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Issues for Aquatic Pedestrian Locomotion[1]

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SYNOPSIS. Aquatic pedestrian locomotion represents an important mode of locomotion for many aquatic and amphibious animals, both extant and extinct. Unlike terrestrial locomotion where weight is the defining force, in aquatic locomotion buoyancy and hydrodynamic forces may be as important as weight. Aquatic pedestrian locomotion differs fundamentally from swimming because pedestrians must maintain contact with the substratum in order to locomote. Ambient water motion may constrain or prevent locomotion of aquatic pedestrians by requiring that they actively grip the substratum. A comprehensive biomechanical analysis of aquatic pedestrian locomotion will require an integration of hydrodynamics with terrestrial locomotor dynamics.

INTRODUCTION

Walking or running along a substratum underwater is an important mode of locomotion for a diversity of aquatic and amphibious animals. Amphibious animals utilizing this mode of locomotion include those that are amphibious on daily, ontogenetic and evolutionary time scales. Many extant animals, such as insect larvae, crustaceans, salamanders, mudskippers and lungfish use pedestrian locomotion underwater rather than or in addition to swimming. Several benthic animal lineages have made the evolutionary transition between aquatic and terrestrial habitats, (notably the arthropods, molluscs, annelids, and vertebrates). Paleontological evidence suggests that many fossil arthropods, such as eurypterids, xiphosurans, and early scorpions, may have not only been amphibious, but may also have used pedestrian locomotion underwater in nearshore environments (Hanken and Stormer, 1975; Gordon and Olson, 1995).

While pedestrian locomotion on land and swimming in water have been well studied, relatively little is known about pedestrian locomotion underwater. Aquatic pedestrian locomotion differs fundamentally from swimming in that pedestrians push on the substratum rather than on the water to generate thrust, requiring that pedestrians maintain close contact with the substratum at all times. A few studies have considered the kinematics (Hui, 1992; Pridmore, 1994), physiology (Houlihan and Innes, 1984; Grote, 1981), hydrodynamics (Pond, 1975; Blake, 1985; Bill and Herrnkind, 1976), or motor patterns (Clarac *et al.*, 1987) of different aquatic pedestrians. In order to more fully integrate these various studies, a comprehensive biomechanical analysis of legged locomotion underwater is needed. Such an analysis would require a synthesis of techniques from terrestrial pedestrian dynamics and fluid dynamics.

Despite the extent to which we understand pedestrian locomotion in the terrestrial environment, these studies generally do not consider fluid forces because for terrestrial pedestrians, gravity produces the predominant external force and aerodynamic forces are usually considered negligible relative to weight. In a case where fluid forces were considered, Pugh (1971) found that for humans running in still air at 6 m/sec, drag accounts for only a 7% increase in the metabolic rate. Full and Koehl (1993), however, found that for small rapidly-running insects, fluid forces can be important, as

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will be discussed later in the text. In contrast to the situation for terrestrial pedestrians, buoyancy and hydrodynamic forces contribute significantly to the balance of forces for aquatic pedestrians. The 800-fold difference in fluid density accounts for the much greater hydrodynamic and buoyant forces on a body in water compared with a body in air; the buoyant force on aquatic pedestrians often approaches the magnitude of their weight, up to 80–99% in benthic crustaceans (Blake, 1985; Hui, 1992; Pond, 1975; Spaargaren, 1979). Perhaps the most profound effect of buoyancy on pedestrian locomotion, is that in reducing the effective weight but not the mass of an animal, it disrupts the pendulum-like exchange of potential and kinetic energy characteristic of terrestrial walking (Blickhan and Full, 1987).

Studying the locomotion of aquatic pedestrian animals will contribute to our ideas about possible constraints on an amphibious lifestyle, and the evolutionary transition between aquatic and terrestrial environments. Recognizing constraints on aquatic pedestrian locomotion in different habitats can help address ecological issues, such as foraging patterns, for these pedestrian animals. These aquatic pedestrians can also serve as biological inspiration for the design of autonomous legged underwater vehicles which are being developed for use in nearshore and aquatic environments. Most robot design currently focuses on neural control mechanisms (*e.g.*, Crisman and Ayers, 1992), rather than physical design principles that consider the environment in which the robot will be operating. Greiner *et al.* (1996), however, have created robots with morphology and behaviors inspired by surfzone organisms, such as a body that minimizes hydrodynamic forces and maximizes stability, as well as behaviors to deal with changing flow conditions, such as changing body posture and digging into the sand to keep from washing away.

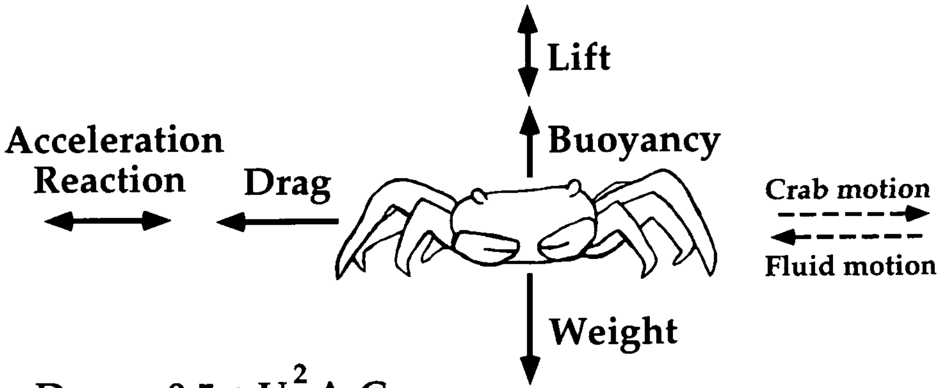
EFFECTS OF A SUBSTRATUM

The requirement of maintaining contact with a substratum confers added significance to ambient water flow for aquatic pedestrians. If waves or currents dislodge a pedestrian, the animal can no longer locomote unless it can reestablish its connection with the substratum. Thus the situation for pedestrian animals differs from that for most swimming animals. While for swimmers water motion either increases or decreases the effort required to locomote, water motion may constrain or even prevent pedestrian locomotion by necessitating that animals actively grasp the substratum to keep from washing away.

The problem of maintaining contact with the substratum is a general one that applies to benthic organisms, including sessile creatures, as described in Koehl (1984) and Denny (1988). Another surfzone locomoter, the swash-riding clam *Donax variabilis,* must maintain contact with substratum at a pivotal point on the shell in order to orient in waves, allowing it to sustain a controlled ride up the beach and gain a foothold in the sand before being swept back in the returning wave (Ellers, 1995).

In addition to providing an anchor against ambient water motion, the substratum can also affect the local flow seen by an animal. In a current flowing over a substratum, a velocity gradient (boundary layer) develops above the substratum, in which pedestrians that are small relative to the thickness of the boundary layer encounter slower flow than freestream flow (flow unaffected by the boundary). Pedestrians in faster flow conditions encounter thinner boundary layers. Under breaking waves, the height of a boundary layer is negligible because there is not sufficient time for it to develop (Denny, 1988). Under typical wind-driven waves, however, boundary layers can reach a height of 5–10 cm above the substratum (Grant and Madsen, 1979). Furthermore, a more rugose substratum or canopies of sessile organisms may disrupt the freestream flow sufficiently to create microhabitats with lower water velocities than freestream velocity (*e.g.*, Nowell and Church, 1979; Lau and Martinez, in prep.; Koehl, 1977).

Presence of a substratum can also directly influence the hydrodynamic forces on aquatic pedestrians. Aeronautical engineers are concerned with the phenomenon of ground effects, in which proximity of the



$$\text{Drag} = 0.5\ \rho\, U^2 A\ C_D$$

$$\text{Lift} = 0.5\ \rho\, U^2 A\ C_L$$

$$\text{Acceleration Reaction} = a\ (m + \rho\ V\ C_a)$$

FIG. 1. Forces on the body of an aquatic pedestrian moving through waves.

ground interferes with air circulation about airplane wings, causing a decrease in drag and an increase in lift on the wing (McCormick, 1979). Ground effects may be important for low-flying birds (*e.g.*, Withers and Timko, 1977; Vogel, 1994) and bottom dwelling fish (Blake, 1979) as well. Since ground effects are significant for objects within about one-quarter chord (length in direction of flow) distance above the substratum, they must be considered when studying the fluid dynamic forces on aquatic pedestrians.

HYDRODYNAMIC FORCES

Forces due to locomotion

The hydrodynamic forces on the body of a pedestrian include drag, lift and acceleration reaction (Fig. 1). Drag acts in the direction of relative fluid motion, tending to resist the animal's locomotion. Lift acts at right angles to the relative fluid motion, usually either toward or away from the substratum. Thus, positive lift will add to the buoyancy, decreasing the effective weight of the animal, and negative lift will augment the weight of the animal. Drag (D) and lift (L) on macroscopic organisms are given by essentially the same equation with different coefficients:

$$D = 0.5\rho U^2 A C_D \qquad (1)$$

$$L = 0.5\rho U^2 A C_L \qquad (2)$$

where ρ = water density, U = velocity, A = reference area, and C_D and C_L = coefficients of drag and lift, respectively. The reference area is often taken to be the area over which the force acts, *e.g.*, projected area (flow's-eye-view) for drag and planform area for lift. Those who deal with swimming animals often use a different convention for the area than those who work with benthic organisms (*i.e.*, planform or wetted area versus projected area), preventing meaningful comparisons unless both types of area measurements are reported. Figures 2 and 3 show coefficients of drag and lift for a few aquatic pedestrians, for comparison with other familiar creatures. Higher drag coefficients for aquatic pedestrians than for swimmers appears to be an emerging pattern, but more data are needed. Lift coefficients show no clear pattern. Interestingly, even though an inclined wing has a greater lift coefficient than pedestrians, its drag coefficient falls within the same range as pedestrians.

Accelerating bodies and appendages experience another hydrodynamic force, acceleration reaction, in addition to drag and

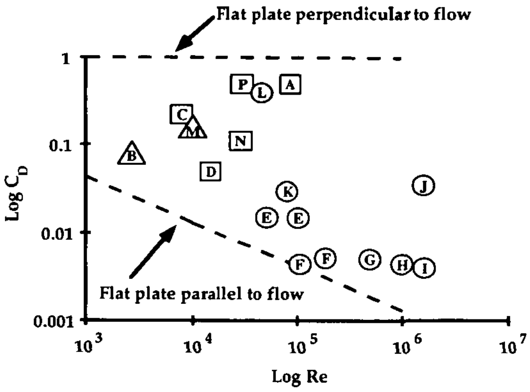


FIG. 2. ○ = swimmer or flier, □ = pedestrian, △ = both swimmer and pedestrian. Drag coefficients in horizontal orientation, based on wetted area. Sources: plates—Ellington, 1991; Thom and Swart, 1940 in Vogel, 1994. (A) Lobster in walking orientation—Bill and Herrnkind, 1976 (area estimate by M. Martinez from molt of same species). (B) Isopod in swimming orientation—Alexander and Chen, 1990. (C, D) Frogs—Gal and Blake, 1987. (E) Trout and (F) mackerel—Webb, 1975. (G) Saithe—Hess and Videler, 1984. (H) Penguin—Nachtigall and Bilo, 1975. (I) Seal and (J) human swimmer—Williams and Kooyman, 1985. (K) Scallop—Hayami, 1991. (L) Duck wing—Withers, 1981 (20° angle of attack). (M, N) Intact crabs and (P) crab with legs removed—Blake, 1985.

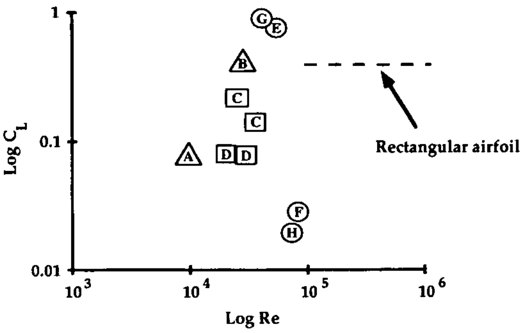


FIG. 3. ○ = swimmer or flier, □ = pedestrian, △ = both swimmer and pedestrian. Lift coefficients in horizontal orientation, based on wetted area. Sources: Rectangular airfoil section (aspect ratio = 5, thickness/chord = 8%)—Hoerner and Borst, 1975. (A) Lobster in escape swimming orientation—Jacklyn and Ritz, 1986. (B, C) Intact crabs and (D) crab with legs removed—Blake, 1985. (E) Plaice—Arnold and Weihs, 1978. (F) Scallop—Hayami, 1991. (G) Duck wing—Withers, 1981 (20° angle of attack). (H) Lasher—Webb, 1989.

lift. Animals virtually never use a constant absolute speed in pedestrian locomotion, but instead accelerate and decelerate their bodies with each step (*e.g.*, Full, 1989). Pedestrian locomotion also involves the cycling of legs, which accelerate and decelerate in each step. Acceleration reaction acts along the axis of water flow relative to the body or appendage, opposing changes in velocity. Therefore acceleration reaction acts in the same direction as drag when an animal or appendage is accelerating, but counteracts drag when the animal decelerates. For an accelerating animal in still water, acceleration reaction (A_p) is given by:

$$A_p = a(m + \rho VC_a) \qquad (3)$$

where a = animal's acceleration, m = animal's mass, ρ = water density, V = animal's volume and C_a = added mass coefficient. The two components of this acceleration reaction force are 1) the force to accelerate the mass of the animal and 2) the force to accelerate a mass of water that behaves as though it were dragged along with the animal (Denny, 1988). While drag and lift scale with velocity squared, acceleration reaction scales with the change in velocity. Note also that acceleration reaction scales with volume rather than area (as in drag and lift), which means that acceleration reaction plays a greater role on larger animals than on smaller ones.

One can determine whether cyclical acceleration forces are likely to be important for an animal locomoting in a fluid environment by calculating the reduced frequency, which is usually employed to gauge the relative importance of the acceleration of oscillating appendages in swimmers (Daniel, 1984; Blake, 1986) and fliers (Lighthill, 1975; Vogel, 1994). This reduced frequency (σ) is given by:

$$\sigma = (2\pi fc)/u \qquad (4)$$

where f = body or appendage cycling frequency, c = length of the animal or appendage in the direction of flow, and u = body velocity relative to the water. Reduced frequency essentially compares the flow speed due to appendage cycling with the animal's forward speed. When the reduced frequency yields a value greater than 0.5, unsteady forces (*i.e.*, acceleration reaction) are important and thus a strict quasi-steady state analysis, which considers only drag and lift, is not sufficient. For example, a person running at 3 m/sec with a stride frequency of 1.4 Hz (He *et al.*, 1991) and leg width of 0.12 m, has a reduced frequency of 0.35, well below the critical value, and thus analyses of human running can safely ignore unsteady fluid forces. Likewise, a medium-sized ghost crab, *Ocypode quadrata,* running on land at 1.6 m/sec with a stride frequency of 6.4 Hz (Blickhan and Full, 1987) and leg width of 0.0045 m, has a reduced frequency of only 0.11. In contrast, a large grapsid crab, *Grapsus tenuicrustatus,* locomoting under water at 0.10 m/sec with a stride frequency of 1.2 Hz and a leg width of 0.008 m (Martinez, in prep.), has a reduced frequency of 0.60, in the region of uncertainty where unsteady forces on the limb may be important. In the case of a swimming water beetle, *Cenocorixa bifida,* a body velocity of 0.08 m/sec, limb oscillation frequency of 10 Hz, and limb width of 0.003 m (Blake, 1986), give a reduced frequency of 2.36, indicating that unsteady forces are extremely important in its locomotion.

An animal's posture may substantially affect the hydrodynamic forces that it experiences. Some mayfly larvae can produce negative lift by tilting their broad headshields into oncoming flow (Weissenberger *et al.,* 1991). The angle at which lobsters hold their antennae can alter the drag on walking lobsters (Bill and Herrnkind, 1976) and produce an impressive range of lift forces, from positive to negative, in swimming lobsters (Jacklyn and Ritz, 1986). Posture affects both the drag coefficient and the added mass coefficient by altering the pattern of flow around an animal (Daniel, 1984; Vogel, 1994).

Forces due to the environment

One cannot adequately assess the hydrodynamic forces on an animal by simply considering it out of the context of its environment. The total hydrodynamic forces on an aquatic pedestrian consist of the forces due to its locomotion plus the forces due to the ambient water flow in its environment. Thus, knowing the field flow conditions, as well as the animal's behavior in those flow conditions, are critical to determining the forces on an aquatic pedestrian.

Forces on a pedestrian due to the environment differ radically depending on the water flow conditions in that environment. Unidirectional flow conditions involve a straightforward hydrodynamic analysis. The forces imposed on a pedestrian by steady unidirectional flow consist of drag and lift due to ambient water velocity relative to the animal. A more complicated hydrodynamic situation exists for aquatic pedestrians in the constantly changing flow of the wave-swept environment. Whereas flow in streams, tidal currents, and water deep enough not to be affected by waves is predominantly unidirectional, wave-swept habitats are characterized by the back and forth motion of waves (Fig. 4), with acceleration and deceleration shoreward and then seaward.

Oscillating flow conditions entail a much more complex analysis than that which is sufficient for unidirectional flow conditions. Drag, lift and added mass coefficients may be affected by oscillating flow; however, when the water moves far enough past an organism before changing direction, drag and lift can be measured with a quasi-steady state analysis, in which the forces are determined for the velocity occurring at each point in time, assuming that time-dependent effects are negligible. Quasi-steady state is a reasonable assumption when an index called the period parameter assumes a value of at least 30 (Keulegan and Carpenter, 1958). Period parameter (K) is given by

$$K = (TU_{max})/l \qquad (5)$$

where T = wave period, U_{max} = maximum water velocity, l = characteristic length of organism in the direction of flow. For a small crab like *Hemigrapsus nudus* (l = 0.04 m) in its flow habitat (T = 3 sec, U_{max} = 0.16 m/sec) (Fig. 4), the period parameter is 12, well into the range where oscillation has a significant effect on lift and drag coefficients. In contrast, a large grapsid crab (l = 0.15 m) in its flow habitat (typical T = 7 s, U_{max} = 1.0 m/sec) (Fig. 5) has a period parameter of 46, so lift and drag

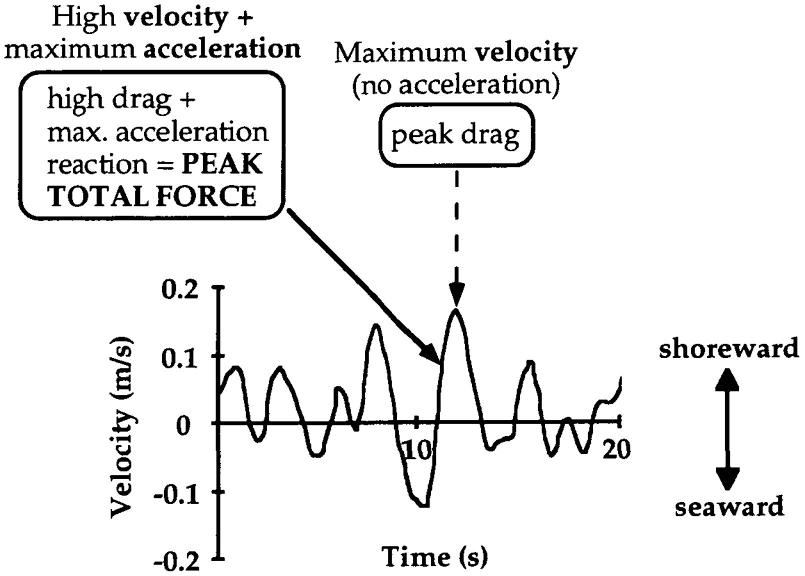


FIG. 4. Velocity record along predominant flow axis, flooding tide, calm conditions in rocky habitat in Friday Harbor, Washington. Data was gathered at approximately the height of a local crab, *Hemigrapsus nudus*, from a Marsh McBirney electromagnetic flow probe (model 511), recorded on a Soltec chart recorder (model 6723) and digitized on a tablet (Jandel) with Sigma Scan Scientific Measurement System software version 3.01 (Jandel) at a sampling rate of 5 Hz.

analyses can be simplified using quasi-steady state assumptions.

Since the water in waves accelerates and decelerates, pedestrians will experience acceleration reaction due to waves. Acceleration reaction due to water accelerating past an animal (A_w) is given by:

$$A_w = \rho VaC_m \qquad (6)$$

where ρ = water density, V = animal's volume, a = acceleration of water relative to the animal, and C_m = the inertia coefficient (1 + the added mass coefficient). This situation (A_w), differs from when an animal is accelerating (A_p), because the animal does not have to exert a force to accelerate its own mass, but rather must decelerate a volume of water that would be accelerating in its place if the animal were not there. When water accelerates relative to the animal, the acceleration reaction acts in the direction the water is moving, (*i.e.*, acts in the same direction as drag and adds to the drag). When water decelerates relative to the animal, acceleration reaction acts in the opposite direction of water movement, opposing drag.

Due to the cyclic nature of waves, the peak water velocity does not coincide with the peak acceleration (Fig. 4). This means that for macroscopic pedestrians, the maximum steady state forces do not coincide with the maximum acceleration forces. Although the lift and drag are maximal at peak velocity, acceleration reaction is zero because the velocity is not changing. Peak forces therefore occur when acceleration is maximal and velocity, hence lift and drag, is moderate. Assuming typical values of 100 m/sec^2 acceleration and 10 m/sec velocity in waveswept sites, Denny (1988) estimates that acceleration reaction would be on the order of 4% of the drag on an animal a few centimeters in length, but would value 40% of the drag on an animal that measured a meter in length. In fact, Denny *et al.*, (1985) suggest that acceleration reaction, rather than lift and drag, may constrain the upper size limit to sessile organisms on waveswept shores.

Total forces on a pedestrian moving through environment

In order to calculate the total hydrodynamic force on the body of an aquatic pe-

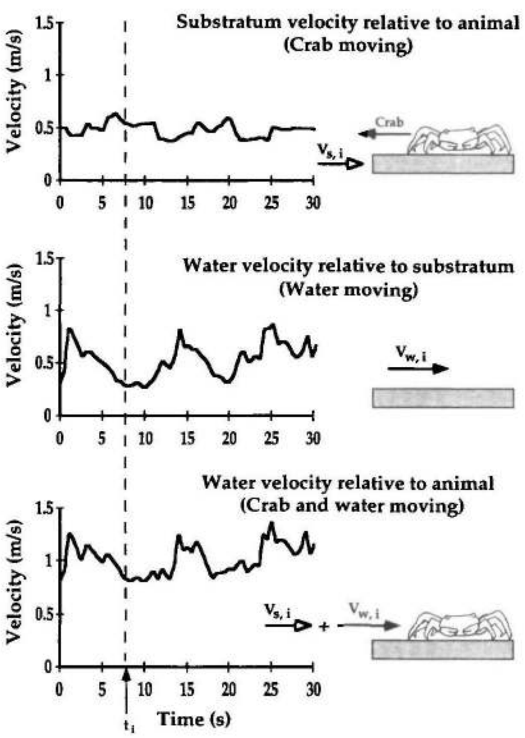


FIG. 5. To determine the water velocity relative to a locomoting animal at any instant (t_i), add the substratum velocity relative to the animal ($V_{s,i}$) with the water velocity relative to the substratum ($V_{w,i}$). Water velocity was recorded at flooding tide under windy conditions in wave-swept rocky habitat of Makapu'u, Hawaii, at the height of a local crab, *Grapsus tenuicrustatus*. Flow record was obtained with a DAQBook data acquisition system (OMB-DAQBOOK-100) on a Texas Instruments 486Dx2/50 Travelmate notebook computer, sampled at 2 Hz from a Marsh-McBirney electromagnetic flow probe (model 511).

destrian subject to ambient water motion, one must first determine the water velocity relative to the locomoting animal by summing the substratum velocity relative to the animal (animal's ground speed) with the water velocity relative to the substratum. (Fig. 5) The total hydrodynamic force at any point in time can then be calculated as the sum of the drag and lift (obtained from a quasi-steady state analysis) plus the acceleration reaction.

The importance of fluid forces to the mechanics of aquatic pedestrian locomotion is really an issue of a more general phenomenon: a high ratio of fluid forces to weight force. Due to the low density of air, the aerodynamic forces on a terrestrial pedestrian are usually negligible compared to the weight force. A rapid runner with a large projected area and low weight, however, could generate enough aerodynamic force to place it in the realm occupied by many aquatic pedestrians, where fluid forces significantly contribute to the force balance on the animal. Full and Koehl (1993) have shown that the cockroach *Periplaneta americana,* which can reach speeds over a meter per second, generates enough drag to account for 20–30% of its power output while running at high speeds. Aquatic pedestrians tend to have high ratios of hydrodynamic force to weight force because water density (to which hydrodynamic forces are proportional) is high and effective weight is lowered by buoyancy.

Many constraints on the size, shape, speed, and kinematics of aquatic pedestrians will be imposed by the water flow conditions in different habitats. Larger animals will not only experience greater absolute drag and lift forces, but also disproportionately greater acceleration reaction. We know that acceleration reaction can limit the size of sessile organisms because their tenacity scales with attachment area while acceleration reaction scales with volume (Denny *et al.,* 1985). We still need to assess how the tenacity of pedestrians scales, considering the variety of mechanisms they use to hold onto the substratum, including grasping hard substrata with lateral leg pairs or digging their legs into sand. Faster flow environments may constrain animals to relatively streamlined shapes, because the drag and acceleration reaction on a non-streamlined, bluff-bodied pedestrian may exceed the animal's tenacity, preventing it from living in that environment. Faster flow environments will restrict the maximum speed of pedestrians more than will slower flow environments. Finally, pedestrians may be required to actively hold on to the substratum as they locomote in faster flow environments, which limits their kinematic options. Pedestrians may be able to partially compensate for these habitat-based constraints by using postural changes to actively control the hydrodynamic forces they experience. Animals could adopt postures that confer negative lift and lower drag, thereby increasing their maximum speed in a given environment.

SUMMARY

Aquatic pedestrian locomotion represents a mode of locomotion quite distinct from terrestrial pedestrian locomotion and from swimming. Unlike the terrestrial situation where weight is most often the defining force, in aquatic realms buoyancy and hydrodynamic forces may be as important as weight to a locomoting organism. The proximity of a substratum distinguishes aquatic pedestrian locomotion from swimming by altering fluid flow and hydrodynamic forces as well as affording greater significance to being dislodged by ambient water motion. Thus ambient water motion may constrain or preclude the locomotion of aquatic pedestrians by requiring that they actively grip the substratum.

Incorporating the field flow conditions as well as field behavior in these studies is essential to correctly interpret the results and identify general principles of aquatic pedestrian locomotion. These general principles which will further our understanding of ecology of these animals, and the evolutionary transition from an aquatic to a terrestrial habitat, are currently being applied to the design of better, more effective legged amphibious robots.

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