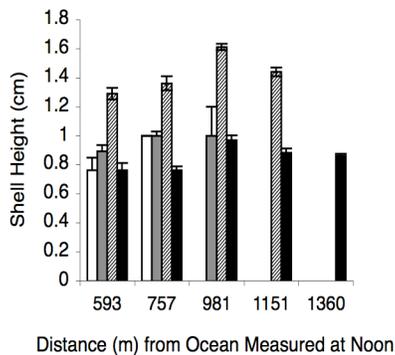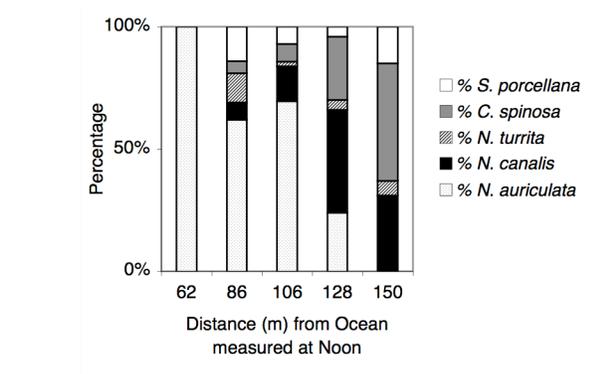
turrita varied between 59% and 26%.

In the Uufau River, the percentage of each species within neritid communities varied with increasing distance from the river mouth (Fig. 3). A Chi-squared test showed this pattern was statistically significant (Likelihood Ratio X^2=382, df=16, p<0.0001). The percent of *Neritina auriculata* decreased overall as distance upstream increased and was completely absent at 150 meters from the river mouth. However, *Clithon spinosa* and *Neritina canalis* increased from 5% and 7% respectively at 86 meters upstream to 48% and 31% respectively at 150 meters upstream. Percentages of *Septaria*
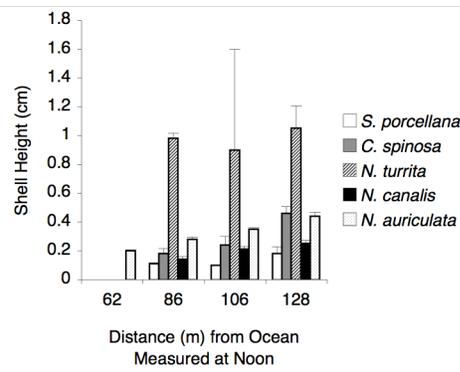

FIG. 4a

FIG. 4b

FIG. 4a-b. This figure shows average shell heights (cm) of species of Neritidae at five distances upstream from the river mouth. An ANOVA test showed a significant difference between average shell height of neritid species in the Amehiti River and average shell height of neritid species in Uufau River (p=0.0184, f=3.3618, df=3). A linear regression test showed average shell heights increased as distance from river mouth increased in the Uufau River for *Septaria porcellana* (p=0.0339, F=5.0887, df=24), *Clithon spinosa* (p=0.0022, F=10.8432, df=37), and *Neritina auriculata* (p=0.0001, F=31.9329, df=153).

    a.   Amehiti River
    b.   Uufau River

porcellana and *Neritina turrita* varied little; percents of both species ranged between 4% and 14% for *Septaria porcellana* and 2% and 12% for *Neritina turrita*.

Shell heights

Average shell heights of neritids were larger in the Amehiti River than average shell heights of neritids in the Uufau River (Fig. 4a-b). An ANOVA test showed this pattern was statistically significant (p=0.0184, f=3.3618, df=3). For example, the average shell height of *Neritina turrita* in the
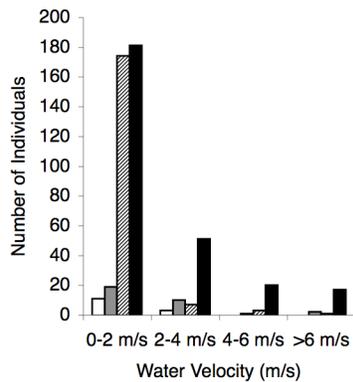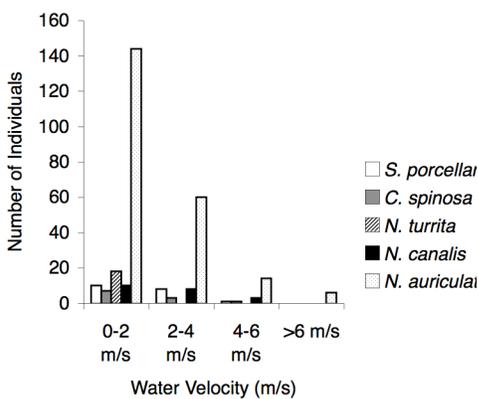

FIG. 5a

FIG. 5b

FIG. 5a-b. This figure shows abundances of species of Neritidae at four different water velocities. A Chi-squared test showed abundances of each species differed significantly at the different water velocities in the Amehiti River (Likelihood Ratio X^2=64, df=9, p<0.0001) and in the Uufau River (Likelihood Ratio X^2=24, df=12, p=0.023).
    a.   Amehiti River
    b.   Uufau River

Amehiti River ranged between 0.76 cm and 0.97 cm; however, in the Uufau River the average shell height of *Neritina canalis* ranged between 0.14 cm and 0.25 cm. In the Uufau River, average shell heights of three neritid species increased as distance from the ocean increased (Fig. 4b). For example, of *Neritina auriculata* and *Neritina canalis* increased steadily from 0.2 cm and 0.44 cm to 0.12 cm and 0.25 cm respectively farther upstream. A linear regression showed these patterns to be statistically significant for *Septaria porcellana* (p=0.0339, F=5.0887, df=24), *Clithon spinosa* (p=0.0022, F=10.8432, df=37), and *Neritina auriculata* (p=0.0001, F=31.9329, df=153).

Species abundances

Abundances of most neritid species declined at water velocities higher than 0-2 m/s in both the Amehiti River and Uufau River (Fig. 5a-b). A Chi-squared test showed this pattern was statistically significant in the Amehiti River (Likelihood Ratio X^2=64, df=9, p<0.0001) and in the Uufau River (Likelihood Ratio X^2=24, df=12, p=0.023). In the Amehiti River, abundances of *Nertina turrita* dropped from 174 individuals in water velocities of 0-2 m/s to 1 individual in water velocities of >6 m/s. In the Uufau River, abundances of *Neritina auriculata* dropped from 114 individuals in water velocities of 0-2 m/s to 6 individuals in water velocities >6 m/s. However, in the Amehiti River, *Neritina canalis* was able to maintain the highest abundances at water velocities >6 m/s.

In the Amehiti River, abundances of neritid species varied between the different locations on substrate (Fig. 6a). A Chi-squared test showed this pattern was statistically significant (Likelihood Ratio X^2=187, df=6, p<0.0001). For example, *Neritina canalis* was found mainly on the bottoms of rocks, where as, *Neritina turrita* was present on the sides and tops of substrate. Abundances of neritid species also varied between locations on substrate in the Uufau River (Fig. 6b). A Chi-squared test showed this pattern was statistically significant (Pearson's X^2=40, df=8, p<0.0001). *Neritina canalis* was found on both the bottoms and sides of rocks, as was *Neritina auriculata*.
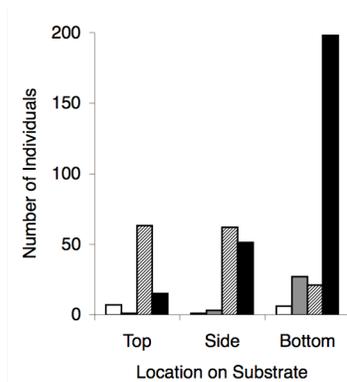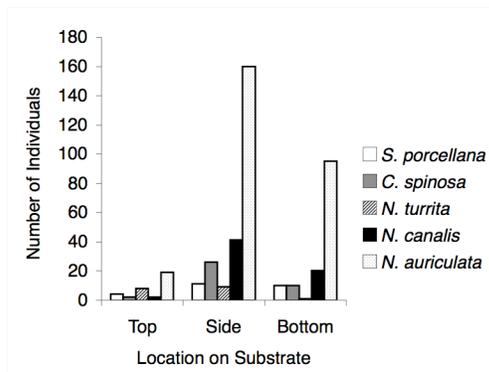
FIG. 6a

FIG. 6b

FIG. 6a-b. This figure shows abundances of species of Neritidae at three different location on substrate (top, side, and bottom). A Chi-squared test showed abundances of each species differed significantly at the different locations in the Amehiti River (Likelihood Ratio X^2=187, df=6, p<0.0001) and the Uufau River (Pearson's X^2=40, df=8, p<0.0001).
   a. Amehiti River
   b. Uufau River

DISCUSSION

Species composition

Neritid communities farther away from the ocean differed dramatically from those communities located closer to the river mouth (Fig. 2 and 3) because the physical environment differs in these two stream locations (Table 1). For example, in the Amehiti River, the salinity was 0 ppt across the entire 700 m reach sampled, but in the

Uufau River the salinity ranged from 0 ppt to 32 ppt. Liu and Resh (1997) found that *Neritina auriculata* had higher survivorship when placed in saltwater than of other neritid species, which included *Neritina canalis*, *Neritina turrita*, *Clithon spinosa*, and *Septaria porcellana*. This ability of *Neritina auriculata* to tolerate the higher salinity levels of marine waters allows it to dominate stream river mouth habitats that become inundated with saltwater during high tides (Liu and Resh 1997). In addition, the average water depths of upstream reaches were shallower than stream reaches closer to the ocean (Table 1). In the Amehiti River, the greatest average depth was only 0.16 m but in the Uufau River, the greatest average depth was 0.33 m. The shallower streambeds in the Amehiti River caused neritids in these locations to be more exposed to hydrologic stresses. It has been documented that some species of Neritidae use deeper waters as "migratory pathways" (Blanco and Scatena 2005), allowing them to find some refuge from the fast moving waters as they travel to upstream reaches. Laboratory experiments have shown *Neritina auriculata* to be more sensitive to hydrologic stress than other common Mo'orean neritid species (Liu and Resh 1997). Thus species like *Clithon spinosa* and *Neritina canalis* comprised upstream neritid communities because they are more tolerant of increased hydrologic stress associated with those habitats.

Shell heights

In the Uufau River, larger individuals of *Neritina auriculata* were located farther from the river mouth and smaller individuals were located closest to the river mouth, because individuals farther upstream were more likely to be older and had more time to migrate upstream (Fig. 4b). These findings agree with a previous study conducted on Mo'orea, which found that the shell length of *Neritina auriculata* increased farther upstream (Morton 2004). Schneider and Frost (1986) proposed that the migrational behavior of neritid snails is an evolutionary adaptation that predominates in young juveniles. Smaller sized juvenile snails are more susceptible to being washed downstream and out of most optimal habitats, because their feet are smaller and less powerful (Vogel 1981 in Schneider and Frost 1986).

It is also possible that this pattern of increasing shell height with increasing distance from ocean was most evident because the young juveniles near the river mouth of the Uufau had not yet begun their upstream migrations. In Puerto Rico, upstream migrations of *Neritina virginea* begin after high-discharge floods (Blanco and Scatena 2005). In Mo'orea, the normal rainy season was delayed and no large floods events occurred until after the study was concluded. This lack of high-discharge events could be responsible for the delayed migrational behavior of neritid species.

The differences of average shell heights of neritid species in the Amehiti River and Uufau River can also be explained by increased hydrologic tolerances of larger individuals (Schneider and Frost 1986). The species of neritids in the upstream reaches of the Amehiti River had larger average shell heights, which suggests that they were overall bigger than the same species found in the Uufau River. The larger individuals most likely had larger feet that they used to attach themselves to substrate. These larger feet allowed them to tolerate the increased hydrologic stress they experienced these shallow high velocity habitats (Schneider and Frost 1986).

Species abundances

The decline in abundance of each species of neritid at higher water velocities in the Amehiti River and Uufau River suggests these species are relatively sensitive to hydrologic stress; however, *Neritina canalis* was able to maintain the highest abundances at the highest water velocities and its decline was more gradual than the other species suggesting it has some advantage over the other species (Fig. 5a-b). An organism's ability to tolerate hydrologic stress and maintain its position within a stream is influenced by its shell morphology (Vogel 1981 in Schneider and Frost 1986). It is possible that *Neritina canalis* has a more hydrodynamic shell that makes it less sensitive to the stress associated with higher water velocity habitats. In addition, *Neritina canalis* dominated the undersides of substrate (Fig. 6a). During flume-tank experiments, Holomuzki and Biggs (2000) found that *Potamopyrgus* snails actively chose locations on the underside of large rocks during high flows to avoid dislodgement. It is possible that *Neritina*

canalis exhibits the same behavior and prefers the undersides of substrate (Liu 1995); where as, species like *Neritina turrita* and *Neritina auriculata*, that were found to have similar abundances to *Neritina canalis* in low water velocities (Fig. 5a-b); were found mainly the sides and tops of substrate, where they are more easily dislodged (Fig. 6a-b).

Conclusion

The distributions of species of Neritidae in two coastal streams on Mo'orea, French Polynesia were influenced by migrational behavior of young juveniles (Frost and Schneider 1986) and physical characteristics, such as, water velocity, water depth, and substrate of stream habitats (Liu 1995); it was the combination of these biotic and abiotic factors interacting with each other that determined the distributions of neritids. The physical characteristics of stream environments, which are created as water flows through the system (Hart and Finelli 1999), determine the number and locations of suitable habitats along the stream reach (Lake 2000) and how difficult it is to reach those optimal habitats (Blanco and Scatena 2006). However, the biology and evolutionary adaptations of organisms living within these aquatic environments determine which species reach these habitats (Blanco and Scatena 2006, Crandall et al. 2005). Understanding the relationship between these biotic and abiotic factors could lead to a better understanding of the distribution patterns of neritid snails of the Pacific.

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