The Relationship between Shell Morphology and Microhabitat Flow in the Endemic Hawaiian Stream Limpet (*Hīhīwai*), *Neritina granosa* (Prosobranchia: Neritidae)[1]

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ABSTRACT: The Hawaiian stream limpet, *Neritina granosa* Sowerby, has three shell morphologies: conic (smooth, narrow shell), intermediate (rugose, narrow shell), and winged (flattened, rugose, and flared shell margin). We studied the relationship between shell morphology and water flow in a laboratory flume and in populations from Palauhulu Stream, Maui. Winged morphs represented 82% of the population at the mouth below the terminal waterfall. At sites above the falls, conic and intermediate morphs dominated. Limpets from the mouth had significantly lower shell-length/shell-width and body-weight/shell-weight ratios and occurred in areas of lower benthic and surface velocities than upstream populations. Field determinations of velocities (measured with a thermistor-based microcurrent meter) around individual *N. granosa* in the field that were oriented parallel to flow demonstrated that conic and intermediate morphs experienced significantly less drag than winged morphs; there was no significant effect when shells were oriented perpendicular to flow. In a laboratory flume, conic and intermediate shells oriented parallel to flow exhibited significantly greater lift and less drag than a winged morph. There was no significant difference in lift and drag for conic and winged morphs in a perpendicular orientation. Because field orientation of the three shell morphs is unpredictable, we hypothesize that microhabitat flow has little or no effect on the phenotypic expression of shell morphology in *N. granosa*. We feel that the transition between winged and conic/intermediate morphs in upstream populations is restricted by bioenergetic constraints on the partitioning of energy between the competing demands of shell and tissue growth.

IT HAS BEEN REPORTED that the streamlined body shape of many macroinvertebrates is a morphological adaptation for reducing lift, drag, and shear forces in rapid-flow environments (Vogel 1981, Denny 1988). The generality of this conclusion has recently been challenged on the premise of a lack of data on the hydraulic regime encountered by benthic macroinvertebrates (Statzner and Holm 1982, 1989, Statzner 1988) and intertidal limpets (Denny 1989). In addition to basic body form, body ornamentations such as ribbed and/or rugose surfaces and body irregularities can potentially act as roughness elements for altering the effects of lift and drag (Vogel 1981, Denny 1989). Statzner et al. (1988) have emphasized the importance of quantifying the microhabitat hydraulic regime at the microhabitat level of benthic macroinvertebrates to more fully understand the ecological, physiological, and behavioral adaptations of these organisms to flow.

The endemic Hawaiian limpet (*hīhīwai*), *Neritina granosa* Sowerby, occurs in streams on all of the major Hawaiian Islands. *N.*

granosa populations are generally found in shallow, well-oxygenated streams on gravel, cobble, boulder, and bedrock substrates and are restricted in distribution to streams with continuous flow (Ford 1979). This distributional restriction is believed to result from the diadromous life cycle of *N. granosa* in which there is an obligatory period of oceanic larval development (Maciolek 1978, Ford 1979). Vermeij (1969), Maciolek (1978), and Ford (1979) have reported the existence of two distinct shell morphologies in *N. granosa*: a conic morph characterized by a smooth, narrow shell and a winged morph that exhibits a flattened, crenulated shell margin and a ribbed and rugose ornamentation. Maciolek (1978) and Ford (1979) have reported a distinct gradient with respect to shell form, with the conic morph being prevalent above the first waterfalls and at higher elevations and the winged morph being found near the stream mouth. Vermeij (1969) hypothesized that the rugose shell ornamentation in this species was an adaptation to minimize the effects of drag in the high-gradient streams characteristic of Hawai'i. Ford (1979) hypothesized that shell morphology and ornamentation were attributable to environmentally induced phenotypic variation and suggested that high velocities were the principal variable affecting the growth of the mantle and an inhibition of lateral wing formation.

The objectives of this study were to: (1) assess the degree of instream morphological variation in *N. granosa*; (2) describe the flow regime encountered by *N. granosa* in the field; and (3) quantify the relationship between shell morphology and orientation and flow in the field and laboratory flume.

Study Area

Palauhulu Stream is a third-order stream on the windward side of the island of Maui. The stream originates at ca. 853 m elevation, is partially diverted at 610 m, 457 m, and 20 m elevations (288 liters day^{-1}), and is continuous until joining Pi'ina'au Stream above the terminal falls that empties into Waialohe Pond 100 m upstream of where it discharges into the Pacific Ocean. The substrate in the stream is a combination of gravel, cobble, boulder, and bedrock, and there is a dense riparian canopy of both native and introduced vegetation. Palauhulu Stream, like most Hawaiian streams, has a stair-step sequence of waterfall, pool, and rapids. A long-term sampling station was established in January 1990 ca. 300 m upstream of the confluence with Pi'ina'au Stream at an elevation of ~40 m (= upstream site). There are three waterfalls between this upstream site and the ocean; a 6-m falls 100 m downstream of the sampling station, a 3-m falls 20 m upstream from the confluence with Pi'ina'au Stream (part of a water diversion into taro fields), and the 4-m terminal falls that empties into Waialohe Pond near the mouth of Pi'ina'au Stream. At the upstream site, water depths at median flows during 1990–1991 ranged from <0.10 m in rapids to 1.5 m in pools, and water temperatures ranged from 16°C to 21°C. The hydraulic regime of Palauhulu Stream was determined on a regular basis during 1990–1991 and is extremely variable and flashy, with daily flows ranging from 0.4 to 283 m^3 sec^{-1}. Median flows ranged from 1.13–1.17 m^3 sec^{-1}. Periodic collections of limpets were also made at the Pi'ina'au mouth at Waialohe Pond (= mouth), a broad (10 m), deep (2–4 m) channel; and at the confluence of Pi'ina'au and Palauhulu streams (= confluence), a shallow (<1 m), high-velocity riffle/run.

MATERIALS AND METHODS

Neritina granosa is common in both Pi'ina'au and Palauhulu streams, with densities ranging from 10 to 50 m^{-2} (C.M.W. and A.J.B., unpublished data). On 17 February 1991, samples of *N. granosa* were collected from three sites: (1) below the terminal falls in Waialohe Pond (mouth); (2) at the confluence of Palauhulu and Pi'ina'au streams above the first falls (confluence); and (3) at 40 m altitude and above three waterfalls (upstream). Individuals used for measurements of shell morphology were collected by randomly selecting 0.25-m^2 sampling quadrats in all habitat types (pools, runs, rapids) and removing all individuals from substrate surfaces and the under-

sides of movable rocks. Instream orientation with respect to flow was noted for each limpet before collection. Limpets were fixed in ~5% neutral formalin in the field for subsequent measurements in the laboratory. Measurements of shell length (SL = greatest anterior-posterior dimension), shell width (SW = greatest lateral dimension), and shell height (SH = greatest dorsal-ventral dimension) were measured to the nearest mm with hand-held dial calipers. Using Ford's (1979) criteria for conic and winged morphs, each shell was categorized as morphologically conic (smooth, narrow, rounded shell) or winged (flattened, crenulated shell margin and a ribbed and rugose ornamentation). The majority of limpets collected at the confluence and upstream sites had heavily ribbed and rugose shells but were conic in shape. We designated this morphology as intermediate (between conic and winged).

Subsamples of 20 limpets spanning the population size range from each of the three sites collected in February 1991 were chosen for the determination of body-weight/shell-weight ratios. Conic juveniles <20 mm SL were excluded from this analysis. Shell length and width of each limpet was measured, the body removed from the shell, and the shell and tissues dried to a constant weight at 60°C for 24 hr. Ambient benthic and surface velocities were determined at the three sites. Measurements were taken 1 cm above the sediment-water interface and 1 cm below the water surface at 10 points spanning the width of the stream.

Field measurements of flow velocities around *N. granosa* were collected for 30 limpets from the upstream site in July and November 1990, and for 21 limpets from the mouth site in February 1991. Current velocities were measured at points around *N. granosa* using a thermistor-based current meter. Velocities were measured 1 cm upstream of the shell edge, ~1 mm above the shell apex, and 1 cm behind the downstream shell edge. Velocity measurements were also taken at 1 cm below the water surface. Velocity measurements were based on a running average of eight readings taken at 10-sec intervals. Data on instream orientation (parallel or perpendicular to primary velocity vectors), shell length, and morphological type (conic, winged, intermediate) of each limpet were recorded. Determinations of the effects of shell shape on ambient flow regimes were approached using two indirect indicators of lift and drag forces. The relative magnitude of lift forces was calculated as the percentage increase in velocities from the leading shell edge to the shell apex, with steeper velocity gradients indicating relatively greater lift forces (directed toward the water surface) imparted on the shell. The magnitude of drag forces was measured as the percentage recovery of ambient upstream velocities 1 cm behind the trailing shell edge, with greater differences between upstream and downstream velocities indicating greater momentum removed from the flow and thus greater drag forces.

The thermistor-based current meter was constructed according to LaBarbera and Vogel (1976) and Vogel (1981). Sensing probes were modified for use in both high-gradient stream habitats and high-velocity flumes (Burky and Way 1991). Calibration of the meter and probe was achieved with a unit that modified and combined designs from Vogel (1981), Muschenheim et al. (1986), and Burky and Way (1991).

Current velocities were mapped around distinct shell morphs (conic, intermediate, and winged) of *N. granosa* in a 12 by 0.5 by 0.5 m (length:width:height) oblong, fiberglass racetrack flume. Shells of *N. granosa* were anchored 20 cm from the trailing edge of a 150 by 1.5 cm piece of clear Plexiglas with modeler's clay and placed at one end of a 5-m raceway. Flows in the flume were created using a small, variable-speed electric boat motor anchored to the beginning of the opposite raceway. The motor was capable of generating flows up to 80 cm sec^{-1} at the point of shell placement. Flow characteristics in the flume at the experimental velocities are given in Table 1. Current velocities were measured at points around *N. granosa* shells using the thermistor-based current meter. The sensing thermistor was held in place by a stainless steel micromanipulator that permitted x, y movements in 1-mm intervals. All velocity measurements were based on a running average of

TABLE 1

HYDRAULIC CHARACTERISTICS OF THE LABORATORY FLUME AT THREE EXPERIMENTAL VELOCITIES

	MEAN WATER COLUMN VELOCITY		
PARAMETER	12 cm/sec	44 cm/sec	61 cm/sec
Flume Reynold's no. (Re)	16,733	55,677	85,060
Boundary Reynold's no. (Re*)	6	23	33
Thickness of boundary layer (mm)	1.8	0.5	0.4

NOTE: Water column velocities were measured at mid-flume depth 10 cm in front of the leading shell edge.
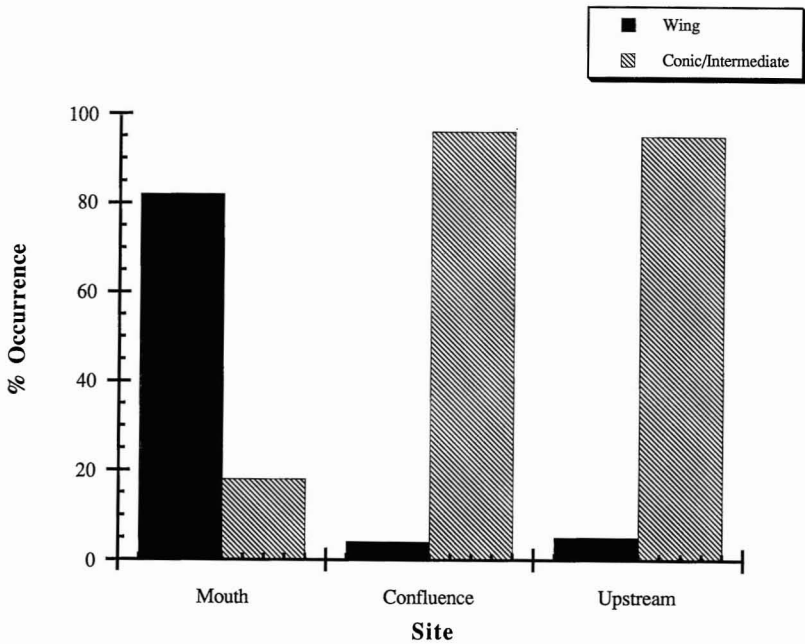

FIGURE 1. Percentage occurrence of winged and conic/intermediate morphs of *Neritina granosa* from the mouth, confluence, and upstream sites in Pi'ina'au and Palauhulu streams, Maui.

eight readings taken at 10-sec intervals. Profiles were measured at three flume velocities spanning measured ambient conditions. Velocities were measured around a conic morph (from upstream site) and a winged morph (from mouth site). In addition, profiles were constructed for one flume velocity around an intermediate morph (a heavily rugose, conic shell from upstream site). All experimental shells had similar shell lengths (40 mm), heights (14 mm), and widths (35 mm conic; 36 mm intermediate; 42 mm winged). Measure-

ments were taken with the anterior end of the shell facing the current (parallel orientation). Also, profiles were measured for each morph with the shells anchored in a position perpendicular to flow (head facing the left descending side of the flume) at one flume velocity.

RESULTS

There was a pronounced difference in the distribution of shell morphs at the three sites.
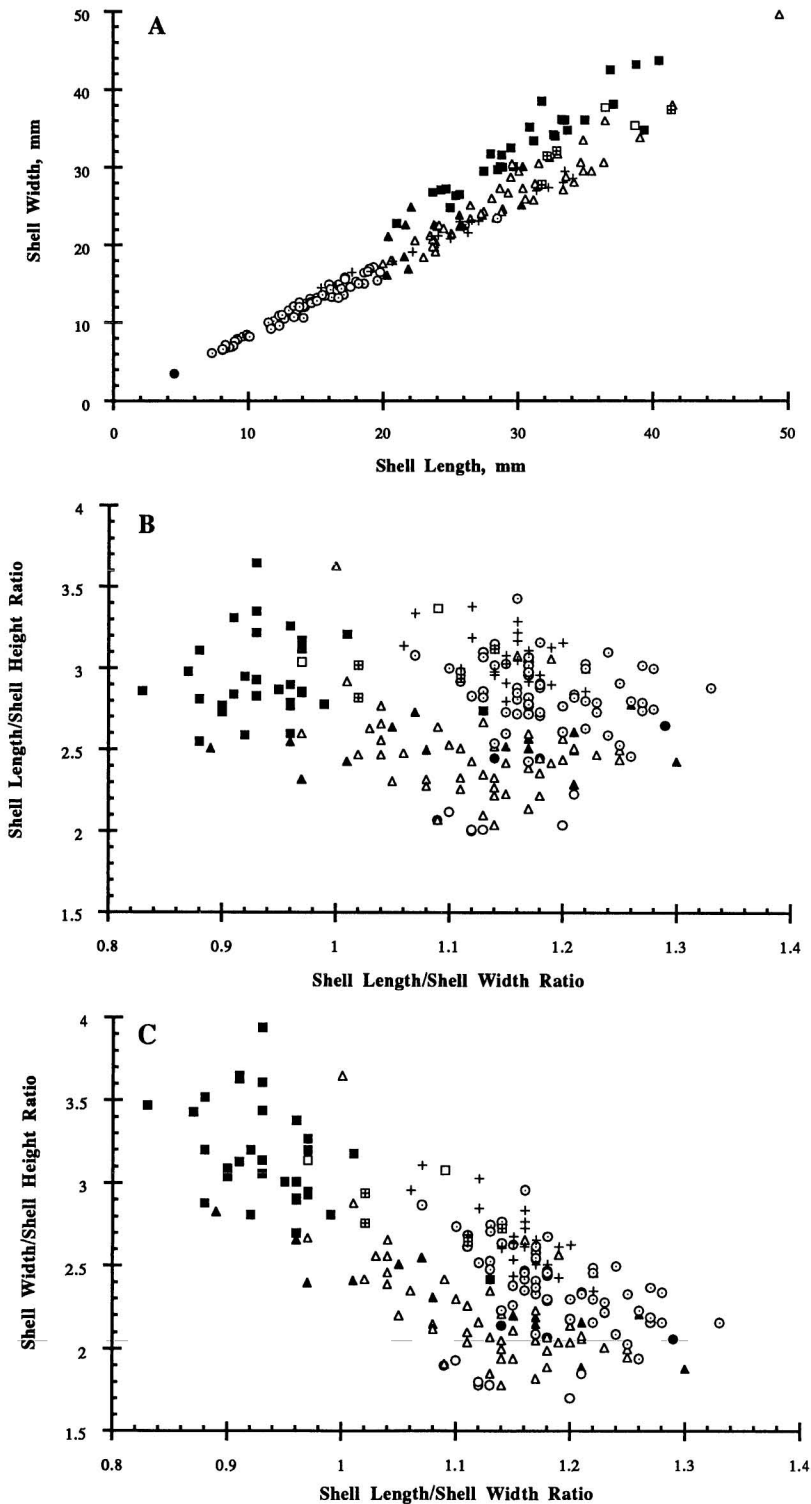
FIGURE 2. Relationships between dimensions of shell length, shell width, and shell height for *Neritina granosa*. Black shapes represent snails from the mouth site, open shapes represent snails from the confluence site; a plus or shapes with either a plus or point represent snails from the upstream site. Circle, triangle, and square shapes represent shells of conic, intermediate, and winged morphs, respectively.

The population from the mouth site was dominated by individuals with prominent wings (82% of the total), but winged individuals were uncommon at the confluence and upstream sites (Figure 1). At these latter sites, large limpets (> 20 mm) were of intermediate morphology and small limpets (< 20 mm) were conic. Conic and intermediate morphs made up 95 and 96% of the total population,

respectively (Figure 1). At all sites, individuals with SL < 12 mm were conic morphs (Figure 2). This observation agrees with that of Ford (1979) that all undifferentiated spat exhibit the conic morphology. In general, shells with pronounced wings (particularly those from the mouth site) had SL/SW ratios < 1.0 and SW/SH ratios > 2.5 (Figure 2). It is possible at these three sites to use quantitative mor-

TABLE 2

MEAN VALUES OF SHELL LENGTH, SHELL WEIGHT, DRY BODY WEIGHT/DRY SHELL WEIGHT, AND AMBIENT BENTHIC
VELOCITIES FOR STUDY SITES IN PALAUHULU AND PI'INA'AU STREAMS, MAUI

SITE	SL/SW (SD)	BODY WT/SHELL WT (SD)	BENTHIC VELOCITY (cm/sec) (SD)
Mouth	0.93 (0.03) a	0.1315 (0.0194) a	29.1 (1.4) a
Confluence	1.15 (0.04) b	0.2640 (0.0564) b	55.8 (3.3) b
Upstream	1.16 (0.05) b	0.2630 (0.0444) b	65.4 (4.2) b

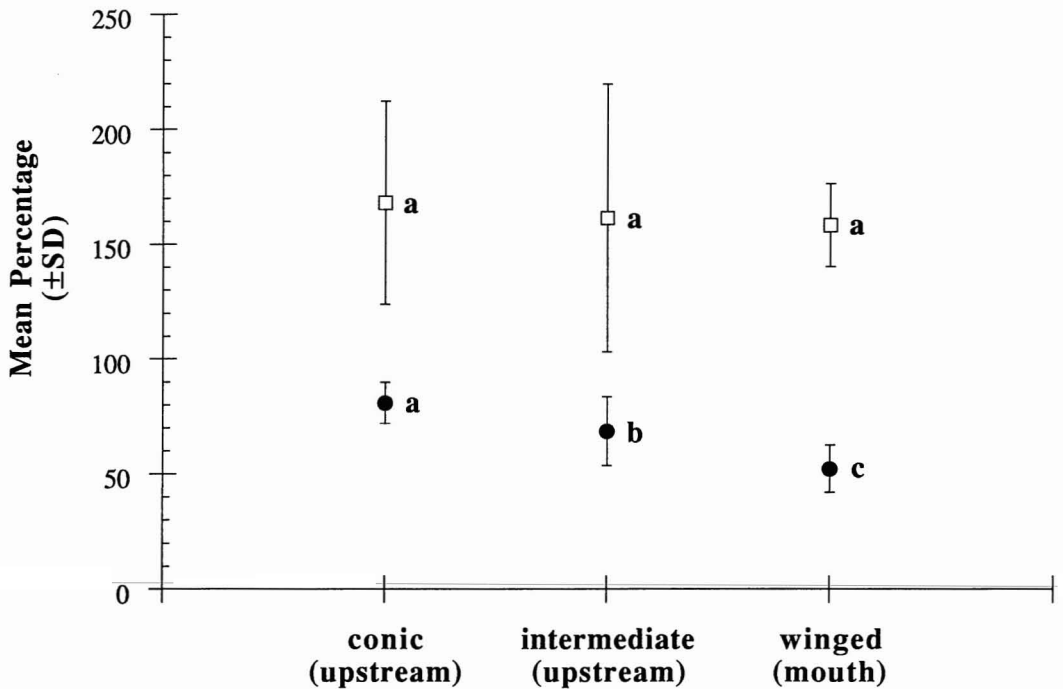Values in a column followed by the same letter are not significantly different (Duncan's test; $P > 0.05$).

FIGURE 3. Mean percentage increase in velocity from leading shell edge to shell apex (lift; open square) and mean percentage recovery of ambient velocities 1 cm behind the trailing shell edge (drag; black circle) for conic, intermediate, and winged morphs of *Neritina granosa* in Palauhulu and Pi'ina'au streams, Maui. Bars represent SD. Means with the same letter are not significantly different ($P > 0.05$).

phometric measurements to reliably separate winged and conic/intermediate morphs.

Limpets from Pi'ina'au Stream mouth had significantly lower body-weight/shell-weight ratios (Table 2). Comparisons of winged and conic limpets of equal tissue mass (1 g) give predictions of larger shell dimensions (SL = 40.6 and 38.7 mm; SW = 44.3 and 34.3 mm for winged and conic morphs, respectively) and shell mass (7.6 versus 3.8 g for winged and conic, respectively) for winged morphs. That is, for limpets of equivalent tissue mass, an individual of the conic form probably expends significantly less energy on shell growth. Winged limpets also had significantly lower SL/SW ratios and occurred in lower benthic and surface velocities (indicating slower-moving water in the mouth) than limpets from the confluence and upstream sites (Table 2).

In the field, there was no significant difference in the anterior velocity gradients around the three morphs oriented parallel to the flow (Figure 3). The variance in the velocity gradient for winged limpets, however, was 10 and 2 times less than those measured for the intermediate and conic morphs, respectively. The large variances measured for the intermediate and conic morphs indicate that there was considerable turbulence in the vicinity of the sensing thermistor. There were significant differences among the percentage recoveries of ambient velocity for all three morphs. Trailing downstream velocities were 81, 69, and 52% of upstream velocities for conic, intermediate, and winged morphs, respectively. There was no significant effect of limpet orientation on either upstream velocity gradients or downstream recovery of ambient velocities (a field sample of four intermediate and five winged limpets).

Substrate heterogeneity (boulder/rock/bedrock) of high-gradient Hawaiian streams provides a multitude of microhabitats with low-velocity shelters in areas of high-velocity sur-
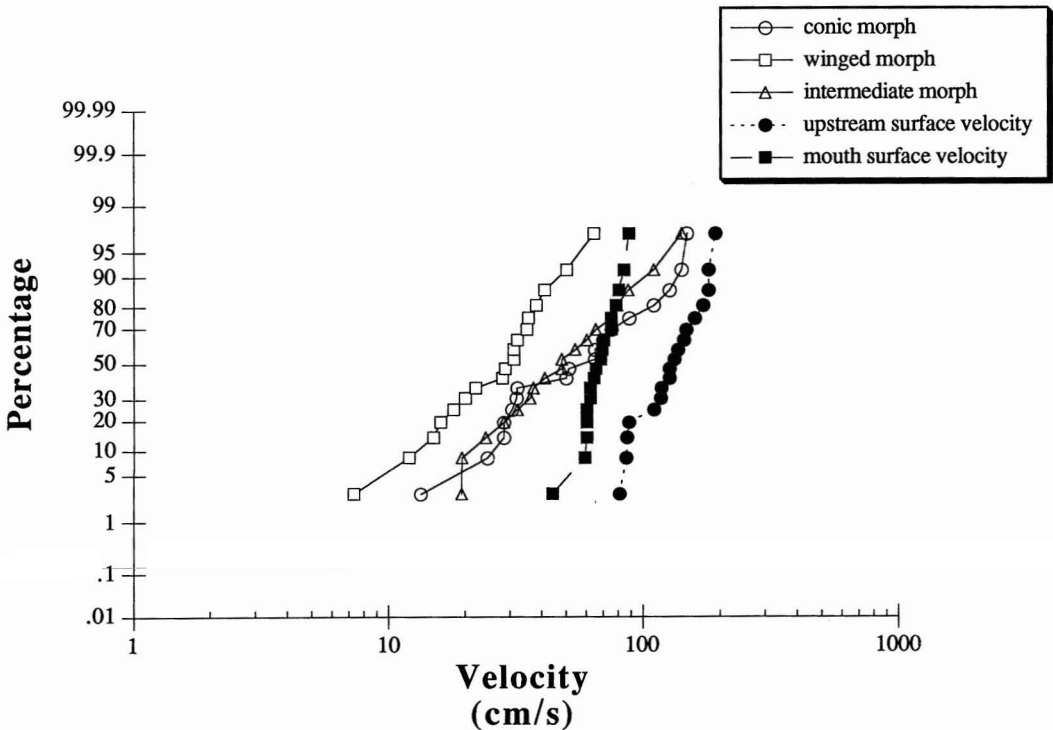

FIGURE 4. Probability of surface and benthic velocities and the percentage (probability) occurrence of conic, intermediate, and winged morphs of *Neritina granosa* at specific velocities at the mouth and upstream sites.

face flows. At the confluence and upstream sites, *N. granosa* was found on substrate surfaces in areas beneath high-velocity water column flows, but snails at the mouth site were found in slower-moving water. Ninety percent of winged limpets measured at the mouth site were found at benthic velocities <40 cm $\sec^{-1}$, but only 40% of the conic and intermediate morphs measured at the upstream site occurred at benthic velocities <40 cm $\sec^{-1}$ (Figure 4).

The pattern of flows measured around *N. granosa* in the laboratory flume is given in Figures 5 and 6. There was an increase in
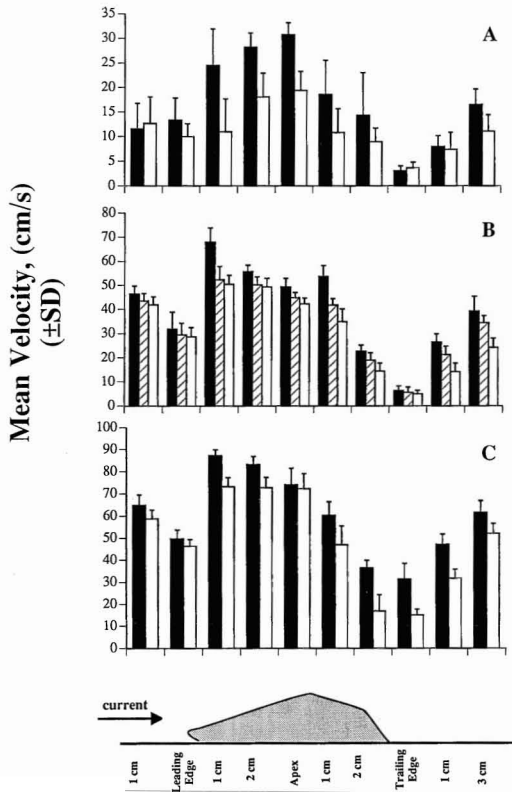

FIGURE 5. Comparison of velocity profiles in a laboratory flume for shells of conic and winged morphs oriented parallel to the flow at three flume velocities. Comparative data for intermediate shell morphs are given in B. Black bars = conic morph, hatched bars = intermediate morph, open bars = winged morph, and vertical lines on a bar represent one standard deviation. The shell schematic below the graphs indicates points where velocity measurements were taken.

velocities from the leading shell edge to shell apex, a decline from the apex to the trailing shell edge, and recovery of ambient velocities 3 cm behind the shell (Figure 5). Above the shell apex, velocities recovered to ambient levels over 3 vertical cm. For all flume velocities, there was a significant difference between conic and winged morphs in the measured anterior velocity gradients and the degree of downstream recovery such that conic forms experienced relatively greater lift and less drag than the winged forms (Figure 5). The magnitude of these differences decreased with increasing flume velocities. The pattern of velocities around an intermediate morph at 42 cm $\sec^{-1}$ was significantly different and in between that of conic and winged morphs. The velocities measured at 42 cm $\sec^{-1}$ for conic and winged morphs in a perpendicular orientation showed no significant differences in either anterior velocity gradients or downstream velocity recovery (Figure 6).

DISCUSSION

Recent research has pointed to the inadequacy of the characterization of the hydraulic regime encountered by organisms in stream habitats (Nowell and Jumars 1984, Statzner et al. 1988, Davis and Barmuta 1989, Statzner and Holm 1989). The importance of water column, benthic, and microhabitat flow in the ecology, behavior, and physiology of stream organisms has become increasingly evident (Statzner et al. 1988). Traditional measurements of the hydraulic stream habitat have included surface, 0.6 depth, and mean water column velocities, mean water depth, wetted perimeter, stream slope, and substrate particle size. However, these "gross-scale" measurements are on the order of meters and tens of centimeters and are inadequate for describing the hydraulic habitat of benthic macroinvertebrates.

In recent years, new techniques and methodologies for measuring have been used in an attempt to more adequately describe the microhabitat flows encountered by benthic stream macroinvertebrates in the field. Laboratory studies using laser doppler anemom-
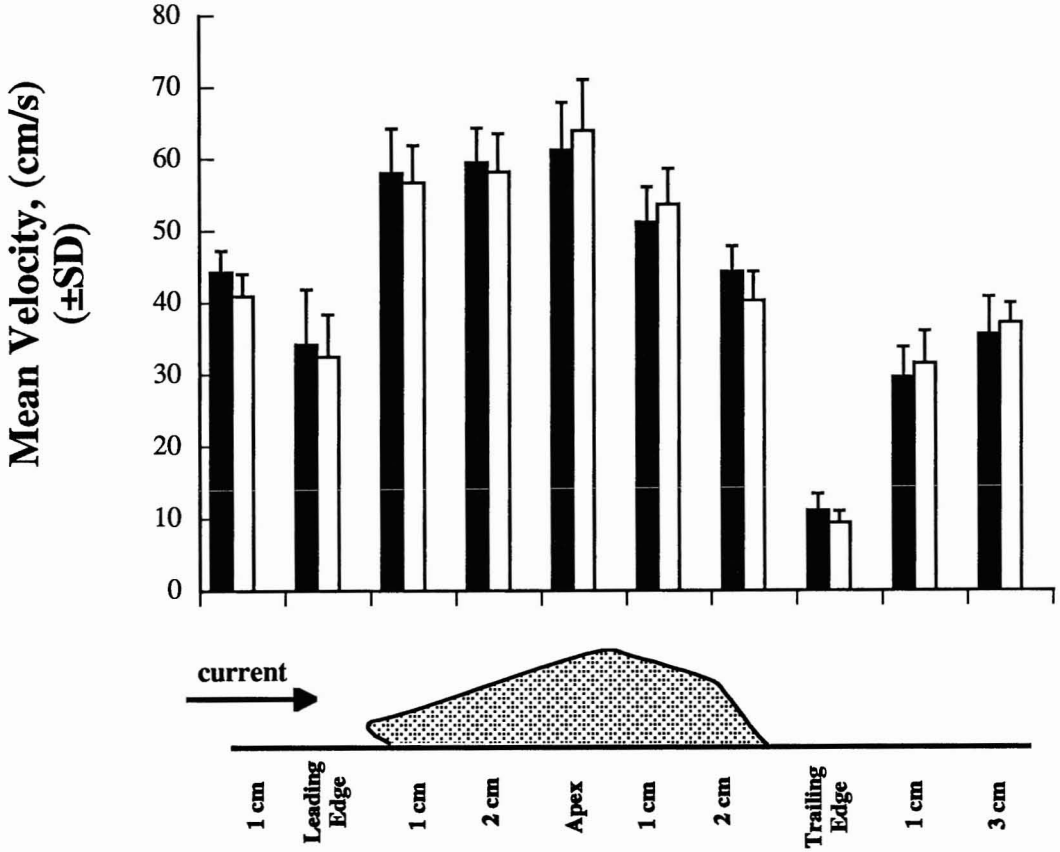
FIGURE 6. Comparison of velocities in a laboratory flume for shells of conic and winged morphs oriented perpendicular to the flow at an ambient velocity of 42 cm sec^{-1} (the velocity used in Figure 5B). Black bars = conic morph, open bars = winged morph, vertical lines on a bar represent one standard deviation. The shell schematic below the graph indicates points where velocity measurements were taken.

etry (LDA; Craig and Chance 1982, Statzner and Holm 1982, Chance and Craig 1986, Statzner and Holm 1989) have shown that flow regimes around benthic macroinvertebrates can vary over a spatial domain of millimeters. Field techniques have included standard hemispheres (Statzner and Muller 1989, Peckarsky et al. 1990), microhabitat substrate samplers (Gore 1978, Statzner et al. 1988), and small, propeller-type current meters (Whetmore et al. 1990). However, these field techniques are unable to directly measure hydraulic variables with spatial resolutions on the order of millimeters. MacIntyre (1986) and Losee and Wetzel (1988) used thermistor-based microcurrent meters to characterize

hydraulic habitats in lentic environments with low flow velocities. We have modified this thermistor-based current meter with sensing probes for field use in high-velocity streams. This field current meter has a spatial resolution of ~2 mm and we have been able to successfully quantify small-scale flow regimes around *N. granosa* in the laboratory and under natural conditions in the field.

Neritina granosa showed a gradient in shell form from the mouth of Pi'ina'au Stream to a site 500 m and three waterfalls upstream in Palauhulu Stream. Winged morphs were significantly more abundant at the mouth of Pi'ina'au Stream, but winged morphs were uncommon at sites above the first and third

falls, respectively. At these sites, individuals > 20 mm were generally intermediate in shell morphology (conic but rugose), but those individuals < 20 mm SL were strictly conic. We found significant differences in SL/SW and SH/SW ratios between a population of *N. granosa* at the mouth of Pi'ina'au Stream (wider, shorter shells = "winged") and populations separated from the mouth by one and three waterfalls (narrower, higher-spired shells = "conic or intermediate"). Maciolek (1978) observed that the winged morph was generally confined to lower stream reaches, and the conic morph was found at higher altitudes. He noted that in some streams there was a gradual change in shell morphology with altitude, but in streams with high waterfalls ('Akaka Falls and Kolekole Falls on the island of Hawai'i) there was a sharp separation between the two morphs. Ford (1979), in Waiohue Stream, Maui, found significant differences in SL/SW and SH/SW ratios between limpets collected at upstream and downstream sites, such that upstream limpets had shells that were narrower and higher spired. He noted that the waterfall nearest to the stream mouth delineated the boundary between the two morphological types. In the three streams he studied (two on the northeast coast of Maui and one on Hawai'i), winged forms were restricted to stream courses below the first falls. In Pua'alu'u Stream conic morphs were found < 20 m upstream of the mouth, which discharged directly into the sea over a steep, terminal cascade. It is important to note that Ford did not distinguish the intermediate morph from the winged and conic morphs at his study sites.

Vermeij (1969) hypothesized that the winged, rugose shell morphology was an adaptive advantage to life in strong currents because a flattened profile would lessen drag and roughness elements would reduce shear forces. Maciolek (1978) and Ford (1979) both rejected this hypothesis after observing that downstream reaches dominated by winged forms had stream flows less than those found at higher elevations. Laboratory flume studies of velocity profiles over *N. granosa* shells showed that conic and intermediate morphs oriented parallel to flow experienced signi-

ficantly less drag and greater lift than a winged morph for all flume velocities. These differences were not significant for conic and winged morphs oriented perpendicular to flume flows. Field velocity measurements around individual limpets showed that conic morphs oriented parallel to flow experienced significantly less drag than winged forms but experienced no differences when oriented perpendicular to flow. Ambient benthic velocities around measured conic limpets at the confluence and upstream sites were significantly greater than those at the stream mouth. However, there was no consistent relationship between the orientation of *N. granosa* and the primary velocity vectors in the stream. This seems intuitive when considering a habitat characterized by an extremely heterogenous particle size distribution, flow velocities varying two orders of magnitude from the surface to the bottom, and benthic velocity vectors that are unpredictable over spatial scales of centimeters (Way and Burky 1991).

Conic and intermediate morphs experience less drag and lift than winged morphs only when oriented parallel to flow, and we have noted that limpets in the field move and graze rocks in a random manner and thus orient randomly to flow. These observations question whether lift and drag are important selective forces for the evolution of shell morphology of *N. granosa*. Ford (1979) noted that the size and strength of the foot of *N. granosa* necessitated the use of force to dislodge specimens from the substrate. We have also noted the tenacity with which *N. granosa* adheres to substrate surfaces. We hypothesize that the strong muscular foot minimizes any observed differences in drag and lift forces on the different morphs between habitat types and argues against the importance of flow in determining shell morphology. Similar conclusions have been reached for the shell shape of the freshwater stream limpet *Ancylus* (Nachtigall 1974, Statzner and Holm 1989).

Ford (1979) hypothesized that environmental variables determined the shell morphology of *N. granosa*. Transplant experiments in which smooth, conic limpets from an upstream site in Waiohue Stream, Maui, were transplanted to a site near the stream mouth

resulted in pronounced wing development over a period of months. Reciprocal transplants were not conducted. It has also been observed that upstream conic forms of *N. granosa* from Palauhulu Stream kept in aquaria develop wings (S. Hau, Hawaii Division of Aquatic Resources, pers. comm.). Ford (1979) stated that a greater exposure to high-velocity currents in upstream sites was associated with a reduction in shell width and ornamentation and an increase in height. Ford hypothesized that the mechanism by which this occurred was the effect of strong currents on mantle growth and inhibition of lateral wing formation in *N. granosa*. A similar observation on changes in shell morphology with changing current velocities has been made for the estuarine neritid *N. violacea* (Gmelin) (Murty and Balaparameswara Rao 1978).

The intertidal neritid *Clithon cariosus* (Wood) and the estuarine (and sympatric for a short distance at the Piʻinaʻau mouth) neritid *N. vespertina* (Sowerby) both have winged shells (Kinzie 1990). In the streams studied to date, most *N. granosa* above the first falls do not have wings. The winged morphology in *N. granosa* probably represents the ancestral morphology and not a morphological adaptation to high-velocity stream flows.

We hypothesize that the development of a lateral wing in upstream populations is restricted by bioenergetic constraints. Analyses of body-weight to shell-weight ratios showed significantly greater ratios in the confluence and upstream populations (conic) when compared with the mouth population (winged). This translates into a 100% decrease in the relative shell mass for the conic morphs at the upstream sites. We feel that there is some limiting environmental variable(s) that requires limpets living in high-velocity environments to allocate a smaller portion of their assimilated energy to shell development, resulting in a shell that still has ornamentation but no lateral wing development.

The energetic cost of upstream migration is one hypothesis to explain the intraspecific differences in shell morphology. Energy is expended for climbing multiple falls and for continuous movement upstream at the expense of shell mass and wing formation. However, this hypothesis predicts a gradient of shell morphs along successive falls. In contrast, we and others have found sharp breaks in morphology of shells between the mouth and sites upstream of the first falls that are separated horizontally by only meters. An alternative explanation for the change in shell morphology is based on a balance of the bioenergetic demands at higher water velocities above the first falls. There may be differences in food quality and quantity at the mouth and upstream sites. Lower food quality above the mouth can potentially result in a lighter shell due to a physiological trade-off between shell and tissue mass. Hard substrates in the Piʻinaʻau mouth are covered by a rich periphyton/algal mat that is actively grazed by the limpets. Preliminary sampling of substrates above the first falls has indicated a relatively sparse periphyton community. Differences in algal densities may be due to reduced water velocities, an open versus closed riparian canopy (increased light penetration), and reduced scouring by spates at the mouth site compared with sites above the first falls. Conversely, because conic and intermediate morphs experience less drag (by greater lift) than winged morphs when oriented parallel to flow, it may be more adaptive to secrete a conic/intermediate shell and divert more energy into a larger foot. Alternatively, the energetic cost of maintaining position in high-velocity waters may require additional energy, which is diverted from shell growth.

Our data indicate that information is needed on the relationship of stream organisms to the flow regime of their microhabitat. We have found that there is little correlation between traditional gross hydraulic measurements of stream flow and flow at the level of millimeters (this study, Way and Burky 1991, Way et al. 1991). *N. granosa* appears to be responding to stream hydraulics on several temporal and spatial scales. Gross hydraulic variables (discharge, mean depth, wetted perimeter, etc.) influence the structural and functional character of a stream and can exhibit long-term periodicities that can ultimately determine species-wide biological responses (e.g., frequency and duration of spawning and the

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timing of upstream and downstream migration). These variables have the potential, however, for indirectly influencing shell growth in *N. granosa* by affecting the distribution and abundance of food. Microhabitat flows, which can vary over spatial and temporal scales of millimeters and minutes/hours, directly influence the daily existence of a limpet by determining paths of grazing, refugia from predators, migratory pathways, and aerial extent of spawning areas. Understanding the manner in which *N. granosa* responds to these two different spatial and temporal scales is necessary to more completely assess the role of stream hydraulics in the life of this organism.

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