

## UNDERWATER PUNTING BY AN INTERTIDAL CRAB: A NOVEL GAIT REVEALED BY THE KINEMATICS OF PEDESTRIAN LOCOMOTION IN AIR *VERSUS* WATER

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### Summary

As an animal moves from air to water, its effective weight is substantially reduced by buoyancy while the fluid-dynamic forces (e.g. lift and drag) are increased 800-fold. The changes in the magnitude of these forces are likely to have substantial consequences for locomotion as well as for resistance to being overturned. We began our investigation of aquatic pedestrian locomotion by quantifying the kinematics of crabs at slow speeds where buoyant forces are more important relative to fluid-dynamic forces. At these slow speeds, we used reduced-gravity models of terrestrial locomotion to predict trends in the kinematics of aquatic pedestrian locomotion. Using these models, we expected animals in water to use running gaits even at slow speeds. We hypothesized that aquatic pedestrians would (1) use lower duty factors and longer periods with no ground contact, (2) demonstrate more variable kinematics and (3) adopt wider stances for increased horizontal stability against fluid-dynamic forces than animals moving at the same speed on land. We tested these predictions by

measuring the three-dimensional kinematics of intertidal rock crabs (*Grapsus tenuicrustatus*) locomoting through water and air at the same velocity ( $9\text{ cm s}^{-1}$ ) over a flat substratum. As predicted from reduced-gravity models of running, crabs moving under water showed decreased leg contact times and duty factors relative to locomotion on land. In water, the legs cycled intermittently, fewer legs were in contact with the substratum and leg kinematics were much more variable than on land. The width of the crab's stance was 19% greater in water than in air, thereby increasing stability against overturning by hydrodynamic forces. Rather than an alternating tetrapod or metachronal wave gait, crabs in water used a novel gait we termed 'underwater punting', characterized by alternating phases of generating thrust against the substratum and gliding through the water.

Key words: locomotion, biomechanics, crustacean, arthropod, gait, crab, *Grapsus tenuicrustatus*.

### Introduction

Several lineages of benthic animals have made the evolutionary transition between an aquatic and a terrestrial habitat, notably the molluscs, annelids, arthropods and vertebrates. Whether a change of habitat takes place on an evolutionary time scale for a lineage or on a contemporary time scale for an amphibious individual (such as one that lives in the intertidal zone), the transition between two distinct physical environments may have significant mechanical consequences for walking and running. As an animal moves from air to water, its effective weight is substantially reduced by buoyancy, while the fluid-dynamic forces (e.g. lift and drag) are increased 800-fold. The changes in the magnitude of these forces are likely to have substantial consequences for locomotion as well as for resistance to overturning. Although pedestrian locomotion in air and swimming in water have been studied extensively (Alexander and Goldspink, 1977; Alexander, 1992; Full, 1997; Gans *et al.* 1997), only a few studies have explicitly considered the kinematics (Hui, 1992; Pridmore, 1994; Jamon and Clarac, 1995), kinetics (Clarac and Cruse, 1982; Grote, 1981; Klärner and Barnes, 1986), energetic cost (Houlihan and Innes, 1984;

Houlihan *et al.* 1984) or hydrodynamics (Pond, 1975; Maude and Williams, 1983; Blake, 1985; Bill and Herrnkind, 1976) of aquatic pedestrian locomotion. No study to date provides a theoretical model of aquatic pedestrian mechanics comparable with those developed for legged terrestrial locomotion (Blickhan, 1989; Blickhan and Full, 1987, 1993; Cavagna *et al.* 1977; McMahon and Cheng, 1990). Most research on aquatic pedestrians has focused on inter-leg coordination and motor control (e.g. Chasserat and Clarac, 1983; Clarac, 1981, 1984; Clarac and Barnes, 1985; Clarac and Chasserat, 1983; Clarac *et al.* 1987; Cruse and Muller, 1986; Jamon and Clarac, 1995; Muller and Cruse, 1991). We contend that a synthesis of these fundamental studies of neural control with analyses of the mechanics of locomoting on underwater substrata is required before we can explain the differences between aquatic and terrestrial pedestrian locomotion and the transition to land.

Previous studies comparing pedestrian arthropods in water *versus* in air have revealed seemingly contrary patterns in locomotor posture and kinematics, including decreased duty factor or power stroke duration (Hui, 1992; Clarac *et al.* 1987),

increased stance width (Grote, 1981; Hui, 1992), no change in stance width (Hui, 1992), increased stride length (Grote, 1981; Pond, 1975), no change in stride length (Hui, 1992), increased stride frequency (Grote, 1981; Pond, 1975; Clarac *et al.* 1987) and no change in stride frequency (Hui, 1992) in water compared with air. The present study seeks a mechanistic explanation of these published observations on postural and kinematic differences. Furthermore, this study seeks to develop a unifying mechanical framework within which to consider pedestrian locomotion under varied conditions (including terrestrial, aquatic and lunar conditions). To accomplish these goals, we make direct kinematic comparisons between individual animals locomoting at the same speed in the same tank filled with either air or water. In doing so, we control for the effects of speed, substratum and the individual animal. We use the kinematic data to test several mechanically based hypotheses of aquatic pedestrian locomotion. This study also reveals basic information about mechanical aspects of the evolution of terrestriality and provides biological inspiration for the design of autonomous legged underwater vehicles (ALUVs; Greiner *et al.* 1996).

#### Experimental system

Crabs provide a useful system for investigation of the mechanics of locomoting in aquatic *versus* terrestrial environments because there are subtidal, intertidal (amphibious) and terrestrial crab species. This diversity permits both comparison across species and comparison of amphibious individuals with themselves as they locomote under water *versus* on land. Using amphibious animals offers the advantage of tighter control with paired comparisons for each individual, rather than comparisons of species averages.

Once we have determined the kinematic differences using amphibious animals, we can then make multiple-species comparisons that focus on quantifying the critical kinematic variables. Furthermore, there is already a rich background of information on the physiology and mechanics of terrestrial locomotion in crabs (e.g. Barnes, 1975; Blickhan and Full, 1987, 1993; Evoy and Fournier, 1973; Full, 1987; Full and Herreid, 1983, 1984; Full and Weinstein, 1992; Hui, 1992). Using this breadth of knowledge from terrestrial locomotion in crabs may allow us more easily to predict how locomotion will change in an aquatic environment. The particular crab we chose was the Hawaiian intertidal rock crab *Grapsus tenuicrustatus*, a large, fleet-footed pedestrian both under water and on land (Johnson, 1965; Martinez, 1996).

#### Hypotheses of aquatic pedestrian locomotion

Using results from previous studies of locomotion in simulated reduced gravity (He *et al.* 1991; Kram *et al.* 1997; Margaria and Cavagna, 1964; Newman, 1992; Newman *et al.* 1994) as well as basic fluid-dynamic principles, we propose three hypotheses about the kinematics of animals locomoting under water *versus* on land.

*Hypothesis 1: the kinematics of aquatic pedestrian locomotion can be predicted from reduced-gravity models of terrestrial locomotion*

Since buoyancy reduces effective weight in water, we hypothesize that, during slow-speed locomotion, to which hydrodynamic forces make very little contribution, the kinematics can be predicted from reduced-gravity models of terrestrial locomotion (Fig. 1).

Like many animals, including humans, crabs locomoting on

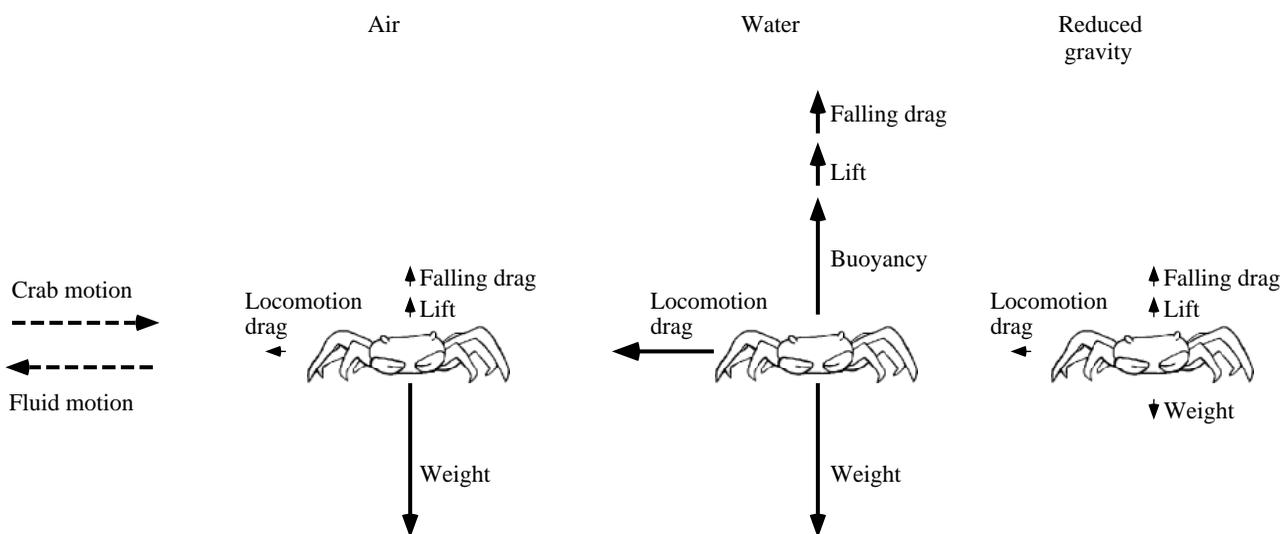


Fig. 1. Comparisons of forces on a crab locomoting in air, in water and under conditions of reduced gravity. In terrestrial pedestrian locomotion, an animal's weight is the predominant force it experiences as it locomotes. In water, buoyant forces can nearly balance gravitational forces, while hydrodynamic drag resists the motion of a body falling towards the substratum between steps. Horizontal locomotion may cause positive hydrodynamic lift on the body, acting at right angles to the direction of locomotion; such lift also supports the weight of the animal. The vertical forces on an animal can be similar in magnitude during aquatic and reduced-gravity pedestrian locomotion.

land at slow speeds use a walking gait, as defined by the inverted-pendulum mechanics of their center of mass (Blickhan and Full, 1987). Maximum exchange between potential and kinetic energy from the inverted-pendulum mechanism occurs when the magnitudes of the potential and kinetic energy fluctuations are equal and the fluctuations occur  $180^\circ$  out of phase with each other. The lower effective weight under water and reduced gravity affect the inverted-pendulum mechanics of pedestrian locomotion in much the same way. The lower effective weight (due to reduced gravity on land or increased buoyancy in water) uncouples the exchange of mechanical energy by reducing the magnitude of fluctuations in potential energy of the body, but not of fluctuations in kinetic energy (Margaria and Cavagna, 1964). This resulting mismatch produces an ineffective pendulum exchange of mechanical energy.

We can make predictions about inverted-pendulum walking using a simple model of dynamic similarity expressed as the Froude number ( $F$ ) (Alexander, 1989):

$$F = u^2/(gl), \quad (1)$$

where  $u$  is the animal's forward speed,  $g$  is gravitational acceleration and  $l$  is the animal's effective leg length. The Froude number is the ratio of the centrifugal force (pulling the animal off the ground) to the gravitational force (pulling the animal back to the substratum). In theory, when centrifugal force balances or exceeds gravitational force (Froude number  $\geq 1$ ), an animal can no longer walk using inverted-pendulum mechanics and switches to a non-walking gait. According to this simple model, a lower effective gravity when in water (due to substantial buoyancy) would cause an animal to change from a walking- to a running-type (bouncing) gait at a lower speed than when in air (if we assume no change in the animal's effective leg length). Since the buoyant force in water decreases the effective gravity on a crab by approximately 10-fold, we expect that, even at the slowest speeds, a crab would use a running-type gait in water, where a running-type gait is defined by spring-mass motion, such as that seen in trotting, galloping and hopping.

Running on land has been successfully modeled as a simple, spring-mass system in a wide diversity of species (Blickhan, 1989; Blickhan and Full, 1993; Cavagna *et al.* 1977; Farley *et al.* 1993; McMahon and Cheng, 1990). The 'leg spring' represents the spring-like characteristics of the entire musculo-skeletal system. The mass is equivalent to body mass, upon which gravity acts. The stiffness of the leg spring is calculated as the ratio of the ground reaction force to the compression of the leg spring when the leg is maximally compressed (Blickhan, 1989). Buoyancy in water counteracts an animal's weight, producing an effect similar to reduced gravitational acceleration on the body mass, thereby decreasing ground reaction forces. Assuming that the stiffness of a crab's leg spring remains the same under water as on land, the spring-mass model predicts that aquatic pedestrians might contact the substratum only briefly and glide more relative to pedestrians on land.

### *Hypothesis 2: aquatic gaits are less constrained than terrestrial gaits*

As gravity pulls an animal towards the substratum, the animal must readjust its legs to ensure support of its body before it falls to the ground. The time available for such an adjustment constrains the footfall patterns and gaits an animal can use while still keeping its body off the substratum. In water, where gravity is effectively less than on land, due to buoyancy, an animal's body is pulled towards the substratum more slowly, allowing more time for the legs to adjust before the animal hits the ground. Falling towards the substratum between steps also generates fluid-dynamic drag on the crab's body acting away from the substratum to support the weight of the animal (Fig. 1). A locomoting crab may even generate fluid-dynamic lift which acts perpendicular to the direction of locomotion. If such lift is positive (i.e. pulling the animal away from the substratum), it will further resist falling. Since drag and lift are proportional to the fluid density, these forces are 800 times greater in water than in air.

The higher buoyancy, drag and lift in water relative to those in air could allow a crab a longer time to fall and, consequently, a longer time to put down a stabilizing foot before its body strikes the substratum. This extra time may allow greater flexibility in the timing and placement of supporting feet during locomotion in water than in air. We therefore predict that a crab can exhibit more variable kinematics in water than in air.

### *Hypothesis 3: pedestrians adopt a more stable posture in water than in air*

A running crab with a given posture incurs a greater risk of overturning in water than on land (Alexander, 1971). An animal will overturn, pivoting about its trailing (i.e. downstream) leg, when the overturning moments about its body exceed the stabilizing moments (Fig. 2). Assuming that all forces act at the center of mass, the overturning moment equals the drag times the vertical distance to the pivot, whereas

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Overturning = drag  $\times$  height

Stabilizing = (weight - buoyancy - lift)  $\times$  distance to trailing leg

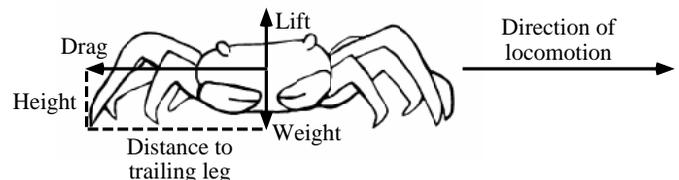


Fig. 2. Stability against overturning. An animal overturns, pivoting about its downstream leg, when the overturning moments about its body exceed the stabilizing moments. The overturning moment is the drag times the vertical distance to the pivot (the height of the carapace above the substratum). The stabilizing moment is the animal's effective weight (weight minus buoyancy minus lift) times the horizontal distance to the pivot (the distance from the center of mass to the trailing leg).

the stabilizing moment equals the animal's effective weight (weight minus buoyancy minus lift) times the horizontal distance to the pivot. Because the density of water is greater than that of air, the overturning moment on a crab locomoting in water is greater (due to higher drag) and the stabilizing moment is lower (due to higher lift and buoyancy) than on a crab in air. We predict that a crab will compensate for the greater likelihood of overturning in water by adopting a more stable posture under water than it uses on land. Crabs may increase the stabilizing moment by adopting a wider stance and may also minimize the overturning moment by adopting a body posture that reduces drag and lift forces on the body.

## Materials and methods

### Animals

Large male *Grapsus tenuicrustatus* Herbst (carapace width  $53 \pm 4$  mm; mean  $\pm$  s.d.,  $N=6$ ; mass  $74 \pm 10$  g,  $N=6$ ) were collected along the rocky shore of Coconut Island, Hawaii. Crabs were maintained in seawater tables at ambient temperature ( $25.5 \pm 0.5$  °C) and local photoperiod, fed freeze-dried brine shrimp daily and video-taped within 1 week of capture. Only intermolt crabs with a full complement of walking legs and chelipeds were video-taped.

### Image capture

Crabs were video-taped as they moved freely along the length of a rectangular arena ( $180 \text{ cm} \times 40 \text{ cm}$ ) through either air or still sea water. The arena was fitted with a felt substratum to provide adequate traction. The water was 20 cm deep, approximately 14 cm above the height of the crab. Before each trial, water motion in the tank was allowed to settle to the point where it could no longer be visually detected. At the beginning of a trial, crabs were occasionally prodded on the leg with a stiff rod to initiate movement. Trials were video-taped with two SVHS camcorders (Panasonic models PVS770 and PVS62) and one 8 mm camcorder (Sony CCD V9/V90) recording at  $60 \text{ fields s}^{-1}$  and synchronized with a light-emitting diode. Two camcorders were positioned  $35^\circ$  from horizontal, one at each end of the arena, and the third was positioned directly above the arena (Fig. 3). A calibration frame ( $12 \text{ cm} \times 6 \text{ cm} \times 5 \text{ cm}$ ) with eight non-coplanar control

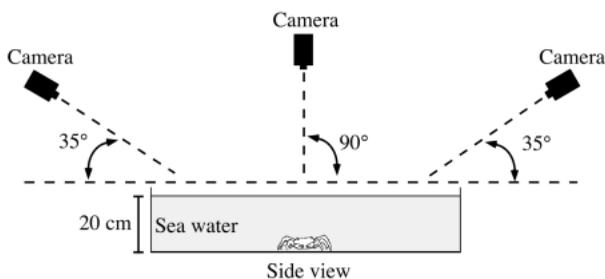


Fig. 3. Diagram of camera positions used to video-tape crabs. The arena ( $180 \text{ cm} \times 40 \text{ cm}$ ) was filled to a depth of 20 cm with sea water for aquatic trials.

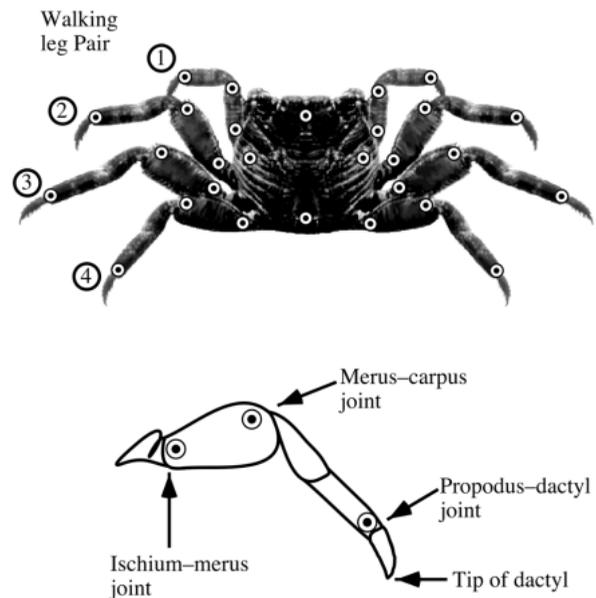


Fig. 4. Location of markers on a crab. Circles indicate points digitized on each crab in three camera views. The tip of the dactyl was also digitized for the first three pairs of walking legs.

points (see Biewener and Full, 1992) was video-taped by all three cameras.

To facilitate digitization of the video recordings, high-contrast white tabs were glued with cyanoacrylate adhesive to the crab's exoskeleton, adjacent to the ischium-merus, merus-carpus and propodus-dactyl joints on the walking legs (Fig. 4). Points on the carapace were marked with white paint (Liquid Paper).

### Kinematic analysis

Video images were digitized using a motion analysis system (Peak Performance Technologies, Inc., version 5.0) to obtain three-dimensional coordinates for the marked points on the legs and carapace as well as the dactyl tips (Biewener and Full, 1992). As our coordinate system convention, we designated positive values of  $x$  as the direction of motion (lateral for a sideways-moving crab; Fig. 5). The resolution of the video images averaged 0.86 mm per pixel. Points in space could be located with mean squared errors of 0.083 mm, 0.098 mm and 0.114 mm for the  $x$ ,  $y$  and  $z$  directions, respectively, yielding a 0.178 mm mean squared error for position. Data were filtered using a low-pass, fourth-order, zero-phase-shift Butterworth digital filter with a cut-off frequency of 10 Hz, a frequency that caused little signal distortion and allowed minimal noise to pass according to a residual analysis (see Biewener and Full, 1992). Filters below 8 Hz added signal distortion, whereas a 12 Hz filter included significant noise. Data from all camera views were filtered before direct linear transformation to three-dimensional coordinates.

### Stride definition

A stride is conventionally defined as the complete motion

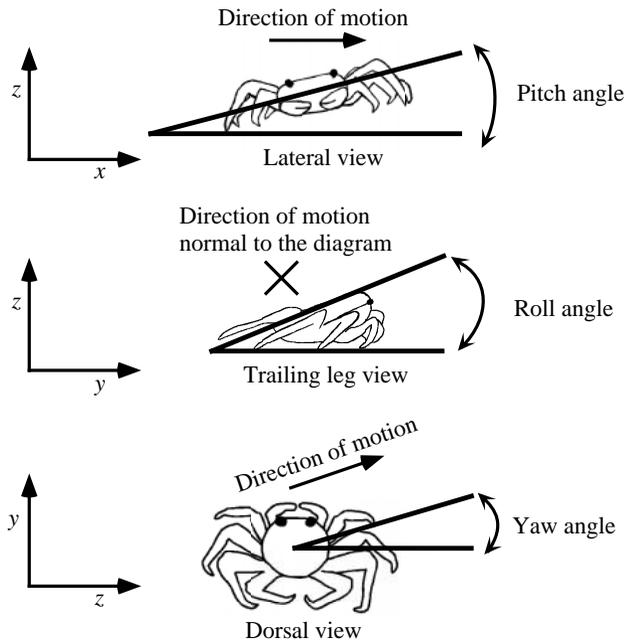


Fig. 5. Coordinate axes and carapace angles defined for a sideways-moving crab. In the trailing leg view, X indicates motion into the page.

cycle of a leg, within which all legs cycle with the same mean frequency. During aquatic locomotion, *G. tenuicrustatus* often cycled different pairs of legs at different rates, with some legs not cycling at all in the time examined. This variability during aquatic locomotion made the application of the conventional definition of a stride impossible. To compare cycles across different legs, we analyzed a complete cycle for legs that cycled throughout the period examined. The time period examined (approximately 2 s) was determined by the length of time that a crab stayed in the view of all three cameras. We defined the maximum stride period to be the longest time period taken by any individual leg to complete one cycle within the sampling period. If a leg did not cycle, it was not analyzed. Likewise, if a leg cycled more than once during that time, each cycle was analyzed and the data for that leg were averaged. A leg was said to cycle completely if it had a period of ground contact associated with protraction and retraction of the leg. The reference point used to determine the start of a cycle was either the beginning or the end of ground contact, whichever occurred first in that trial, for a particular leg. This operational definition of a stride did not bias our results for stride variables (e.g. stride length, duty factor and merus–carpus angle, defined below) because these variables were also analyzed for each individual leg cycle for all legs cycling within the maximum stride period. Defining the maximum stride period with respect to the longest observed leg cycle rather than with respect to the shortest leg cycle allowed inclusion of the greatest number of cycling legs in the time interval examined.

The animals moved at a mean velocity of  $9.7 \pm 0.7 \text{ cm s}^{-1}$  (mean  $\pm$  s.d.,  $N=15$ ) in air and  $11.4 \pm 2.0 \text{ cm s}^{-1}$  ( $N=15$ ) under water, so we chose matched air and water trials at a velocity of  $9 \pm 2 \text{ cm s}^{-1}$  for each of six individuals. One maximum stride

from each of these trials was analyzed, comparing each animal with itself in water *versus* in air. Of the two pairs of walking legs that cycled most consistently across trials, the first pair of walking legs showed the least variance in leg stride period ( $F$ -test of equal variance,  $N=10$ ,  $P=0.005$ ). To analyze a consistent number of fields across trials, we digitized 25 fields of the leg with the shortest leg stride period. Since the first pair of walking legs exhibited the shortest leg stride period of the four pairs of legs, expressing our sampling rate with respect to this leg pair yielded the largest consistent number of samples per maximum stride period. A comparison with 60 Hz sampling demonstrated that our sampling regime did not result in significantly different positions, angles or velocities. Chelipeds were not included in this analysis because *Grapsus tenuicrustatus*, unlike some other species (e.g. Sleinis and Silvey, 1980), were not observed to use them during locomotion.

#### Velocity and stride parameters

Instantaneous forward velocities were calculated by motion analysis software, using a fourth-order central difference algorithm (Biewener and Full, 1992), and were averaged over the trial. These mean velocities were consistent with independent calculations from times to traverse a known distance. For analysis, we chose only constant mean velocity trials in which the sum of increases and decreases in velocity was within 5% of the animal's mean velocity. For each cycling leg throughout the sampling period, stride length was determined from the distance traversed by the tip of a dactyl between successive periods of ground contact. A period of ground contact was defined as a time when a dactyl tip contacted the substratum (as determined from its  $z$ -axis coordinates) and did not move relative to the substratum (as determined from its  $x$ - and  $y$ -axis coordinates). There were no instances of dactyl slippage on the felt substratum. Leg stride period was taken as the time elapsed between successive beginnings or endings of ground contact, with stride frequency then calculated as the inverse of the stride period. Duty factors were calculated as the percentage of a cycle that a dactyl was in contact with the substratum, i.e. the contact time divided by that leg's stride period.

Because individuals almost always cycled more than one leg during a trial, we calculated the mean and variance of stride length, stride period and duty factor for each individual using all cycling legs. Using the mean and variance computed for each individual, we calculated group means and variances in air *versus* water. We compared means in air *versus* water using a Wilcoxon signed-rank test (the nonparametric equivalent of a paired  $t$ -test). Since we hypothesized that reduced gravity could remove the requirement for precise and regular leg movement, we also compared variances in air *versus* water using an  $F$ -test of equal variance. Statistical tests were performed using a statistical program (Statview 4.0 on a Power Macintosh).

#### Distance and angle measurements

For use in estimating overturning moments, we calculated

height at the center of the carapace (midway between the anterior and posterior digitized points on the carapace; Fig. 4) and the width of the stance between contralateral leg pairs using three-dimensional coordinates from the motion analysis software. We calculated maximum stance width as the greatest distance between the tips of the dactyls of any contralateral leg pair, regardless of ground contact, over the maximum stride period. We determined mean, maximum and minimum merus–carpus joint angles (Fig. 4) for every leg over a maximum stride period. We then calculated the means of each of these merus–carpus angles for each individual crab. In addition we determined pitch, roll and yaw angles of the carapace (Fig. 5). For a sideways-moving crab, pitch refers to rotation about the anterior–posterior axis of the carapace and roll refers to rotation about the lateral axis. Yaw is the angle between the lateral axis of the crab and the direction in which the animal moves.

#### Footfall pattern

Footfall patterns were determined from field-by-field analysis of video tapes by noting times of touch-down and lift-off of the dactyl for each walking leg throughout the stride analyzed. The total number of legs in contact with the substratum was determined for each video field. Over the course of the sampling period, the horizontal trajectories of each dactyl relative to the body determined the actual workspaces for each leg, in comparison with the potential workspaces (the area through which a leg could potentially swing, as determined by tracing the range of ground contact that the leg could achieve through maximum extension of all joints while the carapace is at the minimum height observed

during locomotion). Within these actual workspaces, the lateral and anterior–posterior excursion distances were quantified for each leg. In a sideways-moving crab, anterior–posterior excursion refers to the anterior–posterior axis of the animal, which (in the case of 0° yaw) is perpendicular to the direction of motion. Similarly, lateral refers to the lateral axis of the animal, parallel to the line of motion for a sideways-moving crab at 0° yaw. Workspace data for leading and trailing legs were analyzed separately, using Wilcoxon signed-rank tests. To determine the position of the crab's dactyls within the workspace, we compared the crab's lateral with its anterior–posterior stance width.

Whereas stride frequency, stride length, duty factor and contact time were analyzed only on legs that cycled completely, workspaces and stance width were measured without regard to cycling or ground contact, because a leg close to the ground can still provide timely support to a perturbed animal. Conversely, measures such as duty factor and contact time involve interactions with the substratum since they relate to propulsion.

## Results

### Buoyancy

The effective weight of *Grapsus tenuicrustatus* submerged in sea water (salinity 0.33%) was only one-tenth of its weight in air. Subtracting each crab's submerged weight ( $0.073 \pm 0.023$  N, mean  $\pm$  S.D.,  $N=6$ ) from its weight in air ( $0.73 \pm 0.097$  N,  $N=6$ ) yielded its buoyant force ( $0.65 \pm 0.082$  N,  $N=6$ ) in sea water. *G. tenuicrustatus* had a specific gravity of  $1.13 \pm 0.035$  ( $N=6$ ).

Table 1. Kinematic variables in air versus water

	Air	Water	<i>P</i>
Speed (m s <sup>-1</sup> )	0.097 $\pm$ 0.007	0.114 $\pm$ 0.02	0.11 (0.50)
Stride length (m)			
Leg with maximum stride period	0.094 $\pm$ 0.02	0.088 $\pm$ 0.04	0.60 (0.09)
All legs	0.076 $\pm$ 0.0089	0.084 $\pm$ 0.0043	0.17 (0.80)
Stride frequency (Hz)			
Leg with maximum stride period	0.97 $\pm$ 0.14	1.19 $\pm$ 0.49	0.46 (0.008)
All legs	1.17 $\pm$ 0.150	1.13 $\pm$ 0.222	0.75 (0.40)
Stride period (s)			
Leg with maximum stride period	1.05 $\pm$ 0.163	0.94 $\pm$ 0.315	0.35 (0.09)
All legs	0.90 $\pm$ 0.097	0.98 $\pm$ 0.122	0.17 (0.63)
Contact time (s)			
Leg with maximum stride period	0.65 $\pm$ 0.196	0.39 $\pm$ 0.238	0.12 (0.34)
All legs	0.52 $\pm$ 0.047	0.37 $\pm$ 0.087	0.03 (0.20)
Duty factor			
Leg with maximum stride period	0.61 $\pm$ 0.102	0.40 $\pm$ 0.164	0.12 (0.16)
All legs	0.57 $\pm$ 0.021	0.38 $\pm$ 0.080	0.03 (0.01)

Values are means  $\pm$  one standard deviation; for *P*, values are for the means with *P* values for variances in parentheses.

$P < 0.05$  indicates a significant difference between water and air.

$N=6$  crabs except for speed, where  $N=15$  crabs.

Table 2. Kinematic variables of leading versus trailing legs in air and in water

	Leading legs		Trailing legs	
	Air	Water	Air	Water
Stride length (m)	0.079±0.012	0.090±0.017	0.072±0.010	0.073±0.015†
Stride frequency (Hz)	1.11±0.206	1.08±0.154	1.23±0.192	1.28±0.331
Stride period (s)	0.94±0.144	1.00±0.109	0.87±0.112	0.87±0.184†
Contact time(s)	0.53±0.074	0.43±0.092	0.51±0.049	0.28±0.08†,*
Duty factor	0.561±0.022	0.41±0.102	0.58±0.028	0.33±0.095*

Values are means ± one standard deviation; *N*=6 crabs.  
† indicates a significant difference between leading and trailing legs for a given medium.  
\* indicates a significant difference between air and water for a given set of legs.

### Kinematics

Rather than using an alternating tetrapod or metachronal gait, as seen on land, crabs in water usually pushed or pulled with only a few legs, occasionally cycling one leg several times before using a different leg. Thus, in water, the animals often cycled adjacent legs or even leading and trailing legs of the same pair at different rates, with some legs not cycling at all throughout the period examined. There were several instances (12 in water, one in air) where only one leg of a contralateral pair cycled completely during the maximum stride period, and several cases (eight in water, none in air) where neither leg of a contralateral pair cycled.

#### Stride period, frequency and length

During the maximum stride period, neither stride length nor stride period was significantly different between water and air trials (Table 1). Mean stride frequency was not significantly different between water and air trials during the maximum stride period (Table 1), although stride frequency was more variable in water than in air. Neither means nor variances of leg stride frequency, period or length were significantly different in water *versus* air for of all cycling legs (Table 1). In water, leading legs had greater stride lengths and stride periods than trailing legs (Table 2). Leading legs did not show more variable kinematics than trailing legs (Table 2).

#### Contact time and duty factor

Mean leg contact times and duty factors in water were nearly half the values in air for all the legs that cycled completely. Contact time was also significantly lower in water, but was not more variable than in air (Table 1). Contact times for maximum stride periods did not differ in air *versus* water owing to large variations in both values. Duty factors were significantly lower and more variable in water than in air for all legs, but not for the legs with the longest stride periods (Table 1). In water, trailing legs had shorter contact times than leading legs (Table 2). Trailing legs in water also had shorter contact times and duty factors than trailing legs in air (Table 2).

#### Footfall pattern and leg cycling

Rather than an alternating tetrapod or metachronal gait,

crabs locomoting under water used a gait we shall call 'underwater punting,' characterized by alternating phases of gliding and thrust generation. Crabs moving under water had, on average, two fewer legs in contact with the substratum at any point in time than did animals moving on land (Table 3). On land, crabs almost never had fewer than three legs in contact with the ground at any time, whereas in water, they commonly had only one leg in contact with the substratum. We defined 'gliding' as the period when a crab did not have its center of mass surrounded by a tripod of supporting legs in contact with the substratum. Crabs moving on land virtually never glided (one crab for 0.03 s, which was 0.6% of the mean maximum stride period), whereas four of the six crabs moving under water glided for a significant percentage of the maximum stride period ( $57 \pm 27.6\%$ , mean ± s.d., *N*=4). One water trial included an 'aerial' period of 0.07 s, during which no legs contacted the substratum.

Water trials were characterized by a much more variable footfall pattern than air trials (Fig. 6). The number of legs cycling completely was significantly fewer and more variable in water than in air (Table 3), with four fewer legs cycling on average in water trials. In one of the water trials, only one leg cycled through the maximum stride period, whereas in air there was only one incident of a leg not cycling completely through the maximum stride period.

#### Leg stance and workspaces

Crabs adopted a wider stance in water than in air. The maximum lateral stance width in water was on average 1.2

Table 3. Leg participation in air versus water

	Air	Water	<i>P</i>
Number of dactyls in contact with ground	4.8±0.4	2.5±0.5	<0.001 (0.34)
Number of legs cycling through stride	7.8±0.4	4.2±1.6	0.028 (0.005)

Values are means ± one standard deviation; for *P*, values are for the means with *P* values for variances in parentheses.

*P*<0.05 indicates a significant difference between water and air.

*N*=6 crabs.

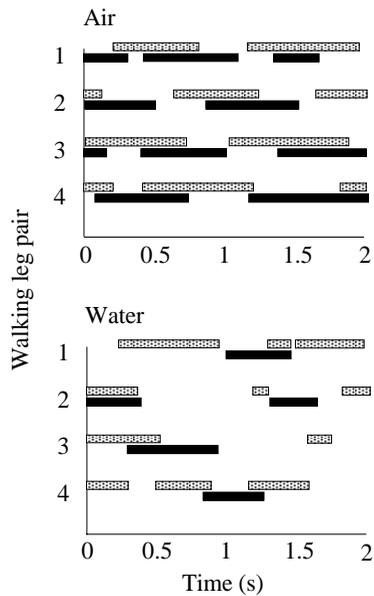


Fig. 6. Representative footfall patterns in air and water for each pair of walking legs plotted as a function of time. Bars represent times when the dactyls were in contact with the substratum. Leading legs (filled bars) and trailing legs (stippled bars) of each walking leg pair are plotted adjacent to one another. Footfall patterns illustrate that a crab locomoting under water showed greater gait variability and fewer legs in ground contact at any time than did a crab locomoting in air.

times that in air, with every individual adopting a greater stance width in water than in air (Table 4; Fig. 7). In fact, the narrowest lateral stance adopted by each crab in water did not differ from the widest stance adopted in air (paired *t*-test, *N*=6, *P*=0.27). In contrast, the maximum anterior–posterior stance width in water was not significantly different from that in air (Table 4). Carapace height was also not different between water and air trials (Table 4).

Dactyl movement within the workspaces differed between air and water trials. The actual workspaces used by the crabs (the two-dimensional horizontal trajectory followed by the dactyls) were very much smaller than the potential workspaces

Table 4. Stance width and carapace height in air versus water

Distance (m)	Air	Water	<i>P</i>
Stance width			
Anterior–posterior position	0.092±0.013	0.085±0.012	0.12 (0.78)
Lateral position	0.164±0.006	0.198±0.006	0.028 (0.90)
Carapace height	0.044±0.004	0.037±0.012	0.12 (0.02)

Values are means ± one standard deviation; for *P*, values are for the means with *P* values for variances in parentheses.

*P*<0.05 indicates a significant difference between water and air.

*N*=6 crabs.

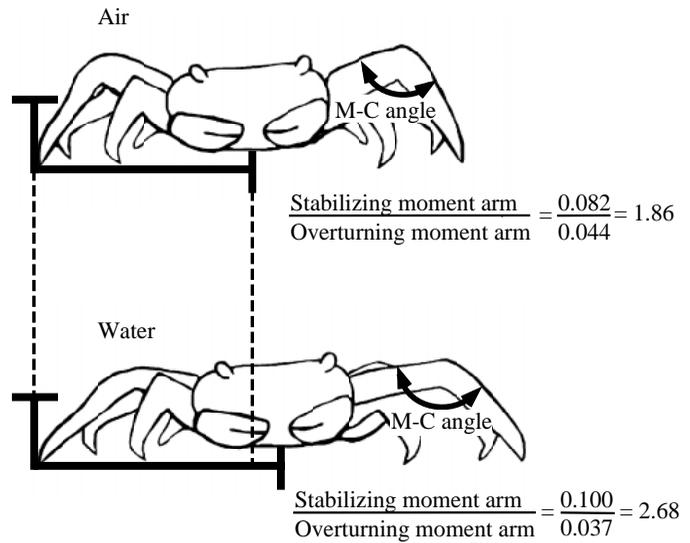


Fig. 7. Moment arms in air and water. Compared with crabs in air, those in water increased the distance between the center of mass and the trailing leg by increasing the merus–carpus (M-C) joint angle (Table 6). The ratio of mean stabilizing to mean overturning moment arms was greater for water postures than for air postures (data from Table 4).

(the range of motion through which dactyls could possibly move; Fig. 8). To compare the motion of a crab’s dactyls relative to its body, we measured the excursions of the dactyls within their workspace along the anterior–posterior and lateral axes of the crab (Table 5; Fig. 8). The workspaces did not differ between the leading and trailing legs in either air or water trials. Water trials showed more variability than air trials in all directions except the lateral excursion of the leading leg (Table 5). The shape of the excursions differed noticeably between air and water trials. In air, the crabs used larger lateral excursions than anterior–posterior excursions for both leading and trailing legs (Table 5); in water, the lateral and anterior–posterior

Table 5. Leg excursions in air versus water

Excursions (m)	Air	Water	<i>P</i>
Anterior–posterior			
Leading	0.0156±0.0033	0.0219±0.0094	0.12 (0.02)
Trailing	0.0145±0.0031	0.0174±0.0093	0.6 (0.016)
Lateral			
Leading	0.0370±0.0050	0.0243±0.0075	0.03 (0.2)
Trailing	0.0356±0.0023	0.0181±0.0058	0.03 (0.03)

Values are means ± one standard deviation; for *P*, values are for the means with *P* values for variances in parentheses.

*P*<0.05 indicates a significant difference between water and air.

*N*=6 crabs.

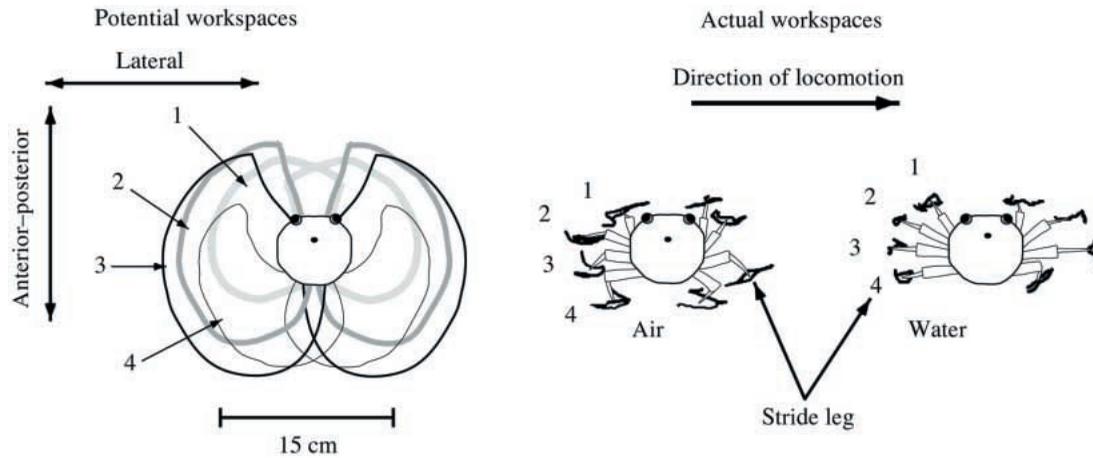


Fig. 8. Potential and actual workspaces. Potential workspaces show the range of motion possible for crab dactyls. Relative shading indicates the potential workspaces that each limb can achieve. Numbers denote the leg pairs corresponding to each of the workspaces. Actual workspaces are for the air and water trials of the same animal moving at  $9\text{ cm s}^{-1}$  for one maximum stride period. Leg movements are shown relative to the stationary dot on the crab's carapace. These workspaces showed that most of the legs in water had smaller lateral excursions than on land. Crabs had a greater stance width when locomoting in water than in air.

excursions did not differ from each other. Crabs used smaller lateral excursions in water than they did in air (Table 5).

#### Joint angles and limb protraction

Mean, maximum and minimum merus–carpus angles were all greater and more variable in water trials than in air trials (Table 6; Fig. 7). Although crabs in water used greater absolute merus–carpus angles, they swept through a smaller range of angles than they did in air. The maximum and mean velocities achieved by a dactyl during its swing phase were significantly slower in water than on land for all four leg pairs (paired *t*-test,  $N=4$ ,  $P=0.00007$  for maximum velocity,  $P=0.02$  for mean velocity).

#### Carapace angles

Mean pitch and roll angles did not differ between water and air trials (Table 7). Whereas variation about the mean angle from a given trial did not differ between air and water,

variation about the group mean angle for all trials was greater in water than in air (Table 7). The roll angles were much greater than the pitch angles. Crabs never achieved negative pitch or roll angles. Yaw angles did not differ between air and water trials and were evenly split between positive and negative values. Mean yaw angles were very small relative to pitch and roll angles.

### Discussion

#### *Hypothesis 1: the kinematics of aquatic pedestrian locomotion can be predicted from reduced-gravity models of terrestrial locomotion*

Reduced-gravity models of locomotion on land provide a framework within which aquatic pedestrian locomotion can begin to be explained (Fig. 1). On the basis of simple inverted-pendulum and spring-mass models (Alexander, 1989; Blickhan, 1989; McMahon and Cheng, 1990), we predicted that *Grapsus tenuicrustatus* would use a running-type gait in water, even at its slowest speeds. While crabs in water did

Table 6. Merus–carpus angles in air versus water

Angle (degrees)	Air	Water	<i>P</i>
Mean	93±4	105±13	0.027 (0.007)
Maximum	119±4	127±11	0.046 (0.033)
Minimum	68±4	82±14	0.027 (0.007)
Range	51±4	45±5	0.027 (0.44)

Values are means ± one standard deviation; for *P*, values are for the means with *P* values for variances in parentheses.

$P<0.05$  indicates a significant difference between water and air.  $N=6$  crabs.

Table 7. Pitch, yaw and roll angles in air versus water

Angle (degrees)	Air	Water	<i>P</i>
Pitch	3±2	10±10	0.12 ( $<0.001$ )
Yaw	1±5	2±7	0.75 (0.20)
Roll	30±5	37±9	0.07 (0.11)

Values are means ± one standard deviation; for *P*, values are for the means with *P* values for variances in parentheses.

$P<0.05$  indicates a significant difference between water and air.  $N=6$  crabs.

exhibit the expected shorter contact times and duty factors (Table 1), the contact time was so brief and the kinematics so variable (Tables 2–5) that we argue that these crabs were not running, but were using a fundamentally different mode of locomotion, a gait we call ‘underwater punting’. The person operating a punt generates thrust by pushing on the river bottom with a pole, allowing the punt to glide before the next push.

At the slow speeds used by crabs during this study, *Grapsus tenuicrustatus* operated at Froude numbers that suggest that they can walk on land but are unlikely to walk under water. Crabs appeared to pivot primarily about their merus–carpus joints both on land and in water. Using the height of this merus–carpus joint as the effective leg length (air,  $0.03 \pm 0.003$  m, mean  $\pm$  S.D.,  $N=6$ ; water,  $0.02 \pm 0.005$  m,  $N=6$ ) and incorporating a factor of 1/10 into the gravity term to account for buoyant force under water, we calculate a terrestrial Froude number of 0.027 and an aquatic Froude number of 0.41 for *G. tenuicrustatus* at  $9 \text{ cm s}^{-1}$ . In water, *G. tenuicrustatus* operate in the range of Froude numbers for which animals usually make a transition from a walking (i.e. inverted-pendulum) to a running (i.e. spring-mass) gait. Mammals and birds switch from a walk to a run at a Froude number of approximately 0.5 (e.g. Alexander, 1989; Gatesy and Biewener, 1991), a value only slightly higher than the aquatic Froude number we calculate for *G. tenuicrustatus*. Crabs in air change gait at the same stride frequency and speed as quadrupedal mammals (Blickhan and Full, 1987). Furthermore, Kram *et al.* (1997) have demonstrated that, even in reduced gravity, humans still prefer to change from a walk to a run at a mean Froude number of 0.45. Therefore, dynamic similarity suggests that crabs would probably not use inverted-pendulum mechanics in water at these speeds. The effective weight reduction in water appears to have forced the crabs at low speeds to adopt a gait more akin to running than to walking. Short contact times, low duty factors (Table 1), a reduction in the number of legs participating in propulsion (Table 3), longer gliding phases and the presence of an aerial phase in *G. tenuicrustatus* are all consistent with the use of a running gait under water at slow speeds. Ghost crabs show these same kinematic changes when running in air at very high speeds (Blickhan and Full, 1987; Burrows and Hoyle, 1973).

Changes in several significant kinematic variables associated with the air-to-water transition are predicted from running or spring-mass models subjected to reduced gravity. Let us assume that weight is reduced by 10-fold and leg spring stiffness does not change. In the mammals measured thus far, leg spring stiffness remains surprisingly constant over a range of speeds (McMahon and Cheng, 1990; Farley *et al.* 1993). Furthermore, leg spring stiffness in humans does not change as gravity is reduced in air (He *et al.* 1991). It has been predicted that, if the spring-mass system is to maintain its velocity and remain stable or re-entrant (i.e. similar initial conditions at landing and take-off) in reduced-gravity conditions, then the landing angle of the leg spring must increase (producing a more vertically orientated leg spring at

ground contact; Cavanga *et al.* 1972). Contact time and duty factor are reduced as the system is only briefly in contact the substratum. The reduced downward force decreases leg spring compression and the oscillation of the center of mass, thus giving the appearance of gliding. The reduction in weight decreases the vertical support forces required, which could then be produced by fewer or different legs than under higher loads.

Actual data on humans running in a reduced-gravity apparatus (He *et al.* 1991; Margaria and Cavagna, 1964) or under water (Newman, 1992; Newman *et al.* 1994) are consistent with some of these predictions. Gait transitions occur at lower speeds in reduced gravity compared with normal gravity (Kram *et al.* 1997). Duty factor always appears to decrease as effective weight is reduced. However, contact times, which are predicted to decrease as gravity is reduced, actually change very little (He *et al.* 1991).

While crabs locomoting in water made many of the same kinematic adjustments predicted from or measured in reduced-gravity studies, their aquatic kinematics were sufficiently different from those of running that we thought the aquatic pedestrian locomotion of this crab should be considered to be a new type of legged locomotion (‘underwater punting’). The exceptional variability allowed in this mode of locomotion prevents us from analyzing it in the same way that we would analyze regularly cycling gaits. In more typical rhythmic gaits, kinematic changes occur within each and every leg cycle. In contrast, leg cycling by this aquatic pedestrian crab can best be characterized as intermittent. We attempted to address this intermittency by determining both the kinematics of individual legs, while they were cycling, and of an overall stride represented by the leg with the maximum stride period (Table 1). Even this attempt failed to produce stride frequency and period data similar to those from studies on reduced-gravity running. When humans run in reduced gravity, they use lower stride frequencies and duty factors, but longer stride lengths, than they do in normal gravity (He *et al.* 1991; Newman, 1992). In contrast, punting crabs did not use significantly longer stride lengths or stride periods than they used on land (Table 1). We found no differences in stride length or frequency between water and air trials, in part because this novel mode of aquatic locomotion does not employ regular cycles of leg motion (Table 3). Rather than having longer leg stride periods, crabs in water used intermittent leg cycling, making use of longer ‘gliding’ times between cycles. A change from regimented leg cycling on land to intermittent leg cycling in water might produce the same dynamic effect as changes in leg stride length and period, but this possibility must be tested by measuring the forces acting on the center of mass. The irregularity of limb support and thrust generation might be understood in terms of controlling the motions of the body, but attempts to correlate ground contact with changes in pitch, roll and yaw of the body did not yield discernible patterns. A follow-up study of single-leg force production and dynamic stability is necessary to link leg function with whole-body dynamics.

Leg kinematics can also affect the hydrodynamic forces experienced by a leg. In the present study, crab legs moved more slowly in water (maximum dactyl velocity for leg pair 3 was  $0.16 \text{ m s}^{-1}$ ) than in air (maximum dactyl velocity for leg pair 3 was  $0.34 \text{ m s}^{-1}$ ) due to longer swing periods and gliding times. Since drag is proportional to the square of velocity, the 47% decrease in maximum velocity of a leg results in a 78% decrease in the drag on that leg in water relative to the drag that leg would experience if it moved at speeds characteristic of terrestrial kinematics.

Kinematic comparisons among aquatic pedestrian data in the literature are difficult because a common set of relevant mechanical variables is lacking. Crustacean pedestrians appear to adopt diverse strategies for locomoting under water, as shown by the varied findings of the few studies that contrast aquatic and terrestrial locomotion (Clarac *et al.* 1987; Grote, 1981; Hui, 1992; Pond, 1975). Whereas Grote (1981), Pond (1975) and Clarac *et al.* (1987) report differences in stride frequency between aquatic and terrestrial pedestrian locomotion, neither Hui (1992) nor the present study found significant differences. Grote (1981) and Pond (1975) found both increased stride length and increased stride frequency under water in forward-moving crayfish. Since both of these variables increased in concert, the animals necessarily moved at faster speeds in water than on land. In fact, Pond (1975) reported speeds in water twice as fast as speeds on land. Since both stride length and stride frequency can change as a function of speed (Blickhan and Full, 1987; Chasserat and Clarac, 1983), Pond's (1975) data do not allow us to determine which kinematic changes are due to a change in medium and which are due to a change in speed. Clarac *et al.* (1987) also found an increased stride frequency under water for sideways-moving crabs, but did not report stride lengths or locomotor speeds, so it is again impossible to know whether the increased stride frequency in water was due to a change in medium or in speed. Even though Hui (1992) found no differences in stride length or frequency in sideways-moving shore crabs in water *versus* in air, the data compare non-overlapping speed ranges or a large range of speeds. The Froude numbers for the shore crabs locomoting under water range from 0.02 to 0.76, calculated using a leg length of 0.015 m and an effective gravity of 20% normal gravity, based on buoyancy measurements from Hui (1992). These calculations show that aquatic data from Hui (1992) span the normal transition Froude number range, suggesting that this study may have included both walking and running gaits within one data set.

Despite the fact that the speed of locomotion has not always been controlled in the measurement of duty factor, all the studies of crayfish and crab locomotion under water *versus* on land, including the present study, report decreased duty factors or power stroke durations in water relative to those in air. Even electromyographic burst durations in shore crabs are shorter and the number of motor neurons activated is smaller during locomotion under water than on land (Clarac *et al.* 1987). While duty factor does change with speed, it is likely to be affected more strongly by a change in medium than by a

change in speed. Data on humans show that, while duty factor decreases with increasing speed, a reduction in gravity produces a larger decrease in duty factor than does an increase in speed (He *et al.* 1991; Donelan and Kram, 1997; Donelan *et al.* 1997). The effect of speed on duty factor is also not as great as the effect of speed on stride period in reduced-gravity studies (He *et al.* 1991). Thus, even though previous studies did not control for speed (Grote, 1981; Pond, 1975; Hui, 1992; Clarac *et al.* 1987), the lower duty factors reported for locomotion in water *versus* on land are likely to be, at least in part, a true effect of changing medium. The inability to detect a speed effect on duty factor in the shore crab *Pachygrapsus crassipes* (Hui, 1992) might be explained by a relatively weak relationship between duty factor and speed in the lower speed ranges as well as by the difficulty of assessing ground contact from only a top view of a crab that moves its dactyls underneath its body.

Sideways locomotion adds further to the challenge of kinematic comparisons because leading and trailing legs can adopt different roles with respect to sensing and propulsion. Primarily on the basis of their more variable kinematics, leading legs are often said to play a sensory role in arthropods (Full, 1997). Variable kinematics in the absence of ground reaction forces and electromyograms, however, leaves leg function less certain. Using electromyographic recordings, Clarac *et al.* (1987) found that the steps of the leading leg of the crab *Carcinus maenas* were more variable and longer in duration than those of the trailing legs both in water and on land. In water, *G. tenuicrustatus* showed a similar trend of longer stride periods and contact times in leading legs relative to trailing legs, but neither the contact time nor the stride period of the leading legs was more variable than in the trailing legs (Table 2). Whether the leading legs actually perform more or less of a sensory role in punting gaits is unknown. In air, *G. tenuicrustatus* showed no kinematic differences between leading and trailing legs (Table 2). Leading and trailing legs may also differ in their propulsive roles. At slow speeds in air, crabs can push with trailing legs or pull with leading legs (Blickhan and Full, 1987; Libersat *et al.* 1987). Burrows and Hoyle (1973) found that, at high speeds, ghost crabs in air use only two trailing legs alternately to generate force, while the leading legs act as skids. Clarac *et al.* (1987) concluded that electromyographic data provide more evidence for pushing propulsion with trailing legs. The present kinematic study showed that *G. tenuicrustatus* may use both the leading and trailing legs for propulsion in air and water. In water, however, crabs may be generating force over shorter periods with the trailing legs than with the leading legs, as suggested by the decreased stride length, stride period and contact time in trailing legs relative to leading legs (Table 2).

Furthermore, the leading and trailing legs could play different roles during locomotion in air *versus* water. Hui (1992) reported greater duty factors for trailing legs than leading legs in water, proposing that *Pachygrapsus crassipes* has to push harder to locomote in water over both rocky and smooth substrata. By contrast, *G. tenuicrustatus* had

significantly lower trailing leg duty factors in water than in air (Table 2). Perhaps as a manifestation of the kinematic variability permitted by lower effective gravity, the trailing legs require only brief periods to generate force effectively at slow speeds in water. Data from the crab *Carcinus maenas* show no effect of air *versus* water on leading *versus* trailing leg function (Clarac *et al.* 1987). Obviously, it is important to remember that kinematic data alone are insufficient to determine leg function. Direct measurements of individual leg ground reaction forces along with electromyograms are required to define a leg's role and will be our next focus.

In summary, data from previous studies clearly demonstrate that differences exist between aquatic and terrestrial pedestrian locomotion, but leave the nature of these differences unresolved. While the pioneering studies (Grote, 1981; Pond, 1975; Hui, 1992; Clarac *et al.* 1987) provided important first steps in exploring the differences between aquatic and terrestrial locomotion, the extreme variability in the variables measured thus far compel us to undertake a complete three-dimensional dynamic analysis of locomotion that includes kinematics, ground reaction forces and fluid-dynamic forces.

*Hypothesis 2: aquatic gaits are less constrained than terrestrial gaits*

Variability in the gaits of aquatic pedestrians has made the synthesis of general motor control principles challenging (Clarac, 1981; Full, 1997). Clarac (1981) reported that steps in crustaceans are incomplete or repeated 25% of the time. Data on crayfish reveal that inter-leg coupling varies depending on the conditions (*i.e.* treadmill *versus* free walking), the individual studied and the trial examined (Clarac and Barnes, 1985). A wide variety of gait patterns appear to be used even within a single locomotory bout of a given individual (Clarac and Barnes, 1985; Jamon and Clarac, 1995).

The slow-speed aquatic gaits of *G. tenuicrustatus* in the present study appeared so unconstrained that they do not conform to any traditionally recognized mode of locomotion. In water, compared with on land, the reduction in support force necessary and the increased recovery time from any instability, in addition to the large number of legs available for propulsion or correction, result in a redundant system in which no single kinematic solution should be expected. Even bipedal Apollo astronauts moving on the moon in one-sixth of the Earth's gravity freely chose new and different gaits (described by Jones, 1995). The inconsistent leg participation in thrust generation noted by Hui (1992) and demonstrated here (Table 3), together with extreme variability in leg kinematics, prompt us to consider underwater punting as a new mode of locomotion. Many kinematic variables of *G. tenuicrustatus*, including duty factor (Table 1), lateral and anterior–posterior excursion distance (Table 5), merus–carpus angle (Table 6) and pitch angle (Table 7) exhibited greater variability under water than on land. Greater variability in the number of legs cycling, the number of legs in the support phase (Table 3) and the overall footfall patterns (Fig. 6) can be tolerated during locomotion under water because animals unsupported by legs

fall to the substratum more slowly in water than they do in air. The relaxation of gravitational constraints on kinematics in water permits the use of gaits that are unavailable to animals locomoting in air at the slow speeds used by these crabs.

The combined effects of increased buoyancy in water and sideways locomotion may suspend the need even for the more tightly coupled ipsilateral leg coordination seen in aquatic walking by some crayfish and lobsters (*e.g.* Clarac, 1984; Jamon and Clarac, 1995; Muller and Cruse, 1991). While buoyancy decreases the requirement for more continuous vertical support, sideways motion allows the legs to move independently without physically interfering with other ipsilateral legs. Even though crayfish and lobsters have a specific gravity similar to that of crabs (*e.g.* the specific gravity of the crayfish *Procambarus clarkii* is 1.07; Grote, 1981) and hence similar buoyant forces, the lateral position of the legs on a forward-locomoting crayfish or lobster may prevent it from using a punting gait because asymmetric propulsion from contralateral legs would subject a forward-moving animal to large roll and yaw moments. Likewise, a forward-moving crab is unlikely to punt because the further a thrust-generating leg is from the axis of locomotion, the greater the moments it will generate about the center of mass.

*Hypothesis 3: pedestrians adopt a more stable posture in water than in air*

Although *G. tenuicrustatus* did not use a significantly lower body height under water, they did adopt a wider, more stable stance (Table 4). Crabs achieved this wider stance by using greater merus–carpus angles in water than they did on land (Table 6; Fig. 7). A wider stance stabilizes the crabs against overturning by hydrodynamic forces due to locomotion or to ambient water currents by increasing the moment arm over which the weight acts (Fig. 2). For example, an increase in stance width from 16 to 20 cm (increasing  $MA_s$  by 2 cm) translates directly into a 25% increase in the drag force ( $D$ ) a crab could withstand before overturning, calculated from Alexander (1971):

$$D = F_v \frac{MA_s}{MA_o}, \quad (2)$$

where  $F_v$  is the net vertical force on the crab (*e.g.* submerged weight 0.07 N),  $MA_s$  is the stabilizing moment arm (the distance from the center of mass to the trailing leg, 0.08 m) and  $MA_o$  is the overturning moment arm (the height of the center of mass above the substratum, 0.04 m; Fig. 2). Hui (1992) found that crabs locomoting sideways on rocky substrata used wider stances in water than they did on land, but he did not detect a difference on smooth substrata. Grote (1981) found that crayfish also used wider stances in water, but since the crayfish move forwards rather than sideways, this wider stance decreased the likelihood of being overturned by a cross current rather than by relative water motion due to locomotion. In contrast, *G. tenuicrustatus* did not show a significant difference in stance width perpendicular to the direction of motion (in the anterior–posterior direction; Table 4) in air *versus* in water.

We predicted that crabs would maintain lower pitch and roll angles of the carapace in water than in air, thereby reducing hydrodynamic forces resisting movement. Drag (resisting locomotion; Fig. 1) and lift (acting upwards) on the carapace due to locomotion are greater at greater positive pitch angles (Martinez, 1996). Greater positive roll angles cause a greater posteriorly directed component of lift on a sideways-moving crab. Contrary to our prediction, crabs used the same pitch and roll angles of the carapace under water as they did in air, but with more variable pitch angles in water (Table 7). The variation in mean pitch angle suggests that, at these slow speeds, crabs may not be subject to large hydrodynamic forces that might constrain gaits or that they are simply less able to control their body orientation under water. The hydrodynamic force due to locomotion in still water was too low to overturn the crabs even at high carapace angles, but the additional force from ambient currents might be sufficient to overturn them (Martinez, 1996).

#### *Dynamics in aquatic versus terrestrial systems*

The variability in the kinematic data of aquatic pedestrian locomotion in this and other studies suggests that we reassess our ideas concerning the neural control of locomotion. Perhaps instead of focusing on the control of leg positions and gait, we should consider the body and its dynamics. An assumption often implicit in the study of gait is that stepping pattern alone is sufficient to characterize the dynamics of the center of mass (e.g. Clarac *et al.* 1987; Cruse, 1990). However, Blickhan and Full (1987) found that whole-body ground reaction forces acting on the center of mass in ghost crabs locomoting in air were remarkably consistent, despite considerable variation in the pattern of leg movements. Determining the motion and forces acting on the body may be even more important in water because, as fluid-dynamic forces begin to dominate, the whole-body dynamics may become increasingly divorced from the pattern of leg movements. We believe new neural control hypotheses concerning the differences between aquatic and terrestrial pedestrian locomotion will emerge when kinematic and kinetic (i.e. fluid and ground reaction force) data are integrated.

Kinematic adjustments between water and land may be best understood in the context of the predominant destabilizing force: the vertical force resulting from the acceleration due to gravity is the principal factor determining locomotor dynamics for most animals on land (Alexander, 1989), whereas the horizontal hydrodynamic forces may equal or surpass the magnitude of the vertical forces under water. *G. tenuicrustatus* responded to this shift in destabilizing forces by adopting a wider stance in water, thereby increasing their resistance to overturning, and by reducing the number of legs in support phase, thereby decreasing their resistance to falling. While the decrease in vertical destabilizing forces may lessen the need for precise neural control of leg placement, the concomitant increase in horizontal destabilizing forces may substantially increase the need for control of the pitch, roll and yaw of the body.

On land, *G. tenuicrustatus* maintained its static stability (as defined by Gray, 1944) by keeping its center of mass within a triangle of supporting legs, whereas in water it relied on dynamic stability by making dynamic adjustments to ensure that, on average, the legs work to counteract gravity. As Pridmore (1994) noted for bottom-walking sharks, the change in overturning and stabilizing moments on an animal in aquatic *versus* terrestrial habitats allows the animal to achieve dynamic stability at much lower speeds under water than on land. Dynamic stability allows greater freedom of leg kinematics since animals do not require regular leg movements, or as many legs in contact with the ground, to ensure continuous support of body weight, so long as a supporting foot is put down in time to save the body from hitting the ground as it falls.

Hydrodynamic forces are likely to be low at slow speeds (Martinez, 1996); hence, reduced gravity makes a reasonable approximation of the forces on crustaceans locomoting under water. As the animals move more rapidly, however, hydrodynamic forces increase with the square of the speed and are likely to become an important component of the force balance on the animal. Using a drag coefficient of 0.1 (M. M. Martinez, in preparation), drag on *Grapsus tenuicrustatus* would equal its apparent weight in water at a speed of  $42\text{ cm s}^{-1}$ . We are currently quantifying the hydrodynamic forces on *G. tenuicrustatus* at appropriate speeds and body postures to understand the mechanical implications for pedestrian locomotion in water.

#### *Biological inspiration for robotics*

The general principles learned from studying how legged locomotion differs on land *versus* under water have already provided biological inspiration for the design of autonomous legged underwater vehicles (ALUVs) which will be able to locomote in a variety of nearshore environments. Greiner *et al.* (1996) have developed an autonomous legged robot featuring the alternating tripod gait and distributed (as opposed to highly centralized) control shown in arthropod locomotion. Their most recent prototype, an amphibious surf-zone robot, emulates the sideways locomotion of a crab and employs a low-profile body to minimize the hydrodynamic forces while in the water. Like a crab, this surf-zone robot uses a wide stance and controls the pitch angle of its body to increase its stability under water. Since control of forces on a body is difficult in the surf-zone, they temporarily opted for a completely invertible design to minimize difficulties in the event of overturning. Most recently, H. Greiner is attempting to add punting behavior to reduce energy consumption and increase battery life. Our understanding of how amphibious animals change their kinematics and kinetics when locomoting in their two natural habitats will make possible even greater advances in the design of underwater pedestrian robots in the future.

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