Running in the surf: hydrodynamics of the shore crab *Grapsus tenuicrustatus*

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Summary

When locomoting in water, animals experience hydrodynamic forces due to ambient water motion and their own motion through the water. Because an aquatic pedestrian must maintain contact with the substratum to locomote, hydrodynamic forces which can dislodge an animal have the capacity to constrain the postures, gaits and speeds an animal can use. This study measured hydrodynamic forces on the amphibious shore crab *Grapsus tenuicrustatus* in aquatic and terrestrial postures. The crabs' locomotory speeds and ambient water velocities in their habitat were considered in predicting the conditions under which a crab is likely to overturn or wash away. A non-moving crab can withstand 200 % faster flow in the aquatic posture than in the terrestrial posture. A crab using the terrestrial posture while locomoting through still water experiences 132 % greater drag and 17 % greater acceleration reaction forces than it does in the aquatic posture. Due to the lower hydrodynamic forces in the aquatic posture, a crab could locomote up to 50 % more quickly or through a faster water flow environment than it could in the terrestrial posture. In faster flow environments like wave-swept rocky shores, a crab in either posture would have to actively grasp the substratum to keep from being dislodged, preventing it from using a punting gait. In slower flow environments, animals can locomote faster and take advantage of different gaits that are not available to them in faster flow environments.

Key words: hydrodynamics, locomotion, crustacean, arthropod, shore crab, *Grapsus tenuicrustatus*.

Introduction

Studies of legged locomotion have historically concentrated on terrestrial locomotion or on swimming (reviewed in Full, 1997; Gans et al., 1997), but have more recently begun to explore aspects of pedestrian locomotion in water (e.g. Pond, 1975; Bill and Herrnkind, 1976; Grote, 1981; Houlihan and Innes, 1984; Houlihan et al., 1984; Clarac et al., 1987; Hui, 1992; Jamon and Clarac, 1995; Martinez, 1996; Martinez et al., 1998). While the increased buoyant force in water explains many of the kinematic differences exhibited by pedestrians when in still water *versus* in air (Martinez et al., 1998), the role of hydrodynamic forces in determining the dynamics of aquatic pedestrian locomotion remains uncertain.

Locomotion in air versus *in water*

Several studies report that amphibious animals using pedestrian locomotion use different kinematics when in air than in water (Pond, 1975; Clarac et al., 1987; Grote, 1981; Hui, 1992; Martinez et al., 1998). The amphibious shore crab *Grapsus tenuicrustatus* changes body posture as well as kinematics, using a different locomotory gait in air than in water (Martinez et al., 1998). The crabs walk on land at slow speeds, but in water at these same speeds, the crabs use a more variable gait (submerged punting), characterized by alternating thrust generation and gliding. Unlike other gaits that crabs might use underwater, the submerged punting gait does not allow crabs to actively grasp the substratum while locomoting.

Animals' kinematic changes between air and water can be understood in terms of the mechanical loads characteristic of these different fluid environments. The increased buoyancy and hydrodynamic forces in water compared to those on land can cause a shift in the predominant destabilizing forces an animal experiences. Whereas on land the destabilizing forces are predominantly vertical (due to gravity), in water the horizontal destabilizing forces (due to hydrodynamic forces) may equal or exceed the vertical forces (Martinez, 1996). Martinez et al. (Martinez et al., 1998) show that many of the kinematic adjustments made by *Grapsus tenuicrustatus* in water at slow speeds can be predicted from reduced-gravity models of locomotion. As animals move more rapidly, however, hydrodynamic forces increase and are likely to become an important component of the force balance on the animal.

Hydrodynamic forces on an animal walking or running underwater are due not only to its motion through the water, but also to the ambient water flow in the animal's habitat. The net hydrodynamic force on an animal affects the force the

animal has to exert to locomote and determines whether the animal washes off the substratum or overturns. Of the few studies that consider hydrodynamic forces on legged animals, most focus on swimming rather than on pedestrian locomotion (e.g. Alexander, 1990; Blake, 1985; Fisher, 1975; Plotnik, 1985; Jacklyn and Ritz, 1986). While the importance of hydrodynamic forces has been demonstrated for many sessile organisms (e.g. Koehl, 1977; Koehl, 1982; Koehl, 1984; Carrington, 1990; Gaylord et al., 1994) and for animals using adhesive locomotion (Denny, 1988; Denny et al., 1985; Dudley, 1985; Denny, 1994; Denny and Gaylord, 1996), little is known about the effects of hydrodynamic forces on aquatic legged locomotion.

The hydrodynamic forces on an animal are not prescribed simply by the water flow environment, but are also modified by the animal's reaction to the flow conditions. Not only do pedestrian animals use different postures in still water than they use in air (Grote, 1981; Hui, 1992; Martinez et al., 1998), but they also change their postures and orientations in response to water flow (Maude and Williams, 1983; Nishimoto and Herrnkind, 1978). Changes in posture and orientation can have large effects on the hydrodynamic forces an animal experiences (Pond, 1975; Bill and Herrnkind, 1976; Koehl, 1977; Koehl, 1982; Jacklyn and Ritz, 1986; Weissenberger et al., 1991). Few studies on aquatic pedestrians have explicitly considered the significance of ambient water flow or an animal's posture on the hydrodynamic forces that it experiences, although Bill and Herrnkind (Bill and Herrnkind, 1976) measured the effect of antennal orientation and inter-lobster spacing on the drag experienced by lobsters walking in a queue.

Consequences of hydrodynamic forces

The hydrodynamic forces on the body of an animal (Fig. 1A) impact the dynamics of aquatic pedestrian locomotion in many ways, including resisting forward motion, keeping the animal in contact with the substratum, or dislodging the animal from the substratum. Dislodgment from the substratum is a serious problem for pedestrian animals since they must maintain contact with the substratum in order to generate thrust. Hydrodynamic forces can dislodge an animal by causing it to overturn or wash away. Assuming that an animal does not actively grip the substratum, it will overturn, pivoting about its downstream leg, when the overturning moment about the animal's center of mass exceeds the stabilizing moment (Fig. 1B) (Alexander, 1971). The conditions under which an animal will overturn can be expressed in terms of the forces on the animal's body, as shown in Equation 1:

$$\frac{(D+A)h}{(W-B-L)d} > 1, \tag{1}$$

where D is the drag force, A is the acceleration reaction force, h is the height of the center of mass, W is the weight of the animal, B is the buoyant force, L is the lift force, and d is the distance from the center of mass to the downstream or trailing

leg. Positive lift (away from the substratum) contributes to the likelihood that an animal will become dislodged, but if an animal generates negative lift, this will assist it in maintaining ground contact.

Another mechanism by which hydrodynamic forces can dislodge an animal is to shear it off the substratum, washing it away. An animal will wash away when the net horizontal force on the body (drag plus acceleration reaction) exceeds the force resisting that motion (Fig. 1C). Unless an animal actively grasps the substratum, only friction between the animal and the substratum keeps it from washing away. The frictional force resisting dislodgment is proportional to the net vertical force on the animal (weight minus buoyancy and lift).

Hydrodynamic forces can constrain aquatic locomotion in several ways. The need to actively hold onto the substratum when exposed to ambient water flow can limit the conditions under which an animal can locomote or the gaits and postures it can use while locomoting. Even if an animal does not become dislodged from the substratum, hydrodynamic forces may limit its speed and accelerations by greatly increasing the horizontal forces and power output it must exert to locomote.

Objectives

The present study addresses three hypotheses concerning the role of hydrodynamic forces in aquatic pedestrian locomotion. (1) Drag, lift and acceleration reaction contribute significantly to the force balance on an animal locomoting through an aquatic environment. (2) Adopting different locomotory postures alters the hydrodynamic forces an animal experiences. (3) Hydrodynamic forces (due to locomotion or ambient water flow) constrain an animal's postures, speeds, accelerations and kinematics as well as the environmental conditions under which it can locomote. These hypotheses are tested using the Hawaiian intertidal rock crab *Grapsus tenuicrustatus*, which inhabits a wide range of water flow environments, from slow-flow lagoons to wave-swept rocky shores. This study employs a quasi-steady state hydrodynamic analysis, considering steady state drag and lift as well as acceleration reaction forces on the body of a crab. These forces are assessed at speeds and accelerations characteristic of locomotion and ambient water velocity measured in three different habitats: a lagoon, a protected bay, and a wave-swept site. Based on the total force on the body of a crab, predictions were made about when a crab will overturn or wash away while locomoting in its natural environment. *G. tenuicrustatus* are convenient animals for this hydrodynamic study, not only because of the diversity of water flow environments they inhabit, but also because they use distinct postures in air and water (Martinez et al., 1998).

To perform meaningful hydrodynamic experiments, one needs first to characterize the hydrodynamic environment of the organism. This study encompasses two parts: (1) characterization of the water flow in several environments inhabited by *G. tenuicrustatus* and (2) hydrodynamic measurements in the laboratory at water velocities representative of those experienced by *G. tenuicrustatus* in the field.

Materials and methods

Animals

Many *Grapsus tenuicrustatus* (not captured) were videotaped in the field to determine their fate in waves. Large adult *G. tenuicrustatus* Herbst (0.070±0.02 kg; mean ± S.D. *N*=9) were collected near Coconut Island, HI, USA. Body mass in air and in water was measured for live crabs to the nearest 0.001 kg with a Mettler balance. Live crabs were videotaped to determine preferred locomotory speeds in air and in water. Different live crabs were used in tenacity measurements. Exoskeletons from these crabs were made into models for lift, drag and added mass measurements. Exoskeletons used for lift and drag measurements had a carapace width of 0.054±0.002 m (mean ± S.D., *N*=5). Exoskeletons with a larger size range were used for acceleration reaction measurements (mean carapace width: 0.052±0.009 m, mean ± S.D., *N*=7). The sizes of crab exoskeletons used in hydrodynamic measurements are representative of large adult crabs in the field, which have been reported to reach up to 0.07 m in carapace width, although specimens over 0.06 m in width are rare (M. M. M., personal observation).

Speeds of locomotion

To estimate a crab's preferred locomotory speed, five crabs were videotaped locomoting freely through air and through still sea water over a flat substratum. Crabs were occasionally prodded to initiate movement. Handling of crabs was minimized and crabs were allowed to rest for several hours between trials. Videotapes were digitized using motion-analysis software (Peak Performance Inc., Version 5.0) to obtain average velocity over a 1 m path. Trials were discarded when crabs tripped, turned, did not move steadily, or ran alongside walls. Crabs used two distinct gears that corresponded to slow and fast speeds underwater (Fig. 2), but this pattern did not show a trial effect; i.e. crabs did not locomote more slowly or more quickly after several trials. Mean slow and fast speeds were calculated for each crab. Group means for slow and fast speeds were then calculated and used in overturning calculations.

Tenacity

Tenacity measurements in air were made on five live crabs on rugose volcanic rock similar to that commonly found in the crabs' habitat. Each crab was allowed to settle on the rock for several seconds and then pulled in the horizontal or vertical direction with an Ametek (LKG-5) force transducer *via* a wire loop attached to the center of the crab's carapace. Each crab was pulled until it detached from the rock. Maximum force was determined to the nearest 0.1 N from ten replicates.

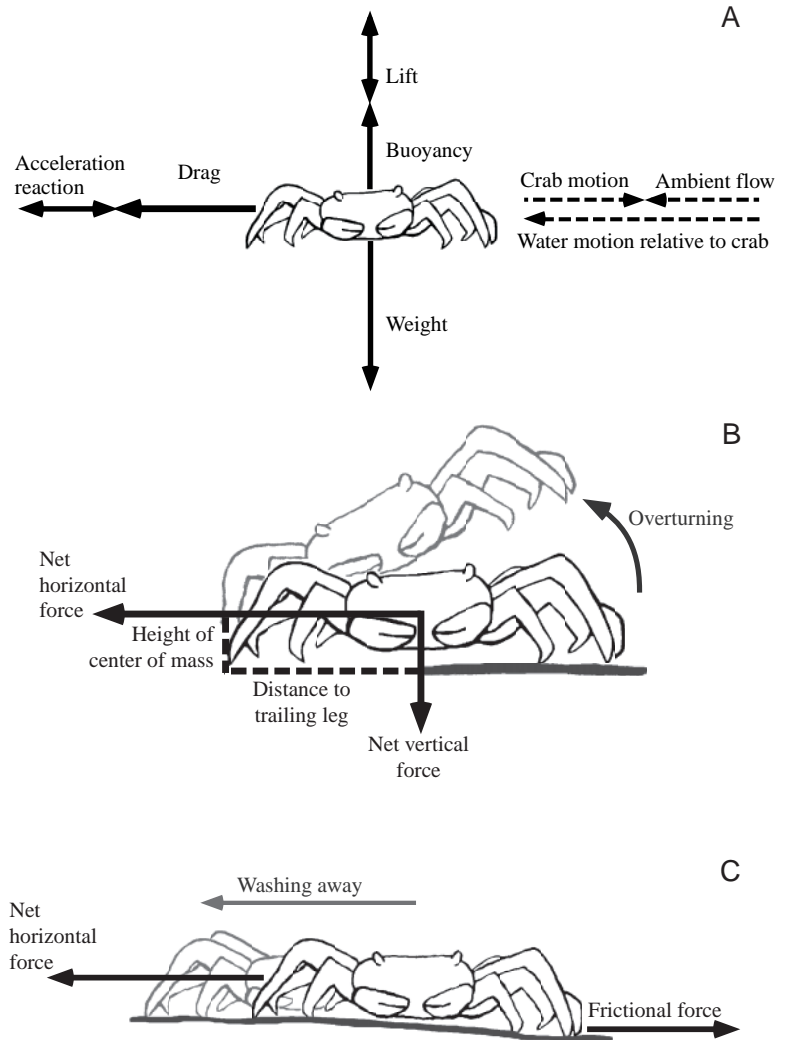The coefficient of friction was determined for each epoxy-

Fig. 1. (A) Forces acting on the body of a crab locomoting through a fluid environment. The crab in the diagram is locomoting with its left side leading and is moving upstream against an ambient water current. The fluid motion relative to the crab is the vector sum of the flow due to the ambient current and the flow due to the motion of the crab. Buoyancy counteracts the crab's weight. Lift, which acts perpendicular to the relative fluid motion, counteracts the weight (positive lift, acting away from the substratum) or augments the weight (negative lift, acting toward the substratum). Drag acts in the direction of relative fluid motion, resisting locomotion and tending to push the crab downstream. Acceleration reaction resists changes in velocity, augmenting drag as a crab accelerates relative to the fluid and counteracting drag as the crab decelerates. (B) A crab overturns, pivoting about its downstream leg, when the overturning moment about its center of mass exceeds the stabilizing moment. The overturning moment is the net horizontal force times the height of the center of mass. The stabilizing moment is the net vertical force times the distance from the center of mass to the trailing leg. (C) A crab that does not actively grasp the substratum washes away when the net horizontal force on its body exceeds the frictional force resisting dislodgment.

filled crab model used in the hydrodynamic experiments. Mass of the models was determined to the nearest 0.01 kg using a Mettler balance. Frictional force (±0.01 N) was measured with a Pesola force transducer as the models were pulled along the wet surface of both the volcanic rock used in tenacity
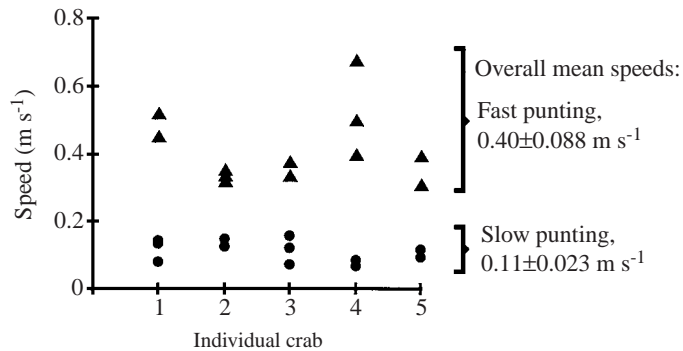
Fig. 2. Speeds of five different crabs locomoting through still water over a flat substratum. Each data point represents one trial for an individual crab. Circles indicate slow punting and triangles indicate fast punting. A mean speed for each of these gaits was calculated for each crab; the overall mean for each gait was calculated as the mean (± S.D.) of the mean speeds of the five crabs.
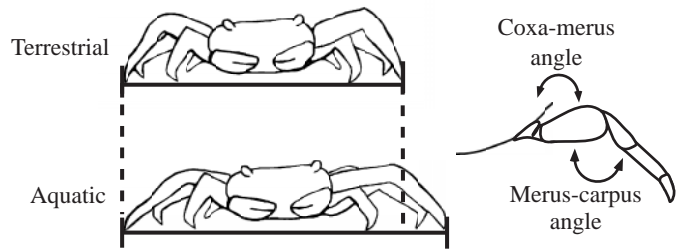

Fig. 3. The two postures of *Grapsus tenuicrustatus* (from Martinez et al., 1998) effected by changes in the coxa/basi-ischium joint, the basi-ischium/merus joint and the merus-carpus joint.

measurements and a flatter, less rugose shale rock. The coefficient of friction was calculated as the frictional force divided by the weight of the model. This coefficient was then multiplied by the weight of live crabs to yield the frictional force between a live crab and the substratum.

Ambient water velocity

For an estimate of the ambient water velocities and accelerations that a crab might encounter, water velocities were measured in *G. tenuicrustatus* habitats on several days in January 1995 along rocky shores on Oahu, Hawaii. These data represent non-stormy conditions over a range of weather conditions, as indexed by wind speed. Three sites were chosen to represent the different water flow environments that the crabs inhabit: a wave-swept site at Makapuu State Beach Park, a protected lagoon at Coconut Island and a semi-protected site in Kaneohe Bay. Ambient water velocity was measured during flooding tide, using an electromagnetic flow probe (Marsh–McBirney, Model 511), the electrodes of which were placed above the substratum at the approximate height of a crab (0.06 m). At all three sites the probe was placed above the substratum at a location where an adult *G. tenuicrustatus* had been observed. The electromagnetic flow probe measures flow in two perpendicular axes. The probe was oriented to measure the horizontal components of velocity, with one axis parallel to the direction of the highest velocity at each site.

Flow velocities were recorded using a DAQBook data-acquisition system (OMB-DAQBOOK-100) on a Texas Instruments 486Dx2/50 Travelmate notebook computer, sampled at 2 Hz. Accelerations were calculated over each 0.5 s sampling interval. While the sensing volume of the flow probe yields accelerations on a spatial scale relevant to *G. tenuicrustatus*, this method of measurement underestimates instantaneous acceleration. Therefore a range of water accelerations were considered for calculations of overturning and washing away. M. Koehl and T. Cooper (unpublished data) have measured water velocities at a sampling rate of 25 Hz with

a sensing volume of $1 \, cm^3$. Their data yield maximum water accelerations of $0.9 \, m \, s^{-2}$ and $1.3 \, m \, s^{-2}$ for sites with similar water velocities and flow characteristics as the lagoon and bay sites used in the present study. Water accelerations in the surf zone on rocky shores may commonly reach $400 \, m \, s^{-2}$ (Denny, 1994). While these values provide a broad sense of the water accelerations in the intertidal zone, their applicability is ambiguous for determining the forces on a large organism such as *Grapsus tenuicrustatus*. Water accelerations cannot generate a force of substantial magnitude on an organism if the bulk of accelerating water encompasses only part of the organism at a given time (Gaylord, 1999).

Hydrodynamic forces

Models and postures

Crab exoskeletons were filled with epoxy and positioned in different postures by adjusting the angles between the coxa and the merus (*via* the coxa/basi-ischium joint and the basi-ischium/merus joint) and between the merus and the carpus (Fig. 3). These joint positions were secured with remeltable plastic (Friendly Plastic), which was smoothed and sanded to the contour of the legs. Threaded hexagonally shaped nuts were embedded in the ventral and posterior side of the crabs' bodies and made flush with the surface of the body with epoxy.

By holding a crab's posture constant, the effects of different water flow conditions can be evaluated. Yet at any particular speed and gait, the instantaneous posture of a locomoting crab can differ markedly from the average posture used by the crab. To assess the effect of instantaneous posture on hydrodynamic forces, drag was measured on both an extreme instantaneous posture and the average posture used by *G. tenuicrustatus* during aquatic locomotion (Martinez et al., 1998). Since the difference in drag on these two postures was less than 5 %, all subsequent hydrodynamic measures were made using the average posture.

Hydrodynamic forces were measured on each crab model in two average postures, a sprawled aquatic posture and a more upright terrestrial posture, as determined from a three-dimensional kinematic analysis of these crabs locomoting in air and water (Martinez et al., 1998). In this kinematic study, Martinez et al. showed that the differences in posture were due mainly to changes in the angles of the joints described above. For the aquatic posture, crabs were positioned with a relatively

wide lateral stance (0.20 m, 364 % of the mean carapace width). For the terrestrial posture, crabs were positioned with a narrower lateral stance (0.16 m, 291 % of the mean carapace width), with smaller merus-carpus joint angles (Fig. 3). Crabs in both aquatic and terrestrial postures were positioned with their centers of mass approximately 0.04 m above the substratum, as determined from the kinematic analysis (Martinez et al., 1998). The crab models were attached to force transducers *via* the ventral nut (for drag and acceleration reaction measurements) and then *via* the posterior nut (for lift measurements).

In water at high speeds, *G. tenuicrustatus* uses a slightly different posture than it does in water at slow speeds. At high speeds, the crabs use multiple legs for propulsion simultaneously, resulting in two or more of the leading legs bent back toward the body at the merus-carpus joint for a greater percentage of the time than is seen in the slow-speed posture in water. At the highest water velocity, where the differences in drag will be the greatest, drag on the high-speed and slow-speed aquatic postures differed by less than 5 %. Thus all subsequent measurements and calculations for crabs using an aquatic posture were made for the slow-speed aquatic posture only.

Kinematic analysis (Martinez et al., 1998) showed that *G. tenuicrustatus* used angles of attack (the angle at which the animal meets the oncoming flow, rotation about the anterior–posterior axis for a sideways-moving crab) between 0 ° and +4 ° for more than 65 % of the time when locomoting through air or still water. Although *G. tenuicrustatus* did not use negative angles of attack at slow speeds (Martinez et al., 1998), negative angles of attack provide a potential stabilizing mechanism against overturning and consequently were considered in this study.

Assessing the effect of swinging legs

Fluid dynamic forces act not only on the body of a crab as it locomotes, but also on its legs as they swing through a stride. Drag on a leg was measured to assess the effect of a swinging leg on the drag experienced by a crab locomoting in water. Since *G. tenuicrustatus* primarily swings its legs from the merus-carpus joint while locomoting underwater (Martinez et al., 1998), drag was measured on the distal half of the leg with the carpus segment mounted on a force transducer (as described for a whole crab model). The mounted leg was one of the third pair (numbered from anterior, not including chelipeds) because it is the largest leg and frequently used during submerged punting (Martinez et al., 1998).

Drag on the leg was measured at velocities used by a leg as it swings during aquatic locomotion. The velocity of a swinging leg was obtained from the video sequence of a crab's fastest aquatic trial. Kinematic analysis of this video using the Peak Performance Motion Analysis System and the methods described by Martinez et al. (Martinez et al., 1998) yielded simultaneous records of leg velocity and body velocity as a function of time. Using the velocity data from this kinematic analysis and the drag coefficients from the hydrodynamic

measurements, instantaneous drag on the body and on the swinging leg were calculated at each time interval. The drag coefficient of the leg and the velocity of the leg with respect to the body of the crab were used to calculate the component of drag on the leg due to its swinging. The instantaneous drag on the leg (due to swinging) was added to the instantaneous drag on the body during the swing phase and subtracted from the drag on the body during the stance phase, to give the total drag on the crab as it locomotes with one swinging leg.

Justification of a quasi-steady state approach

To verify the validity of a quasi-steady state approach in analyzing the hydrodynamic forces on *G. tenuicrustatus*, the period parameter was calculated for the epoxy-filled crab models, assuming conditions of a wave-swept environment. The period parameter is used as an index of whether time-dependent effects will have a significant influence on hydrodynamic coefficients. Period parameter (K) is given by Equation 2:

$$K = (TU_{max})/l, \qquad (2)$$

where T is wave period, U_{max} is maximum water velocity and l is a characteristic length of the organism in the direction of flow. Using the crabs' maximum length in the flow direction (width of lateral stance in aquatic posture: 0.2 m), the average wave period (average of ten consecutive waves at the wave-swept site: 12.5 s), and the mean maximum water velocity (mean of the maximal water velocity from each wave: 0.5 m s^{-1}), yields a period parameter value of 31.3. A period parameter greater than 30 allows one reasonably to assume quasi-steady state conditions (Keulegan and Carpenter, 1958).

Importance of a substratum

It is important to consider proximity to a substratum when measuring hydrodynamic forces on a benthic animal because the substratum can affect the local flow and thus affect the fluid dynamic forces experienced by the animal. The proximity of a surface can interfere with fluid flow around an animal, decreasing drag and increasing the lift experienced by the animal (Martinez, 1996). When fluid flows over a substratum, a velocity gradient (boundary layer) develops above the substratum (Vogel, 1981). Reduced flow and high shear in the steep gradient of a boundary layer can significantly alter the forces an animal experiences.

When an animal locomotes through still water, the substratum and the water move with respect to the animal but not with respect to each other; therefore no boundary layer develops over the substratum. However, for an animal either standing or locomoting in ambient water flow, the water also moves with respect to the substratum, creating a velocity gradient. Yet *Grapsus tenuicrustatus* are unlikely to feel the effects of a boundary layer in their environment because these large crabs do not dwell within the steep gradient of a boundary layer that would develop over rough substrata in shallow water (Denny, 1988). In addition, crabs do not experience boundary layer effects on wave-swept shores because thick boundary

layers do not have sufficient time to develop under these conditions (Denny, 1988).

Using a unidirectional flow tank, I modeled three situations: a crab locomoting through still water, a crab standing still in moving water, and a crab locomoting through moving water. In a typical unidirectional flow tank (Vogel, 1981), water moves past a specimen which is fixed relative to the substratum. In order to simulate a crab locomoting in still water, I positioned the crab model over an underwater treadmill with the belt speed matched to the speed of the water. To simulate water moving past a crab standing still, I circumvented the effects of a boundary layer by placing the crab model at the leading edge of a flat plate. This method is effective because boundary layers do not appear instantaneously, but take time and distance to develop. Preliminary measures of drag force on a crab model positioned over the underwater treadmill did not differ from drag measured on the model positioned at the leading edge of a flat plate (within 1 cm of the edge) (paired two-tailed t-test, $P=0.82$, $N=6$ speeds). Therefore, all subsequent hydrodynamic measurements were made over a flat plate rather than over a treadmill.

Drag and lift

Drag and lift were measured on five crab models in a unidirectional water flow tank with a working section of $0.35\,\text{m} \times 0.50\,\text{m} \times 2.00\,\text{m}$. Forces were measured at seven different water velocities ranging between 0.15 and $1.00\,\text{m s}^{-1}$, approximating my measurements of both the crabs' locomotory speeds in water and water velocities in the habitat. Water velocity in the flow tank was measured with an acoustic Doppler anemometer (SonTek, Inc.) to the nearest $0.001\,\text{m s}^{-1}$. The crabs did not significantly affect flow through the flow tank since they obstructed less than 3 % of the flume's cross section (largest crab cross-sectional area: $0.003\,\text{m}^2$, cross section of tank: $0.13\,\text{m}^2$) (Vogel, 1981).

Since crabs locomote with their left or right sides leading, the models of *G. tenuicrustatus* were placed with their left side facing upstream in the flow tank. Drag and lift on the models were measured with force transducers (e.g. Vogel, 1981; Koehl, 1977). The force signal was passed through a bridge amplifier (Measurements Group, Model 2100) to a desktop computer (Gateway 2000) *via* LabView software (Version 3.0.1, National Instruments). Force signals were sampled at 10 Hz and averaged over 2 min intervals. Three replicate measures of forces were made on each crab in each posture and angle of attack at each speed. Mean forces and coefficients were calculated for each crab and group means were calculated for each posture.

Crabs' projected areas and planform areas were measured on video images (to the nearest $0.01\,\text{cm}^2$), using NIH Image software (version 1.52) on a MacIntosh PowerPC 7200/120 desktop computer. Since some studies report drag coefficients (C_D) calculated using frontal area and others using planform area, this study includes values for C_D calculated in both ways for comparison. The choice of which area to use for this calculation can profoundly affect the interpretation of the data

(Alexander, 1990). The ratios of planform to frontal areas are probably not the same for two animals being compared. Therefore, determining which animal has a lower drag coefficient may depend on which reference area is used in the calculation.

Drag coefficient (C_D) was calculated from Equation 3:

$$C_D = D/(0.5\rho u^2 S), \qquad (3)$$

where D is the measured drag force, ρ is the fluid density, u is the water velocity relative to the crab, and S is the projected or planform area of the crab. Lift coefficient (C_L) was calculated from Equation 4:

$$C_L = L/(0.5\rho u^2 S_P), \qquad (4)$$

where L is the measured lift force, and S_P is the planform area (top view). Preliminary hydrodynamic measurements indicated that lift, but not drag, was sensitive to these small changes in angle of attack (Kruskal–Wallis test, d.f.=2, $P=0.006$ for lift, $P=0.97$ for drag). Thus lift measurements were made at $+4°$, $0°$ and $-4°$. Drag measurements were made only at $0°$ angle of attack.

Acceleration reaction

Using the apparatus and methods described in Denny and Gaylord (Denny and Gaylord, 1996), acceleration reaction forces were measured on crabs accelerating in a tow tank. During the force measurements, crab models were oriented as for drag and lift measurements and positioned next to a substratum that accelerated with the crabs. Ten force measurements were made for each of seven individual crab models (body mass of live crabs=0.070±0.013 kg, mean ± S.D.) in each posture. Inertia coefficients (C_M) (for modeling fluid accelerating past a crab) were calculated from Equation 5:

$$C_M = A/(\rho Va), \qquad (5)$$

where A is acceleration reaction force, ρ is water density, V is volume of the crab, and a is acceleration of water relative to the crab. Accelerations were measured by a force transducer acting as an accelerometer as it was towed along with the crab model. Crab volumes (V) were calculated from the models' weights in air and submerged weights using Equation 6:

$$V = (m - m_{app})/\rho, \qquad (6)$$

where m is mass of the crab, m_{app} is apparent mass of the crab in water (submerged weight divided by gravity), and ρ is water density. Added mass coefficients (C_A) (appropriate for modeling a crab accelerating through still fluid) were calculated from Equation 7:

$$C_A = C_M - 1, \qquad (7)$$

(Denny, 1988). Mean coefficients were calculated for each crab and group means were calculated for each posture.

Critical velocity calculations

Overturning

Critical velocities required to overturn a crab under various

conditions were calculated using Equation 1. The crabs' mean slow and mean fast punting speeds (measured from videotape) were used to determine whether or not it would overturn while punting through still water. Even during locomotion at a constant average speed, an animal accelerates and decelerates its body during each stride (e.g. Full, 1989). The only data available for body accelerations of *G. tenuicrustatus* were determined from kinematics (Martinez et al., 1998), a process that returns questionable values for accelerations. Therefore a sensitivity analysis was used to explore the effects of body accelerations on the likelihood of a crab overturning using different postures and angles of attack. Since in punting there are times when a crab has no legs in contact with the substratum, they cannot actively grasp the substratum while using the submerged punting gait (Martinez et al., 1998). Accordingly, calculations of overturning during punting locomotion excluded active tenacity.

For a crab in ambient water flow, the maximum water velocities and accelerations measured at each of three sites were used in the calculations. All calculations involving ambient water flow were made on the assumption that crabs were fully submerged in shallow water, either in oscillatory flow characteristic of flow along the substratum under waves passing overhead or in the shoreward surge and seaward backwash after a wave has broken. Under these assumptions the present study did not address the effects of pressure distribution or air bubbles under breaking waves or the impact forces associated with a wall of water hitting an emersed animal (Denny, 1988). A crab locomoting in ambient flow was considered during the worst-case scenario of punting upstream. Accelerations used in these calculations were the maximum accelerations measured for comparable water velocities in the crab's habitat; e.g. for velocities less than $0.30\,\mathrm{m\,s^{-1}}$, the maximum acceleration measured in the lagoon environment was used; for velocities greater than $0.50\,\mathrm{m\,s^{-1}}$, the maximum acceleration measured at the wave-swept site was used.

Washing away

Critical velocities for washing away were calculated for a crab in each posture at an angle of attack of $0\,°$. For these calculations, the crab was assumed to wash away if drag (in steady currents) or drag plus acceleration reaction (in waves) exceeded the frictional force resisting a crab's lateral movement across the substratum. The frictional force (F_f) is given by Equation 8:

$$F_f = (W_{app} - L)\Phi,\qquad(8)$$

where W_{app} is the crab's apparent weight in water (weight minus buoyancy), L is the hydrodynamic lift on the body of the crab (where positive lift acts away from the substratum), and Φ is the coefficient of friction for a crab on rock. For a crab actively grasping the substratum, the maximum horizontal tenacity of a crab was added to the frictional force. Critical water velocities for washing away were calculated over a range of water accelerations for crabs in the aquatic and terrestrial postures.

Fate of crabs in waves

Using a zoom lens so as not to disturb the natural behavior of these skittish crabs, *Grapsus tenuicrustatus* were videotaped (Panasonic model PVS62, $60\,\mathrm{fields\,s^{-1}}$) in the field along the coast of Hawaii at several locations representing a range of water flow conditions: (1) a protected lagoon (Coconut Island), (2) semiprotected sites (Kaneohe Bay, Aloha Tower), and (3) rocky shores exposed to heavy wave action (Makapuu, Kona Coast of Hawaii, Kapapa Island). The videotapes were analyzed to determine the fates of crabs in waves. Each crab and each wave was only counted once, yielding statistically independent samples. In video sequences where several crabs were subjected to many waves, events were sampled systematically in a counter-clockwise direction from the top right corner of the camera view. Approximate wave heights were determined from the videotapes, using crabs as a size scale. Crabs were assumed to have a carapace width of 0.05 m. With this method, wave heights were approximated with a precision of 0.2 m. Waves were categorized as small (0–0.5 m), medium (0.5–1 m) or large (1.0–2.0 m).

Statistics

Hydrodynamic forces and coefficients were compared using Wilcoxon signed-rank tests. All statistical tests were performed on a MacIntosh PowerPC (6100/60), using Statview (Version 4.5).

Results

Speeds of locomotion

When locomoting under water, crabs used a slow punting speed of $0.11\pm0.02\,\mathrm{m\,s^{-1}}$ and a fast punting speed of $0.40\pm0.09\,\mathrm{m\,s^{-1}}$ (Fig. 2). The fastest speed recorded for underwater punting was $0.67\,\mathrm{m\,s^{-1}}$, whereas for terrestrial running the fastest speed recorded was $1.4\,\mathrm{m\,s^{-1}}$.

Tenacity

Crabs' mean maximum tenacity on rugose rock exceeded their weight in air by more than an order of magnitude (horizontal tenacity 13.0±7.7 N, vertical tenacity 11.3±3.3 N; means ± S.D., $N=5$ crabs). On the slate rock, the crab models had a mean friction coefficient of 0.32±0.06 (mean ± S.D., $N=5$). On the volcanic rock, the dactyls of the models caught in holes, greatly increasing the force needed to drag the models across the rock. The force required to pull crab models across the volcanic rock was in excess of 5.6±0.7 N (mean ± S.D., $N=5$), which is the force required to break a leg off the model. The pliant legs of live crabs grasped the substratum with 130 % more force than it took to break a model crab's leg.

Measurements of water flow in the field

Water flow in the lagoon and bay environments was characterized by turbulent velocity fluctuations superimposed upon relatively slow unidirectional currents. The wave-swept environment was characterized by oscillatory water movement, with much greater water velocities and
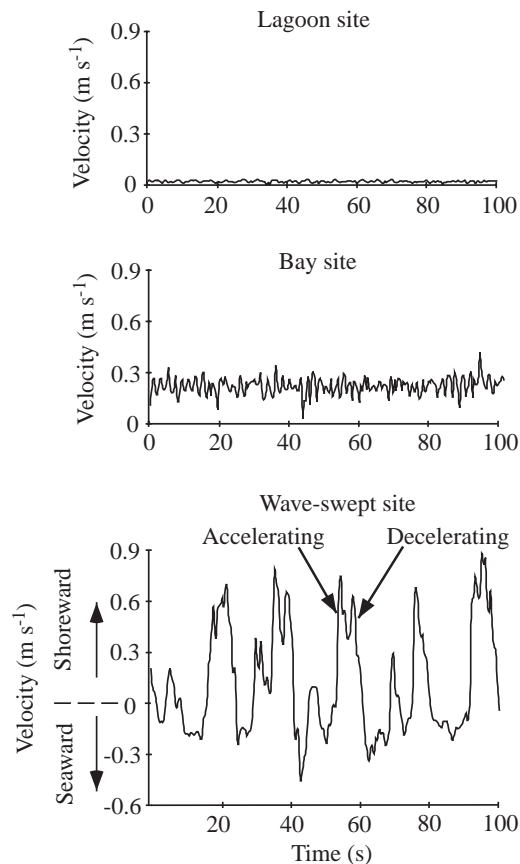
Fig. 4. Water flow records from the lagoon, bay and wave-swept sites, measured at the approximate height of a crab (0.06 m above the substratum). Mean and maximum velocities measured for the trials shown were $0.02\,\mathrm{m\,s^{-1}}$, $0.04\,\mathrm{m\,s^{-1}}$ (lagoon), $0.21\,\mathrm{m\,s^{-1}}$, $0.40\,\mathrm{m\,s^{-1}}$ (bay) and $0.30\,\mathrm{m\,s^{-1}}$, $0.91\,\mathrm{m\,s^{-1}}$ (wave-swept site).

accelerations than at the other sites (Fig. 4). The peak water velocity in the wave-swept site was almost three times the peak velocity at the bay site and 13 times the peak velocity at the lagoon site (Fig. 4). The peak acceleration measured at each site was $0.17\,\mathrm{m\,s^{-2}}$ at the lagoon site, $1.05\,\mathrm{m\,s^{-2}}$ at the bay site, and $1.71\,\mathrm{m\,s^{-2}}$ at the wave-swept site.

Hydrodynamic forces

Drag

Differences in posture sometimes affected the magnitude of the drag on crab models. The difference between drag on models in the fast- and slow-water postures was less than 5 %, so all subsequent results reported will be for the slow-water posture. In contrast, the difference between air and slow-water posture at this same speed was 50 %.

As expected for this Reynolds number range (10^4–10^5), drag increased with the square of the velocity for crabs in both postures ($r^2>0.997$). Crabs experienced greater drag in the terrestrial posture than they did in the aquatic posture (Wilcoxon signed-rank test, $P<0.05$, $N=5$) at all speeds except the slowest speed (Fig. 5A). Drag coefficients (C_D) did not show a significant association with Reynolds number for either
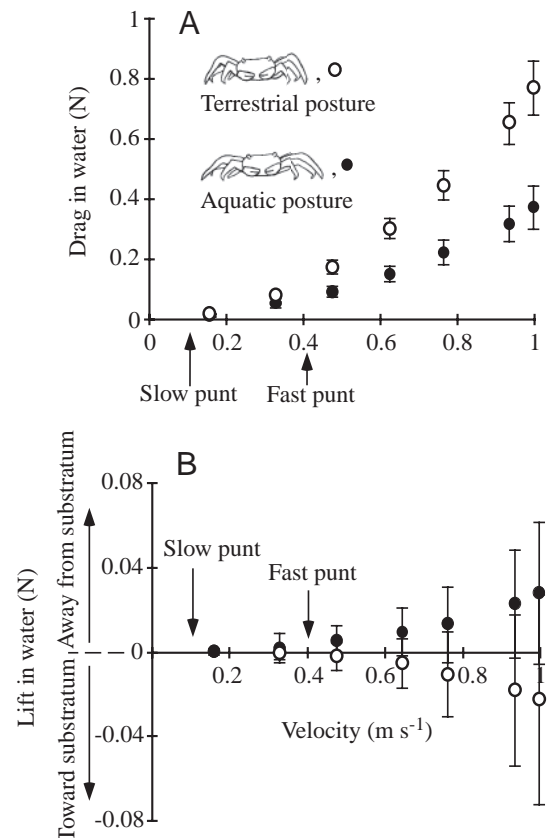

Fig. 5. Hydrodynamic forces on the body of a crab using the terrestrial (open circles) and aquatic (filled circles) postures at $0\,^{\circ}$ angle of attack. Each data point represents the mean of five trials for an individual crab, and values are means $\pm$ 1 S.D. Reynolds numbers (based on maximum lateral width of a crab) range from 2.5×10^4 to 2.0×10^5. Drag force (A) was significantly different for the two postures at all velocities except $0.15\,\mathrm{m\,s^{-1}}$. Lift force (B) was not significantly different for the two postures. Arrows indicate the mean slow and mean fast punting speeds.

posture (Kendall rank correlation, $P>0.05$, $N=7$). Mean drag coefficients were greater at each speed for crabs in the terrestrial posture than for crabs in the aquatic posture (Wilcoxon signed rank test, $P=0.018$, $N=7$ speeds) (Table 1). While models in the terrestrial posture had a smaller planform area than they did in the aquatic posture, this change accounted for only 14 % of the difference in drag coefficient (based on planform area) between these two postures. Drag measures were at $0\,^{\circ}$ angle of attack because angle of attack did not affect drag coefficients on either posture (see Materials and methods).

Effect of leg swinging

Due to the timing of the direction of the drag vector with respect to the timing of speed of the whole crab, the effect of swinging a leg is to reduce the total drag on the whole crab over a stride, although this reduction is very small (Fig. 6). Maximum drag measured on the leg was 12 % of the drag on the whole body at an average locomotory speed of $0.67\,\mathrm{m\,s^{-1}}$.

The drag on the leg should be added to the drag on the body when the leg swings forward, but subtracted from the body when the leg is stationary and generating thrust. Due to the timing of a leg swinging relative to the acceleration and deceleration of the body during locomotion, a crab model with one swinging leg experiences a 1.0 % decrease in the average drag over a complete cycle of the leg, compared to a crab model with non-swinging legs.

Lift

The lift force was sensitive to angle of attack for both the aquatic and the terrestrial postures (Fig. 7). Over the span of just a few degrees, the effect of the lift force switched from pulling a crab off the substratum to pushing it down onto the substratum. At 0° angle of attack, crabs in the aquatic posture experienced, on average, positive lift (away from the substratum), while crabs in the terrestrial posture experienced, on average, negative lift (toward the substratum) (Fig. 5B, Table 1). A +4° angle of attack produced positive lift and a −4° angle of attack produced negative lift. At all angles of attack, the aquatic posture generated lift of greater magnitude than did the terrestrial posture (Wilcoxon signed-rank test, *P*=0.02, *N*=7), although due to the difference in planform areas,

Table 1. *Hydrodynamic coefficients*

Coefficient	Aquatic posture	Terrestrial posture	*P*
Drag coefficient			
Planform area, S_p	0.10±0.02	0.24±0.01	0.018
Projected area, S	0.47±0.08	0.68±0.02	0.018
Lift coefficient			
Angle of attack			
+4°	0.038±0.003	0.026±0.006	0.028
0°	0.005±0.001	−0.003±0.004	0.018
−4°	−0.033±0.002	−0.036±0.003	0.091
Added mass coefficient	0.48±0.08	0.67±0.18	0.018

Values are means ± 1 S.D. for all crabs at all speeds (*N*=7 speeds, except for added mass coefficient for which *N*=7 crabs).

P<0.05 indicates a significant difference between aquatic and terrestrial posture.

the lift coefficients for −4° angle of attack are similar for the two postures (Wilcoxon signed-rank test, *P*>0.05, *N*=7) (Table 1).

Lift coefficient showed a significant negative association with Reynolds number for the terrestrial posture, but not for the aquatic posture, at all three angles of attack measured (Kendall rank correlation, *P*<0.005, *N*=7). At 0° and +4° angle of attack, lift coefficients on crabs were greater in the aquatic posture than in the terrestrial posture (Wilcoxon signed rank test, *P*<0.05, *N*=7) (Table 1).
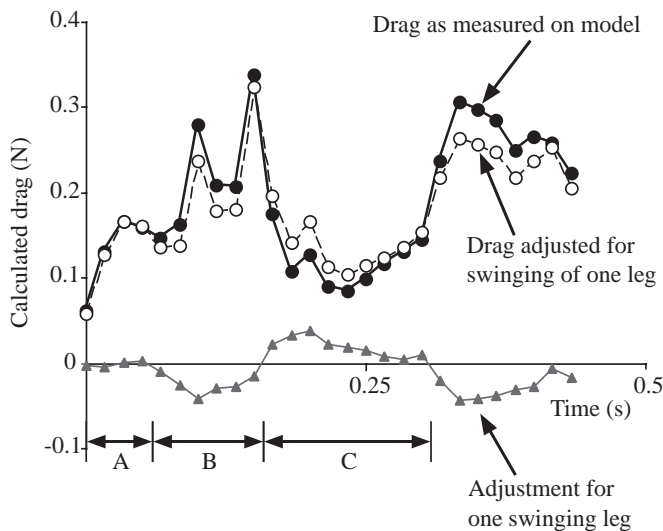

Fig. 6. Calculated contribution to drag on the crab due to drag on the swinging of one leg. Positive drag indicates drag acting in the opposite direction from the direction the whole crab is moving through the water (i.e. resisting forward movement). Negative drag indicates drag acting in the same direction as the crab is moving through the water (aiding forward movement). Filled circles indicate calculated drag on a crab model with legs not swinging. Open circles indicate the calculated drag on a crab model when adjusted for the contribution of one swinging leg. Grey triangles indicate the adjustment in drag due to one swinging leg. A, the time when a leg is not swinging relative to the body; B, the time when a leg is in the stance phase, generating thrust against the substratum and thus swinging with respect to the body; C, the time when a leg is in the swing phase and swinging with respect to the body.
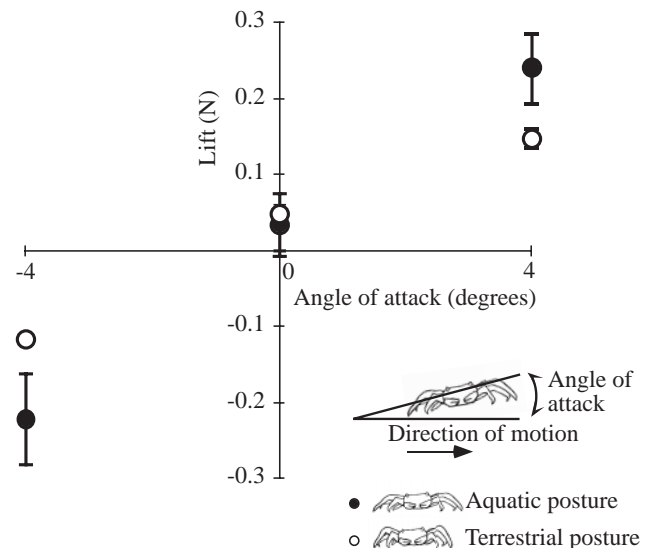

Fig. 7. Lift force on the body of a crab as a function of angle of attack. Values are means ± 1 S.D. of three replicate measurements at a velocity of 0.98 m s⁻¹ for one individual crab in the aquatic and the terrestrial posture. The actual values varied: the absolute value of the magnitude of the lift at angles of attack of +4° or −4° were greater for the aquatic posture than for the terrestrial posture, and lift acted upwards at angle of attack +4° but downwards at angle of attack −4°.
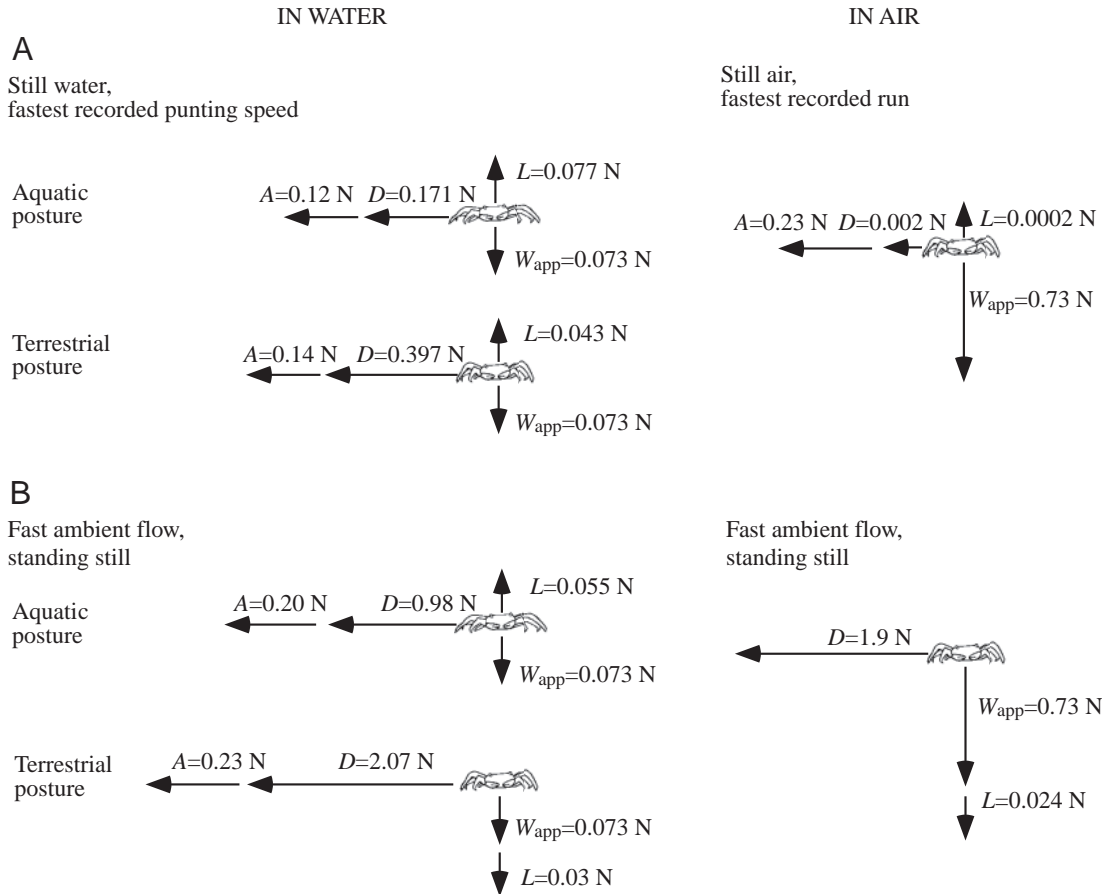
Fig. 8. The means of the mean values for all crabs were used to estimate the forces acting on the body of a crab using different postures in various flow conditions. Fluid motion relative to the crab is right-to-left. Longer arrows represent larger forces. In air, crabs are shown only in the terrestrial posture. W_{app}, apparent weight (= weight−buoyancy); A, acceleration reaction; D, drag; L, lift. (A) Crab is locomoting through still fluid (water or air). Fastest punting speed in water=$0.67\,\mathrm{m\,s^{-1}}$. Fastest recorded run on land=$1.4\,\mathrm{m\,s^{-1}}$. Crab is locomoting at $+4\,^\circ$ angle of attack. Body acceleration=$1.13\,\mathrm{m\,s^{-1}}$. (B) Crab is standing in moving fluid (water or air). Fastest water flow measured in the field at wave-swept site=$1.6\,\mathrm{m\,s^{-1}}$, acceleration=$1.71\,\mathrm{m\,s^{-2}}$. Air speed in hurricane $\approx 45\,\mathrm{m\,s^{-1}}$. Crab is standing with $0\,^\circ$ angle of attack relative to oncoming flow. Acceleration reaction force was not calculated in the terrestrial hurricane condition because acceleration data appropriate to the size scale of a crab was not available. Note that a crab locomoting in water at its fastest punting speed generates positive lift greater than its effective weight if the crab uses a $+4\,^\circ$ angle of attack.

Acceleration reaction

Added mass coefficients were greater for crabs in the terrestrial posture than in the aquatic posture (Table 1). Since added mass coefficients did not show a significant correlation with crab size in either posture (Kendall rank-correlation tests, $P>0.05$, $N=7$), group mean coefficients for each posture were used in overturning calculations.

Comparison of forces

At locomotory speeds in air, weight was by far the greatest force on a crab, whereas at locomotory speeds in water, the hydrodynamic forces were sometimes much larger than a crab's submerged weight. In still air at a crab's maximum recorded terrestrial speed ($1.4\,\mathrm{m\,s^{-1}}$), weight was 384 times greater than the drag force (on a crab using the terrestrial posture) (Fig. 8A). Even at an angle of attack of $+4\,^\circ$, drag was 10 times greater than the lift force, but only 0.3 % of the weight (Fig. 8A). By contrast, in still water at their maximum recorded locomotory speed in water ($0.67\,\mathrm{m\,s^{-1}}$), drag on *Grapsus tenuicrustatus* was 2.3 times greater than the crab's submerged weight and 17 times greater than lift at $0\,^\circ$ angle of attack for a crab using the aquatic posture. At an angle of attack of $+4\,^\circ$ at this speed, *G. tenuicrustatus* generated positive lift greater than its apparent weight in water. Lift at this angle of attack was still less than half the drag on a crab (Fig. 8A).

For a crab standing still in a wave-swept environment, drag was still the predominant force, but acceleration reaction also imposed a significant force. On a wave-swept shore with water velocities and accelerations of $1.6\,\mathrm{m\,s^{-1}}$ and $1.7\,\mathrm{m\,s^{-1}}$, the magnitude of the acceleration reaction force was 20 % of the drag force on a crab using the aquatic posture and 11 % of the drag force on a crab using the terrestrial posture (Fig. 8B).

Table 2. *Calculated critical speeds (m s⁻¹) in aquatic versus terrestrial postures at 0 ° angle of attack*

Condition	Critical speed ($m\,s^{-1}$)	
	Aquatic posture	Terrestrial posture
Washing away*		
Without active tenacity	0.09	0.03
With maximum tenacity	5.72	3.98
Overturning‡		
Without active tenacity (e.g. punting)	0.66	0.44
With maximum tenacity	8.20	5.50

*Critical water velocity (with appropriate accelerations measured in the field) to wash away a crab standing still.

‡Critical speed to overturn a crab locomoting through still water, assuming no body accelerations.

Aquatic versus *terrestrial posture*

Posture greatly influenced the hydrodynamic forces on the body of a crab. Compared to a crab using the aquatic posture, a crab using the terrestrial posture in wave-swept conditions (water velocity=1.6 m s⁻¹, water acceleration=1.7 m s⁻¹) experiences 111 % greater drag, 53 % less lift (and negative rather than positive lift) and 12 % more acceleration reaction force (Fig. 8B). The different forces cause a crab in the terrestrial posture to wash away in slower water flow than a crab in the aquatic posture. In fact, a crab in the aquatic posture could withstand 44 % faster flow in a steady current and 200 % faster flow in waves (slow flow regime, water acceleration= 0.17 m s⁻²) than it could withstand in the terrestrial posture (Table 2) before washing away. Furthermore, the difference in forces imposed on the two postures affects the maximum speed at which a crab could locomote underwater. A crab could locomote 50 % faster in the aquatic posture than in the terrestrial posture before overturning in still water (at 0 ° angle of attack, without tenacity), assuming that it is not accelerating its body during the maximum acceleration of the water around it (Table 2).

Calculations
Overturning

Even if crabs do not accelerate their bodies at the same time that waves maximally accelerate over them, crabs punting upstream while using the terrestrial posture overturn in any of the three flow environments considered (Table 3), even without consideration of acceleration reaction forces. In contrast, crabs punting upstream in the aquatic posture (at 0 ° angle of attack) are stable against overturning in the lagoon environment at both slow and fast punting speeds if water accelerations are low (Table 3). In the wave-swept environment, crabs punting at the slow speed are unstable in either posture even without water acceleration. The critical speed for overturning in still water (at 0 ° angle of attack, no body accelerations) is 0.66 m s⁻¹ for a crab in the aquatic posture and 0.44 m s⁻¹ for a crab in the terrestrial posture (Table 2). For comparison, a crab locomoting on land (using the terrestrial posture at 0 ° angle of attack, no body accelerations) would overturn at 41.3 m s⁻¹.

Critical speeds for overturning are highly dependent on the body acceleration assumed (Fig. 9A). Crabs in the terrestrial posture must punt with accelerations lower than 1.3 m s⁻². In contrast, crabs in the aquatic posture can punt with accelerations up to 2 m s⁻². A crab using a −4 ° angle of attack in the aquatic posture does not overturn at any speed for body accelerations less than 2 m s⁻². For 0 ° and +4 ° angle of attack as well as for the terrestrial posture, using higher accelerations

Table 3. *Washing away and overturning at three field sites*

Condition	Lagoon (u=0.12 m s⁻¹)	Bay (u=0.55 m s⁻¹)	Wave-swept (u=1.57 m s⁻¹)
Wash away standing still?*			
Aquatic posture	No (0.15 m s⁻²)‡	Yes	Yes
Terrestrial posture	No (0.12 m s⁻²)‡	Yes	Yes
Overturn punting upstream?§			
Aquatic posture slow punt	No (1.47 m s⁻²)‡	No (0.04 m s⁻²)‡	Yes
Aquatic posture fast punt	No (0.50 m s⁻²)‡	Yes	Yes
Terrestrial posture slow punt	Yes	Yes	Yes
Terrestrial posture fast punt	Yes	Yes	Yes

Calculations assume 0 ° angle of attack and no active tenacity.

u=peak water velocity measured at site.

*Due to drag and lift forces only.

‡Critical acceleration to wash away or overturn crab under these conditions, assuming that crab does not accelerate into accelerating flow.

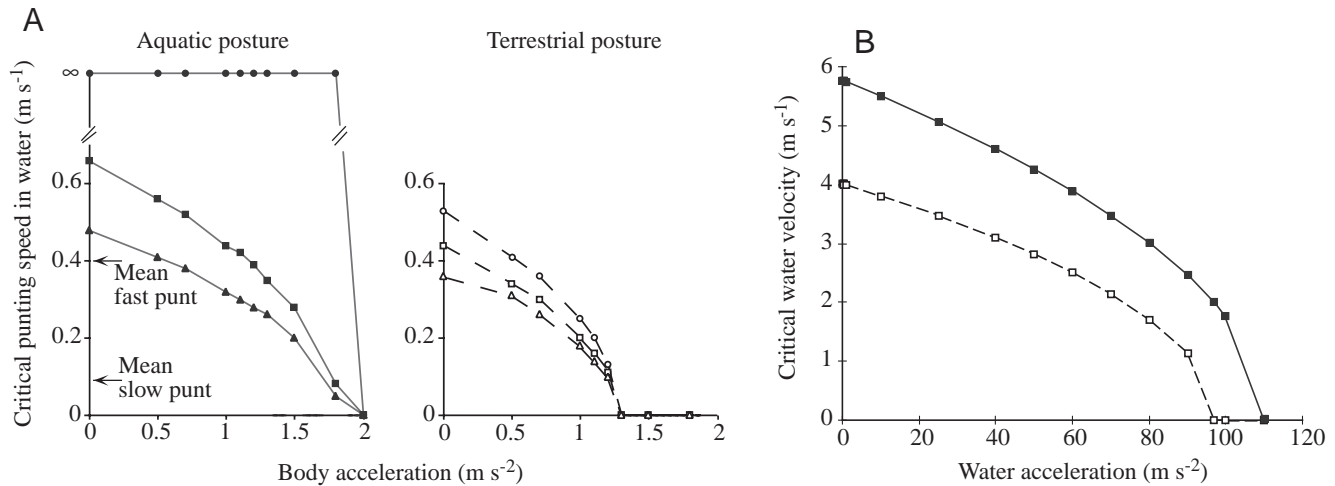§Slow punting speed=0.11 m s⁻¹. Fast punting speed=0.40 m s⁻¹.

Fig. 9. (A) Effect of body acceleration on the critical punting speed to overturn a crab in still water. Means of mean measurements for five crabs were used to calculate critical punting speed. Filled symbols and solid lines represent a crab in the aquatic posture. Open symbols and dashed lines represent a crab in the terrestrial posture. Angles of attack were $-4°$ (circles), $0°$ (squares) and $+4°$ (triangles), respectively. (B) Effect of water acceleration on the critical ambient water velocity necessary to wash away a crab standing with an angle of attack of $0°$. Calculations assumed that crabs grasped the substratum with maximum horizontal tenacity (13 N). Means of mean measurements for five crabs were used to calculate critical water velocities. Filled symbols indicate a crab using the aquatic posture. Open symbols represent a crab using the terrestrial posture in water.

drastically reduces the speeds at which a crab can punt without overturning.

Washing away

Critical speeds for washing away are lower than critical speeds for overturning. Furthermore, the critical speed at which a crab washes away depends on whether it relies on friction or actively grasps the substratum. If a crab in steady currents (i.e. with no water acceleration) relies on friction, it washes away at $0.25\,\mathrm{m\,s^{-1}}$ in the aquatic posture and at only $0.17\,\mathrm{m\,s^{-1}}$ in the terrestrial posture. However, if a crab grasps the substratum with its maximum horizontal tenacity, it can resist washing away at velocities up to $5.81\,\mathrm{m\,s^{-1}}$ in the aquatic posture and $4.01\,\mathrm{m\,s^{-1}}$ in the terrestrial posture, greater than the peak water velocities measured at all sites (Table 3). Increasing water acceleration decreases the water velocity a crab can withstand before washing away (Fig. 9B)

Table 4. *Fate of crabs in waves*

Type of wave (N)	Fate (% of total)		
	Washed away	Did not move	Kept walking
Small (17)	24	76	0
Medium (32)	6	88	6
Large (17)	6	88	6

5.5 h of videotape yielded 66 independent crab-waves from six different sites.

Wave heights (before breaking) were estimated from video images, using crabs as a size scale. Small waves, 0–0.5 m; medium waves, 0.5–1.0 m; large waves, 1.0–2.0 m.

N, number of crabs.

Behavior in waves

While most crabs maintained their positions, a few crabs washed away in waves in all three size categories (Table 4). Surprisingly, 6 % of the total number of crabs were observed to continue walking through waves of medium and large sizes. No crabs were observed walking through waves of the smallest size, although this may be due to the small sample size. Sometimes as a large wave broke over a crab, the crab flattened itself against the rock. This flattening behavior appeared to prevent crabs from washing away.

Crabs were observed to use non-punting gaits in the field, especially while climbing a vertical wall or while locomoting upside-down under a ledge. These non-punting gaits were characterized by constant contact with the substratum. Usually a crab had at least two legs in contact with the ground, one on either side of the body, allowing the crab to grip the substratum with a pinching behavior. Occasionally a crab dangled from one leg while climbing.

Discussion

An animal using pedestrian locomotion under water must contend with hydrodynamic forces that can prevent it from locomoting quickly or that can cause it to overturn or wash away. Thus, hydrodynamic forces can limit how and when an animal can locomote. In addition to an animal's morphology, factors such as posture, behavior and water flow environment dramatically influence the hydrodynamic forces the animal experiences.

Comparisons with other animals

Comparison of hydrodynamic coefficients with those of

other animals gives a relative measure of how an animal's morphology influences the hydrodynamic forces it experiences. Comparing benthic crustaceans using data from the literature is difficult, primarily because these data are collected under different circumstances. To determine the hydrodynamic forces an aquatic pedestrian experiences, measurements should be made on intact animals, in appropriate postures, in biologically relevant flow conditions, and next to a substratum. Blake (Blake, 1985) and Plotnik (Plotnik, 1985) determined the components of force generated by crabs' carapaces, but did not measure forces on entire animals. Both Pond's data (Pond, 1975) and the present study (Fig. 5, Fig. 7, Fig. 8) show that leg positions influence the forces experienced by an animal, suggesting that legs can contribute significantly to the hydrodynamics of the whole body. While several studies have measured hydrodynamic forces on benthic crustaceans, most of these studies (Pond, 1975; Blake, 1985; Plotnik, 1985; Jacklyn and Ritz, 1986; Alexander, 1990) have focused on swimming rather than on pedestrian locomotion and have thus measured forces on bodies far from a substratum. Animals very near a surface experience decreased drag and increased lift relative to animals far from a surface (Withers and Timko, 1977; Martinez, 1996).

Given these caveats, hydrodynamic comparisons can still be made among benthic crustacean data in the literature. The drag coefficients measured for *Grapsus tenuicrustatus* are smaller than those reported for benthic and swimming crabs (Blake, 1985), lobsters (Bill and Herrnkind, 1976), crayfish (Maude and Williams, 1983; Pond, 1975, calculated in Maude and Williams, 1983), and isopods (Alexander, 1990) (Fig. 10A,B), indicating that *G. tenuicrustatus* has a relatively streamlined shape. The only other crab that has a drag coefficient as low as that of *G. tenuicrustatus* is *Callinectes sapidus* (Blake, 1985; Plotnik, 1985), a crab known for rapid swimming (Spirito, 1972) (Fig. 10B).

Few data are available for lift on benthic crustaceans. *G. tenuicrustatus* has a large planform area, yielding a very low lift coefficient compared to crabs measured without legs (Blake, 1985) and for lobsters executing tail flips (Jacklyn and Ritz, 1986) (Fig. 10C).

The present study is the first to report added mass coefficients for a benthic animal using legged locomotion, enabling evaluation of the hydrodynamic forces imposed by accelerating water in the intertidal habitat. *G. tenuicrustatus* have added mass coefficients in the range reported for various sessile or slowly moving intertidal invertebrates (Denny et al., 1985), but lower than reported for sea urchins (Denny and Gaylord, 1996).

Drag on swinging legs

The drag on swinging legs damps out peaks and troughs in the magnitude of drag experienced by the whole animal over time as it locomotes through water (Fig. 6). The magnitude of this damping effect is small, even if two legs swing simultaneously. Measurements in a flume on models with legs
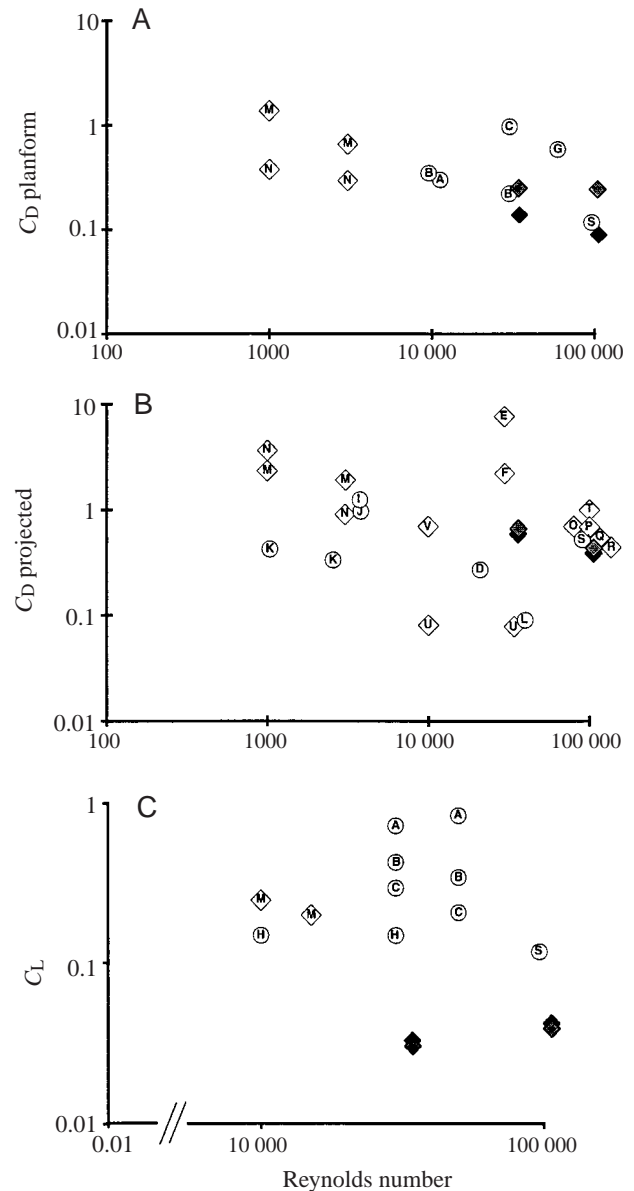

Fig. 10. Drag C_D (A, planform; B, projected) and lift C_L (C) coefficients as a function of Reynolds number for various animals. Black and grey diamonds indicate data for *Grapsus tenuicrustatus* in the aquatic and terrestrial postures, respectively. Diamonds represent data measured on animals near a substratum. Circles represent data measured on animals far from a substratum. Symbols are labelled as follows: A–C, crabs (Blake, 1985); D, crab (Plotnik, 1985); E,F, crayfish (Maude and Williams, 1983); G, lobster (Bill and Herrnkind, 1976); H, lobster in tail-flip posture (Jacklyn and Ritz, 1986); I,J, isopods (Alexander, 1990); K, euphausid (Torres, 1984); L, eurypterid (Plotnik, 1985); M,N, cockroaches (Full and Koehl, 1993); O, barnacle, (P, snail, Q,R, limpets (Denny et al., 1985); S, scallop (Hayami, 1991); T, sea urchin (Denny and Gaylord, 1996); U, inclined sand dollar (Nakamura, 1994); V, sea anemone (Koehl, 1977). Lift coefficients were measured at positive angles of attack: *G. tenuicrustatus* +4°; A–C, +5°; S, +25°.

not swinging give a good approximation of the hydrodynamic forces on a locomoting animal.

Mechanisms for resisting dislodgment

One mechanism by which a crab can avoid dislodgment from the substratum is by altering its posture. Of the two postures examined in this study (described for *Grapsus tenuicrustatus* in Martinez et al., 1998), the aquatic posture confers greater stability against overturning and washing away than does the terrestrial posture. This greater stability allows a crab to locomote up to 50 % faster through water in the aquatic posture than in the terrestrial posture (Table 2). Using the aquatic posture also allows a crab to be active in faster flow environments than it could be if it used the terrestrial posture (Table 3).

Two mechanisms contribute to the greater stability of the aquatic posture relative to the terrestrial posture: (1) the aquatic posture's wider stance increases the moment-arm over which the stabilizing forces act (Fig. 1B; Martinez et al., 1998); and (2) the lower drag coefficient and added mass coefficient associated with the aquatic posture result in smaller forces acting about the overturning moment-arm (Fig. 1B, Table 1). Martinez et al. (Martinez et al., 1998) predicted that a crab in the aquatic posture could withstand 25 % more drag than in the terrestrial posture before overturning in a steady current. However, the present study reveals that the stability of the aquatic posture is somewhat reduced by positive lift, resulting in a smaller increase in drag force (6 %) that a crab could withstand before overturning.

Another aspect of posture that affects hydrodynamic forces is the angle of attack. Since the lift on *G. tenuicrustatus* is very sensitive to angle of attack, a crab could substantially alter its stabilizing moment simply by changing its angle of attack by a few degrees (Fig. 7). The aquatic posture affords more opportunity for control of lift than does the terrestrial posture because the aquatic posture shows greater sensitivity of lift to changes in angle of attack (Fig. 7). Yet in faster flow environments, a small increase in angle of attack could result in a much larger lift force, causing the crab to overturn or wash away as it climbed over rugose terrain. Crabs punting slowly in still water do use variable angles of attack, but this variation is limited to shallow positive angles (Martinez et al., 1998). A crab's risk of overturning increases at faster relative water velocities and accelerations. Since negative angles of attack greatly increase a crab's stability (Table 1), crabs may use negative angles of attack at higher locomotory speeds and in ambient water flow to help them maintain contact with the substratum and to keep from overturning. It is possible for an animal to be stable at any speed (below a critical acceleration value) if it generates negative lift such that the lift times its moment-arm is greater than the drag times its moment-arm (Fig. 9A).

A crab's tenacity provides a very effective mechanism to resist overturning or washing away. A crab's tenacity augments its weight, increasing the hydrodynamic force necessary to dislodge it from the substratum. On a substratum with sufficient availability of footholds, tenacity could increase the relative water flow an animal could withstand by more than an order of magnitude (Table 2). Actively grasping the substratum (hence using a different gait than submerged punting) allows *Grapsus tenuicrustatus* to locomote in its wave-swept habitat, even through breaking waves (Table 4).

Hiding in a crevice allows a crab to withstand greater ambient water velocities. Koehl (Koehl, 1977) showed that flow microhabitats can be protected even in high flow sites. Furthermore, wedging against the sides of the crevice increases the water velocity necessary to wash away a crab, although the crab's behavior is still limited by the flow.

Hydrodynamic forces constrain locomotion

Hydrodynamic forces have the potential to constrain the speeds and accelerations an animal can attain while locomoting because at high velocities or accelerations these forces contribute a large portion to the force balance on the animal (Fig. 8). Unlike crabs such as *Callinectes sapidus*, *Grapsus tenuicrustatus* does not swim when removed from the substratum; it rows its legs in an anterior–posterior direction with little locomotory effect (M. M. M., personal observation). The power output to locomote at a constant speed is given by the product of the speed at which an animal locomotes and the drag force on the animal at that speed. Assuming a power output of $1.2\,\mathrm{W\,kg^{-1}}$ (value for *Ocypode quadrata* running on land; Blickhan and Full, 1987), a $0.07\,\mathrm{kg}$ *G. tenuicrustatus* could locomote at a constant speed of $4.45\ \mathrm{m\,s^{-1}}$ on land, $0.59\,\mathrm{m\,s^{-1}}$ in water using the aquatic posture, or $0.46\ \mathrm{m\,s^{-1}}$ using the terrestrial posture. Aside from the power to overcome drag at a given speed, an animal must generate power to accelerate, which can be calculated as the product of acceleration reaction force and the change in speed. The power output required to accelerate a crab using the aquatic posture is 53 % greater in water than on land.

Ambient water flow in a habitat can constrain the gait choice and kinematics of aquatic pedestrians. While *Grapsus tenuicrustatus* uses a punting gait in slow water (Martinez et al., 1998), the present study reveals that it could not use this gait in faster water flow because it would overturn (Table 3) unless it used negative angles of attack (which it does not use in slow punting). Maude and Williams (Maude and Williams, 1983) have shown that while standing still, crayfish adopt a lower, more streamlined posture and a negative angle of attack in response to increasingly faster water flow. Because flow habitat can greatly affect pedestrian kinematics (Martinez et al., 1998; Hui, 1992; Maude and Williams, 1983; Grote, 1981; Clarac et al., 1987), the next step in kinematic studies will be to incorporate field flow conditions as well as an animal's behavior in those flow conditions.

In addition to influencing an animal's gait, ambient water motion can constrain or completely inhibit an animal's locomotion. In the very slow flow of the lagoon environment, *Grapsus tenuicrustatus* (using the aquatic posture) incur very little risk of dislodgment; however, in the faster flows of the bay and wave-swept environments, crabs are constrained to actively grasp the substratum while locomoting or to locomote downstream (Table 3). The lobster *Homarus gammarus* stops locomoting in moderately slow flow and washes away in flow

approaching $50\,\mathrm{cm\,s^{-1}}$ on a gravel substratum (Howard and Nunny, 1983). Similarly, crayfish may be limited in their distribution by hydrodynamic interaction and their ability to hold onto the substratum to keep from washing away (Maude and Williams, 1983). Likewise, Le Roux et al. (Le Roux et al., 1990) have suggested that green crabs *Carcinus maenas* do not invade the wave-swept shoreline because they are inhibited by the ambient flow. Restrictions on mobility affect not only an animal's behavior, but consequently its interactions with other organisms. Sea urchins reduce their locomotion and feeding rates in faster flow (Kawamata, 1998). In the intertidal zone, limpets forage less when waves are high (Wright, 1978) and carnivorous gastropods impose low predation intensity at high flow sites (Leonard et al., 1998).

Not only are the dynamics of pedestrian locomotion drastically different in air from in water, but also in still water as opposed to currents or waves. The hydrodynamic forces imposed by ambient water flow constrain how, when, and where a pedestrian may locomote because the animal must generate enough force to overcome hydrodynamic resistance to movement as well as keep from being dislodged from the substratum. In order to assess the role of hydrodynamic forces in pedestrian locomotion, it is critical to consider water flow conditions in the environment as well as the postures and behaviors an animal uses in those water flow conditions.

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