

WALKING OF THE SHORE CRAB *PACHYGRAPSUS CRASSIPES* IN ITS TWO NATURAL ENVIRONMENTS

By CLIFFORD A. HUI*

*Chemistry and Biochemistry Branch, Code 521, Naval Ocean Systems Center,
San Diego, CA 92152-5000, USA*

Accepted 31 December 1991

Summary

Video analyses of crabs walking on smooth and rocky terrains when in air and when submerged in water were conducted. Modifications of walking in the two environments, between which the animal's weight changes sixfold, are consistent with the goals of maximizing ease of walking and minimizing risk of injury. The duty factor (fraction of step cycle in which the dactylus is in contact with the substratum) was greater than 50% when in air compared to less than 46% when submerged, indicating a need for greater stability against the destabilizing vertical force of gravity when in air. The duty factors of the trailing and leading leg rows were the same for the two terrains in air but the trailing leg row had a larger duty factor when submerged, indicating a greater pushing effort to overcome drag forces. Width of stance differed among the four conditions and was narrowest in animals walking over rocky terrain in air, the condition which has the greatest potential for injury. The mean phase difference (percentage of a step cycle by which ipsilateral legs differ) between leading and trailing rows did not differ under any condition except for submerged smooth terrain, meeting the unique requirements of that condition. The observed walking speed range had no effect on stance, duty factor or phase difference.

Introduction

Shore crabs inhabit two environmental regimes while their brachyuran relatives inhabit only one. There is no shore crab more successful than the lined shore crab *Pachygrapsus crassipes* Randall. This crab is found along rocky shores on the west coast of North America from 24°20' to 45° latitude and in Japan and Korea between 34° and 37° (Hiatt, 1948). Its habitat extends from the upper low intertidal zone to the highest high intertidal zone (Hiatt, 1948), and the crab has been maintained out of water for up to 4 days (Gross, 1957).

An important element in the successful competition of *P. crassipes* is locomotion. Locomotion enables migration (Bovbjerg, 1960a; Gross, 1961), foraging

* Present address: U.S. Fish & Wildlife Service, c/o Wildlife & Fisheries Biology Department, University of California, Davis, CA 95616, USA.

Key words: walking, crabs, locomotion, kinematics, *Pachygrapsus crassipes*.

(Hiatt, 1948), courtship (Bovbjerg, 1960*b*) and predator escape (Hiatt, 1948). All these activities, except courtship, occur in both air and water. However, the physical requirements for locomotion differ between the two regimes. In air, it is the vertical force of gravity that may destabilize (cause loss of control) a walking crab, but in water, buoyancy neutralizes the effects of gravity and it is the horizontal forces of currents or drag resistance that are destabilizing.

These crabs may change locomotion variables to accommodate the different physical constraints of each regime. Other animals change locomotion patterns to minimize energy expenditure (Hoyt and Taylor, 1981; Dawson and Taylor, 1973), maximize ventilation (Jackson and Prange, 1979; Carrier, 1987; Hui, 1987, 1989) or reduce mechanical stresses (Farley and Taylor, 1991). Some spiders have different walking patterns when walking on land to those when walking on water (Schultz, 1987). In the light of these observations and because a change in environmental regime triggers a change in social behaviour of *P. crassipes* (Bovbjerg, 1960*a*), it seems reasonable to expect that a change in environmental regime, with its concomitant change in physical forces, would also trigger a change in locomotory patterns.

There are many studies of walking crustaceans (e.g. Pond, 1975; Barnes, 1975; Chasserat and Clarac, 1980; Grote, 1981; Hessler, 1982; Clarac *et al.* 1987; Blickhan and Full, 1987; Muller and Clarac, 1990*a,b*), but the nature of modifications in locomotion effected in compensation for changes in normal environmental conditions has not been thoroughly explored. I report here on the differences in locomotion patterns of *Pachygrapsus crassipes* walking in the two environmental regimes and two terrains of its normal habitat.

Materials and methods

Animals

Male *Pachygrapsus crassipes* were collected at Hospitality Point on Mission Bay in San Diego, California, using bait on a line during the month of August. Only the largest individuals with all appendages intact were retained for recording. The range for the maximum widths of the carapaces was 33.6–38.8 mm, well above the 14.0 mm width of minimum size for sexual maturity (Hiatt, 1948). The animals were maintained in aerated sea water at collection site temperature but not fed. All recordings were completed and the crabs released within 26 h of capture. Eight crabs were used for recording.

Recording

Video recordings (Panasonic WV-F2 camera, Panasonic AG2400 recorder, at 30 frames s⁻¹) of the crabs were made using a mirror arrangement enabling a vertical view (Fig. 1). Each crab was placed in a plastic pan (47 cm × 35 cm × 12 cm deep) under one of two regimes: in air or submerged in sea water. In each submerged case the water was of a depth (approximately 9 cm) adequate not only to cover the crab but also to preclude the formation of surface ripples (energy

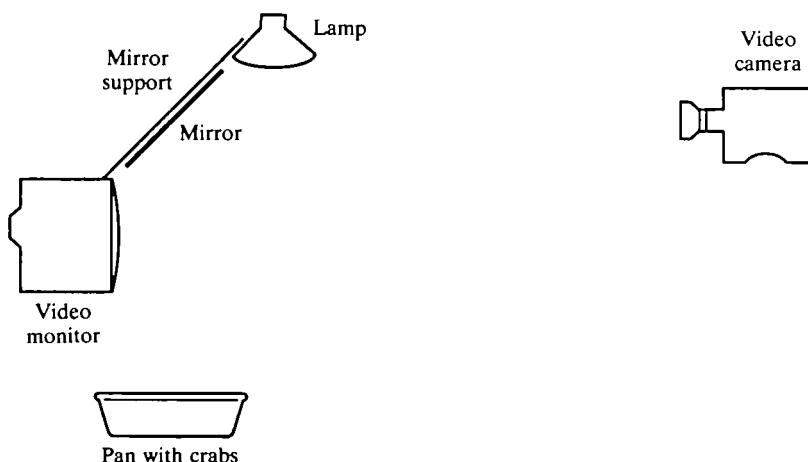


Fig. 1. Schematic drawing (not to scale) showing the general configuration of the observation set-up.

consuming) when the crab was walking. Each regime had two terrains: smooth (a large paper towel was fastened to the bottom for traction) and rocky. The rocky substratum consisted of several layers of randomly placed broken quartz-like material. The thickness of the layers was adequate to ensure that, if a space between rocks opened directly to the floor of the plastic pan, the distance was greater than the reach of the crab's leg. The broken nature of the rocks and their random placement ensured an irregular walking surface. The rocks had a mean maximum length (\pm s.d.) of 42.8 ± 9.9 mm and mean maximum width of 30.5 ± 7.8 mm ($N=20$). The third dimension was the smallest but was not measured because the first two dimensions will impart the nature of the rocky terrain. Although not the dark type of the crabs' natural habitat, this rock contrasted with the dark body colour of the crabs and facilitated video analysis.

Each crab was individually recorded walking over both terrains (one at a time) of only one of the regimes. A minimum of five walking sequences for each terrain for each crab was selected for analysis. Criteria for selection were a straight path, an even sideways gait and clarity of the images. Ground contact by the dactylus is evident because (1) horizontal displacement ceases and (2) the dactylus changes orientation from vertical to horizontal. A mark of known length was placed in the camera's view for each walking session and used for scaling adjustments. Measurements were taken directly from a 48-cm (diagonal) video screen. The stop-action capability of the player (Panasonic AG500) and the on-screen time record allowed reacquisition of the same images for re-examination when necessary.

The data collected were the mean walking speed, the time that each dactylus moved onto and off the substratum, the length of each step (distance between the substratum contact points for a dactylus) and stance (maximum distance between

the dactyli of a contralateral leg pair within one step sequence). The stance measurement did not require that both dactyli of the pair be on the substratum simultaneously. The number of steps measured for each dactylus for each walking sequence varied from 0 to 7.

Buoyancy

The weights of this species of crab in water and in air were determined using 13 individuals not used in the locomotion recordings. The range of the maximum carapace widths was 26.9–35.3 mm. The crabs were divided into two groups (mean carapace widths: 32.00 ± 2.38 mm, 34.05 ± 1.23 mm) and the individuals in each group were weighed together as a single group in both air and water. Weighing them as groups increased the total weight, thereby reducing relative error.

Results

Eighty-two walking sequences were examined: 32 in air (3 crabs, 17 sequences on smooth terrain, 15 sequences on rocky) and 50 submerged (5 crabs, 25 sequences each on smooth and rocky terrain). Occasionally a crab walked forwards, backwards or obliquely or turned, but these sequences were not considered. Sample size was inadequate for paired comparisons. On careful observation, the fourth (last) leg on each side appeared to be used as a tactile sensor too frequently to be considered a participant in the general walking pattern displayed by the other legs (Fig. 2). Statistical results were more random when data from the fourth legs were included. Therefore, the results presented here exclude data from the fourth legs unless otherwise noted. The crabs displayed the various gaits expected by Wilson (1966) at the higher walking speeds for insects although the crabs were walking slowly. The alternating tripod gait Wilson described for the highest speeds occurred in crabs as the alternating tetrapod gait but appeared at the slowest speeds. The crabs never appeared to stumble. When a dactylus mis-stepped into a hole on rocky terrain, the leg continued through the stepping motion cycle until it made contact with the substratum.

At a constant framing rate of 30 frames s^{-1} , the relative precision of the timing measurements decreases as the walking speed increases. Using the relationships among stepping frequency, framing rate and maximum error described in error analysis for stepping locomotion (Ward and Humphreys, 1981), the maximum error at the fastest walking speed I measured (41.2 cm s^{-1}) is 9.3% of the step duration. The maximum error of the 85% of the total walking speeds that were below 12 cm s^{-1} (Fig. 3) is well within the 4% error considered acceptable. The mean errors are half of the maximum error values (Ward and Humphreys, 1981). The variability in precision does not bias the measurement estimate systematically in any direction but increases the variance about the mean or presumed true value. Accordingly, none of my analyses regarding the time measurement is dependent on the precision of a given set of measurements. The analyses consist of

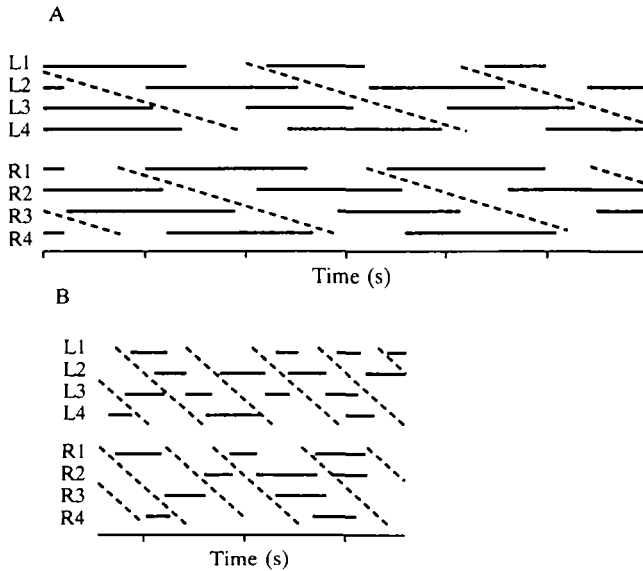


Fig. 2. Examples of stepping patterns. Solid lines indicate that the dactylus is in contact with the substratum. Dotted lines separate metachronal sequences. Metachronal sequences can be depicted as starting with the last leg, as described by Wilson (1966) for insects, instead of the first leg, but the slow walking speed data for crabs do not support the walking sequence paradigm presented by Wilson based on slow speeds. Marks on the time axis denote 1-s intervals. Individual legs are denoted on the left margin (L1 and R1 are the most anterior legs on the left and right sides, respectively). (A) Classic metachronal pattern; air regime, smooth terrain; speed= 2.1 cm s^{-1} . (B) Metachronal pattern with inconsistent participation of various legs; submerged regime, rocky terrain; speed= 6.1 cm s^{-1} . The duty factor is essentially the same for the two leg rows (39.4% and 39.5%) when all eight legs are considered, but when the fourth legs of each row are eliminated the leading row has a duty factor of 39.8% while the trailing row has a factor of 44.0%. The change may reflect the time for tactile exploration by the legs of the leading row. Note the 'missing' steps as dactyli are held off the substratum.

comparisons of means using non-parametric tests so that equality of variances of the tested groups is not required.

Owing to distortion near the edge of the screen, no measurements were taken within 8% of the distance to the margin. No other measures were taken to compensate for possible distortion due to screen curvature. Repeated examination of several sequences resulted in duplication of length measurements to within 1 mm. Therefore, length measurement errors are considered to be negligible. Length data analyses also used non-parametric tests.

Speeds of the four conditions differed among each other (two-sided Mann-Whitney test, $P < 0.02$) except that the speeds on the two terrains of the submerged regime were the same (two-sided Mann-Whitney test, $P > 0.38$; Fig. 3). The range of speeds was greatest in air on smooth terrain but smallest in air on rocky terrain (Fig. 3).

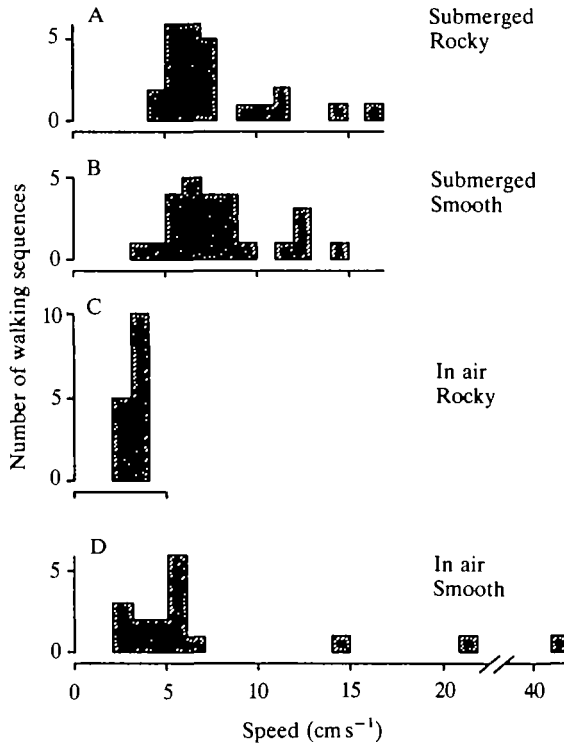


Fig. 3. Distribution of observed walking speeds among the various test conditions: (A) submerged regime, rocky terrain (mean= 7.6 cm s^{-1} , s.d.= 3.0 cm s^{-1}); (B) submerged regime, smooth terrain (mean= 8.0 cm s^{-1} , s.d.= 2.8 cm s^{-1}); (C) air regime, rocky terrain (mean= 3.0 cm s^{-1} , s.d.= 0.5 cm s^{-1}); (D) air regime, smooth terrain (mean= 8.3 cm s^{-1} , s.d.= 9.8 cm s^{-1}). Caution must be used against over-interpretation of speed frequency distribution data because data collection was optimized for stepping data, not speed distribution.

Stepping frequency is more closely correlated with walking speeds than is step length for every condition except the case of the leading leg row in air over rocky terrain (Table 1). The relative importance of frequency and length between the leading row and trailing row of legs differs between terrains of each regime (Table 1). The relationships of walking speed to stepping frequency are fitted to power functions (Table 2; Figs 4, 5, 6, 7): at the higher speeds the relationships approach a straight line and at walking speeds of 0 cm s^{-1} the stepping frequencies are zero. In the one condition for which speed is better correlated to step length, that relationship is also a power function (Table 1).

The ratios of the step lengths between the leading and trailing leg rows are the same for all the conditions except for walking in air on rocky terrain (Table 3). These ratios do not change with walking speed under any of the four conditions (r^2 range 0.06–0.46). A summary of the step length data is presented in Table 4.

The metachronal pattern (Fig. 2) was quantified by measuring the mean phase difference of the step cycle among adjacent ipsilateral legs (Table 1). The pattern

Table 1. *Some walking variables of Pachygrapsus crassipes leg rows in different walking conditions*

Condition (regime, terrain, leg row, <i>N</i>)	Phase differences* (% \pm s.d.)	Frequency† (<i>r</i>)	Length‡ (<i>r</i>)	Duty factor§ (% \pm s.d.)
Air, smooth, leading, 17	50.1 \pm 18.1	0.98	0.17	50.7 \pm 7.2
Air, smooth, trailing, 17	45.6 \pm 12.2	0.98	-0.20	54.8 \pm 5.8
Air, rocky, leading, 15	47.3 \pm 13.3	0.67	0.70¶	55.6 \pm 4.4
Air, rocky, trailing, 15	41.5 \pm 7.2	0.78	0.17	53.1 \pm 6.1
Submerged, smooth, leading, 25	43.8 \pm 8.3	0.92	0.10	40.7 \pm 4.5
Submerged, smooth, trailing, 25	49.8 \pm 7.6	0.90	0.47	45.9 \pm 5.8
Submerged, rocky, leading, 25	47.0 \pm 13.2	0.79	0.61	39.7 \pm 4.9
Submerged, rocky, trailing, 25	46.7 \pm 10.1	0.94	-0.06	42.3 \pm 5.0

Only the anterior six walking legs are considered.

N, number of sequences.

* Mean phase differences.

† Correlation of walking speed with stepping frequency.

‡ Correlation of walking speed with step length.

§ Mean duty factor.

¶ Regression data: step length (mm) = 22.49 \times speed^{0.55} (cm s⁻¹).

Table 2. *Regression coefficients for stepping frequency (steps s⁻¹) as a function of walking speed (cm s⁻¹)*

Condition (regime, terrain, leg row)	<i>a</i>	<i>b</i>	R	<i>N</i>
Air, smooth, leading	0.22	0.91	2.6-41	17
Air, smooth, trailing	0.27	0.76	2.6-41	17
Air, rocky, leading	0.43	0.48	2.1-3.8	15
Air, rocky, trailing	0.26	0.84	2.1-3.8	15
Submerged, smooth, leading	0.18	0.98	3.7-14.7	25
Submerged, smooth, trailing	0.26	0.82	3.7-14.7	25
Submerged, rocky, leading	0.38	0.64	4.1-16.8	25
Submerged, rocky, trailing	0.25	0.91	4.1-16.8	25

Regression coefficients are for the relationship $y = ax^b$.

Only the anterior six walking legs are considered.

R, speed range.

N, number of sequences.

Degrees of freedom = *N*-2 in each case.

did not differ between leading and trailing leg rows for three of the conditions (two-sided Mann-Whitney test, $P > 0.42$), but the trailing leg row had a significantly greater phase shift than the leading row on the smooth terrain of the submerged regime (two-sided Mann-Whitney test, $P < 0.008$). The phase difference did not change with the walking speeds I measured under any condition for either the leading or trailing leg rows (r^2 range 0.00-0.24).

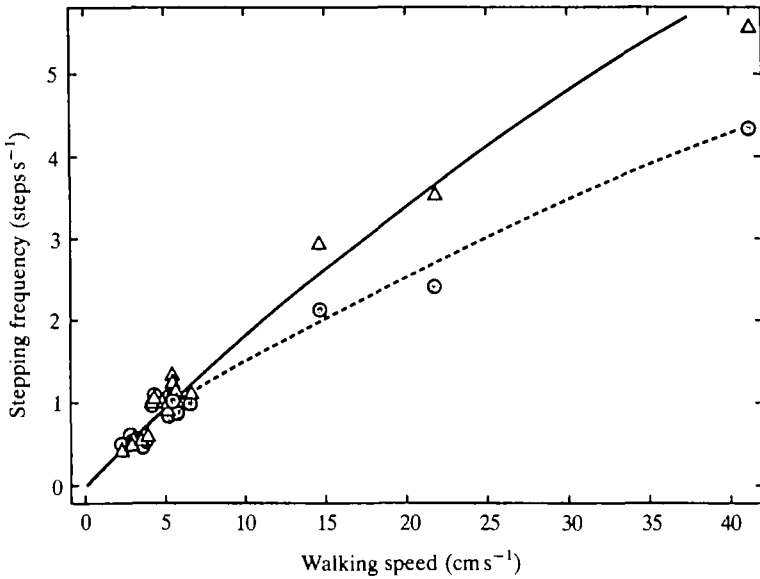


Fig. 4. The relationship of stepping frequency to walking speed for shore crabs travelling over smooth terrain in air. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 17; each point represents an average value computed from 7–15 steps (mean=10.1 steps; s.d.=1.86 steps).

Table 3. *Step-length ratios of leading:trailing leg rows and the stance width*

Condition (regime, terrain, <i>N</i>)	Step-length ratios	Stance width (mm)
Air, smooth, 17	1.05±0.12	130.2±16.2
Air, rocky, 15	0.90±0.11	79.6±8.5
Submerged, smooth, 25	1.15±0.19	111.7±9.1
Submerged, rocky, 25	1.07±0.19	103.9±8.9

Values are mean±s.d.

Only the anterior six walking legs are considered.

N, number of sequences.

The duty factor (fraction of the step cycle in which the dactylus is in contact with the substratum) of the leading row was less than that of the trailing row in the submerged regime (two-sided Mann–Whitney test, $P < 0.01$ over smooth terrain and $P < 0.04$ over rocky terrain). In the air regime the duty factors between leg rows were the same (two-sided Mann–Whitney test, $P > 0.07$ over smooth terrain and $P > 0.26$ over rocky terrain). In air, the duty factor of the trailing leg rows over the two terrains is the same (two-sided Mann–Whitney test, $P > 0.57$), but it is greater in the leading row over rocky than over smooth terrain (two-sided

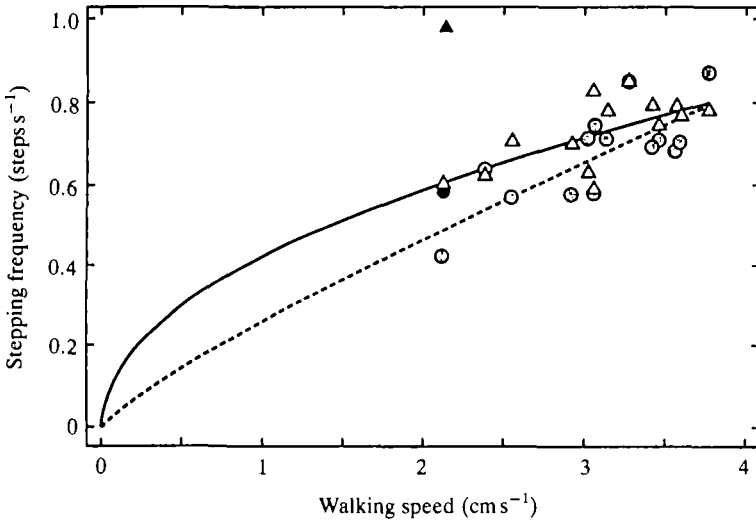


Fig. 5. The relationship of stepping frequency to walking speed for shore crabs travelling over rocky terrain in air. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 15; each point represents an average value computed from 9–16 steps (mean=12.4 steps; s.d.=2.18 steps). Filled symbols were not used in computations for the lines.

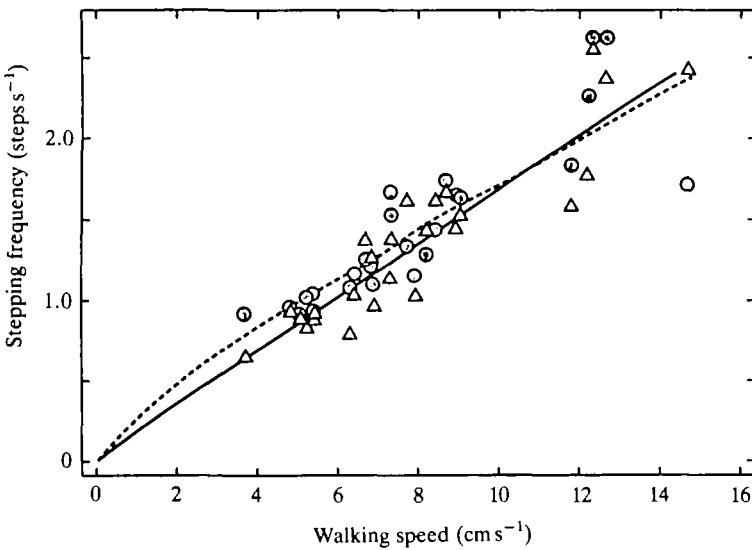


Fig. 6. The relationship of stepping frequency to walking speed for shore crabs travelling over smooth terrain while submerged. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 25; each point represents an average value computed from 5–20 steps (mean=12.4 steps; s.d.=3.42 steps).

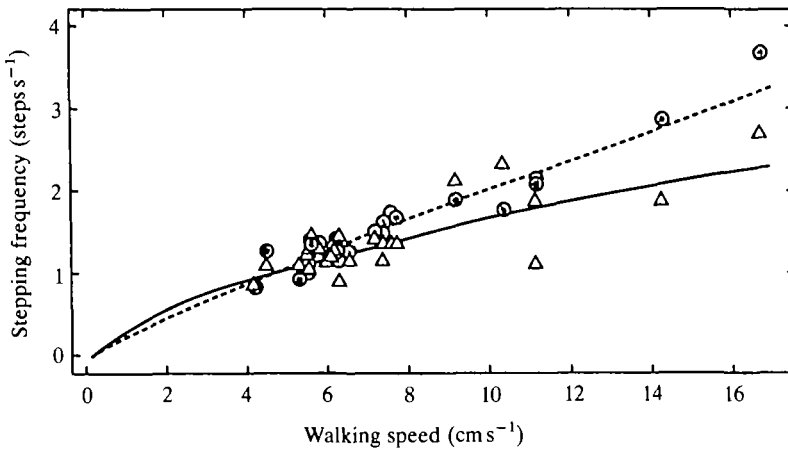


Fig. 7. The relationship of stepping frequency to walking speed for shore crabs travelling over rocky terrain while submerged. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 25; each point represents an average value computed from 7–19 steps (mean=12.7 steps; s.d.=2.75 steps).

Table 4. *Step lengths (mm) of Pachygrapsus crassipes when walking in different conditions*

Condition (regime, terrain, leg row)	Mean	±s.d.	Range	N
Air, smooth, leading	54.9	6.64	41.3–65.8	17
Air, smooth, trailing	51.7	4.63	43.5–59.2	17
Air, rocky, leading	41.8	5.86	29.5–51.8	15
Air, rocky, trailing	47.2	4.32	42.3–56.9	15
Submerged, smooth, leading	60.2	10.59	45.0–91.6	25
Submerged, smooth, trailing	53.9	9.10	44.0–85.7	25
Submerged, rocky, leading	51.5	8.24	33.1–68.8	25
Submerged, rocky, trailing	49.7	6.53	33.4–60.9	25

Only the anterior six walking legs are considered.

N, number of sequences.

Mann–Whitney test, $P < 0.03$; Table 1). There was no significant relationship with walking speed (r^2 range 0.00–0.39 for all four conditions), possibly due partly to the large variability of the duty factor at the lower speeds and the small sample size at the higher speeds (Fig. 8).

The stances differed significantly among conditions (two-sided Mann–Whitney test, $P < 0.005$). The widest and narrowest stances occurred in air while the two conditions of the submerged regime had stances closer together and between the values for the air regime (Table 3). Stance did not change with walking speed (r^2 range 0.01–0.22 for all conditions).

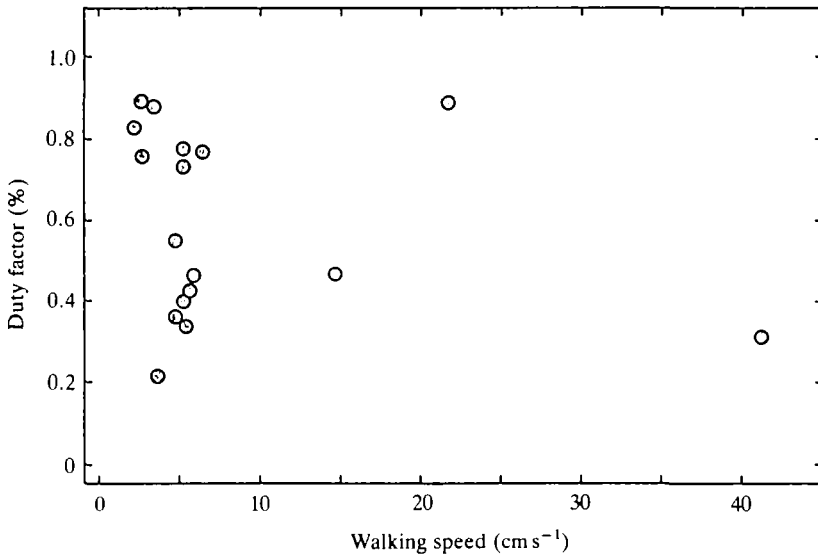


Fig. 8. Example of the variability of duty factor (fraction of the stepping cycle during which the dactyl is in contact with the substratum) values relative to walking speed of shore crabs. These data ($N=17$) are for the trailing leg row when on smooth terrain in air. The obvious variability is similar when walking under the other test conditions. There is no significant relationship between walking speed and duty factor in any condition.

Buoyancy eliminated over 80% of in-air weight when the crabs were submerged. One group lost 83.5% of its in-air weight while the other lost 85.0%. The difference may be due to incomplete filling of the branchial chamber when immersed for measurement. These results indicate a specific gravity of 1.2 for these shore crabs.

Discussion

Because I made no effort to examine the full range of walking speeds for these crabs under any of the conditions, these speed ranges are probably not representative of the crabs' abilities. Therefore, my interpretations of speed-related behaviours are conservative and may be shown to be erroneous by subsequent studies. However, because the overlap of the ranges is so extensive, comparison of the walking variables for each of the different conditions seems reasonable.

Pachygrapsus crassipes obviously modify walking variables according to regimes and terrain. Although various aspects of the crabs' ecology may be the causes of these modifications, the behaviours are consistent with a locomotion paradigm. The primary habitat of rocky shores (Hiatt, 1948; Gross, 1957) carries with it a risk of accidental damage to carapace or appendage due to a mis-step. Therefore, the walking modifications may be to maximize ease of walking and to minimize risk of injury.

The rocky terrain in air offered the highest risk and the crabs displayed the slowest walking speeds and the narrowest stances. The narrow stance may be to maximize the distance between the body and the uneven, unpredictable surface. Such a surface is more likely to injure the body in the event of a mis-step. The narrow stance also offers stability by allowing a step-length reserve: if a satisfactory foot-hold does not occur at an optimum short distance, the crab can lower its body to allow the dactylus to extend farther in its search for another site. By lowering its body, the centre of gravity can remain within the boundaries of its base of support. This type of stability may be safer for the crab because it is functional under both standing and walking conditions but does not have the potential for falling that 'dynamic stability' has (Hildebrand, 1980). Because it has many legs, more dactyli can be in contact with the substratum as the duty factor increases. With more than three dactyli on the substratum, the base of support expands from a triangle to a polygon of greater area. The larger area will reduce the opportunities for the crab's centre of gravity to move beyond its base of support. Therefore, with its multiple legs stepping in a metachronal pattern, the crab can increase its static stability by increasing its duty factor. The largest duty factor of all leg rows occurred over rocky terrain in air (Table 1), where poor stability may have the worst consequences in terms of accidental injury.

The effect of buoyancy when submerged reduces the risk of damage when over any terrain compared to being in air. This reduced risk is reflected in walking speeds, stances and duty factors. The speeds over rocky terrain were not reduced compared with those over smooth terrain. The stance over rocky terrain was wider than its counterpart in the air regime, perhaps because buoyancy reduces the strength required for standing, enabling obtuse angles in the leg joints to be maintained with less effort and simultaneously providing a lower profile that reduces interaction with drag forces of currents. Currents are reduced within the boundary layer that occurs at the substratum surface (Vogel, 1981). The duty factors were less than 46% for all leg rows over both submerged terrains. The larger duty factors of the trailing leg rows when submerged may be necessary to provide adequate thrust to counteract the drag forces encountered. Other crabs push with their trailing legs instead of pulling with their leading legs (Hafemann and Hubbard, 1969; Burrows and Hoyle, 1973).

When submerged, constant propulsive effort against drag forces may be more energetically efficient than intermittent effort for animals with rigid bodies (Weihs, 1974) and low fineness ratios (Blake, 1983) like these crabs. A phase difference of 50% for the trailing (propulsive) leg row would allow more uniform propulsive effort and is possible only over smooth terrain, because secure dactyli placement without searching is assured by the predictability of the terrain. This rationale is supported by results showing that the only condition in which the trailing row had a phase difference of 50% occurred over smooth terrain when submerged.

The forces needed to overcome locomotory drag can be roughly estimated and compared to the force needed to overcome gravity. Let us assume the following.

Frontal area of the crab to the direction of motion (A) is 4 cm^2 ; speed (U) is 10 cm s^{-1} ; drag coefficient (C_D) is 0.5 (blunt body with rounded corners); and the density of water (ρ) is 1000 kg m^{-3} . Using drag (D)= $0.5\rho AC_D U^2$, $D=0.001\text{ N}$. If the crab has a mass of 35 g in air, then it has an underwater weight of 0.05 N ($0.035\text{ kg in air}\times 9.8\text{ N kg}^{-1}\times 0.16$ negative buoyancy). Therefore, at the majority of underwater walking speeds I observed, the forces required to overcome drag appear to be approximately one order of magnitude lower than those required to overcome gravity.

Crabs apparently recognize the general nature of the terrain and remember the details as they encounter them, at least for the short term. The risk of injury due to a mis-step in air over rocky terrain would make learning more imperative there than over the other terrains. In air over rocky terrain the leading legs generally have shorter steps than the following legs (Table 3), a pattern to be expected if the crab is learning the irregularities with the leading legs but not the trailing legs. Consequently, the trailing legs can be placed directly on a known stable site and not used for tactile searching, resulting in a longer step length. Over smooth terrain in both regimes the leading legs do not need to search and, over rocky terrain in the submerged regime, buoyancy diminishes problems from mis-steps. Correspondingly, under these three conditions not requiring tactile searching, the leading legs take longer steps than do the trailing legs (Table 3). Neuromuscular activity of *Carcinus maenas* over smooth terrain in the two regimes also indicates longer steps by the leading legs (Clarac *et al.* 1987).

Vision plays an important role in ascertaining the general nature of the terrain (Hiatt, 1948). The eyes can be elevated and rotated in their stalks to maximize their visual capacity (Hiatt, 1948). However, because the eyes are located anteriorly and the crab walks sideways, the eyes may not be ideally located to view the terrain in the path of travel. Perhaps in partial compensation, the fourth leg of each side, located at the opposite end of the body from the eyes, is used for tactile feedback about the terrain and is not a consistent direct contributor to *P. crassipes* walking or to ghost crab running (Milne and Milne, 1946; Hafemann and Hubbard, 1969). The tactile feedback of the fourth legs can also be instrumental when the crab walks backwards and when it seeks refuge (Hiatt, 1948; Bovbjerg, 1960a).

Locomotion in two regimes is a key adaptation for shore crabs. The ability to walk from a submerged regime onto land requires adjustment to a sixfold increase in gravitational effects, an issue that must have been one of the first addressed to facilitate adaptations for terrestrial excursions. Terrestrial adaptations for desiccation, respiration and thermal gradients can develop in small increments after the advent of terrestrial excursions. Real proficiency in terrestrial locomotion enables searching for separate bodies of water compatible with survival and propagation. Escape from the aquatic regime when dissolved oxygen decreases to levels approaching zero, as has been observed in coastal lagoons (Carpelin, 1961), offers survival. Escape to the terrestrial regime offers avoidance of aquatic predators and exposure of another habitat for foraging. Coastal lagoons may have afforded ideal

conditions for the evolution of terrestrial crabs (Gross, 1961), but the ability to walk in both regimes must have been one of the first steps in that evolution.

I thank R. R. Hessler and two anonymous reviewers for helpful comments on the manuscript and F. S. Shipp for technical assistance. This effort was supported largely through NAVSEA Program Element 63721N and NAVFAC IR Project NOSC-89-05.

References

- BARNES, W. J. P. (1975). Leg co-ordination during walking in the crab, *Uca pugnax*. *J. comp. Physiol.* **96**, 237–256.
- BLAKE, R. W. (1983). Functional design and burst-and-coast swimming in fishes. *Can. J. Zool.* **61**, 2491–2494.
- BLICKHAN, R. AND FULL, R. J. (1987). Locomotion energetics of the ghost crab. II. Mechanics of the centre of mass during walking and running. *J. exp. Biol.* **130**, 155–174.
- BOVBJERG, R. V. (1960a). Behavioral ecology of the crab, *Pachygrapsus crassipes*. *Ecology* **41**, 668–672.
- BOVBJERG, R. V. (1960b). Courtship behavior of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pacific Sci.* **14**, 421–422.
- BURROWS, M. AND HOYLE, G. (1973). The mechanism of running in the ghost crab, *Ocypode ceratophthalma*. *J. exp. Biol.* **58**, 327–349.
- CARPELIN, L. (1961). Salinity tolerances of some fishes of a southern California coastal lagoon. *Copeia* **1961**, 32–39.
- CARRIER, D. R. (1987). Lung ventilation during walking and running in four species of lizards. *Expl Biol.* **47**, 33–42.
- CHASSERAT, C. AND CLARAC, F. (1980). Interlimb coordinating factors during driven walking in Crustacea. *J. comp. Physiol.* **139**, 293–306.
- CLARAC, F., LIVERSAT, F., PFLÜGER, J. J. AND RATHMAYER, W. (1987). Motor pattern analysis in the shore crab (*Carcinus maenas*) walking freely in water and on land. *J. exp. Biol.* **133**, 395–414.
- DAWSON, T. J. AND TAYLOR, C. R. (1973). Energetic cost of locomotion in kangaroos. *Nature* **246**, 313–314.
- FARLEY, C. T. AND TAYLOR, C. R. (1991). A mechanical trigger for the trot–gallop transition in horses. *Science* **253**, 306–308.
- GROSS, W. J. (1957). A behavioral mechanism for osmotic regulation in a semi-terrestrial crab. *Biol. Bull. mar. biol. Lab., Woods Hole* **113**, 268–274.
- GROSS, W. J. (1961). Osmotic tolerance and regulation in crabs from a hypersaline lagoon. *Biol. Bull. mar. biol. Lab., Woods Hole* **121**, 290–301.
- GROTE, J. R. (1981). The effect of loads on locomotion in crayfish. *J. exp. Biol.* **92**, 277–288.
- HAPEMANN, D. R. AND HUBBARD, J. I. (1969). On the rapid running of ghost crabs (*Ocypode ceratophthalma*). *J. exp. Zool.* **170**, 25–32.
- HESSLER, R. R. (1982). The structural morphology of walking mechanisms in eumalacostracan crustaceans. *Phil. Trans. R. Soc. Lond. B* **296**, 245–298.
- HIATT, R. W. (1948). The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pacific Sci.* **2**, 135–213.
- HILDEBRAND, M. R. (1980). The adaptive significance of tetrapod gait selection. *Am. Zool.* **20**, 255–267.
- HOYT, D. F. AND TAYLOR, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.
- HUI, C. A. (1987). The porpoising of penguins: an energy-conserving behavior for respiratory ventilation? *Can. J. Zool.* **64**, 209–212.
- HUI, C. A. (1989). Surfacing behavior and ventilation in free-ranging dolphins. *J. Mammal.* **70**, 833–835.

- JACKSON, D. C. AND PRANGE, H. D. (1979). Ventilation and gas exchange during rest and exercise in adult green sea turtles. *J. comp. Physiol.* **134**, 315–319.
- MILNE, L. J. AND MILNE, M. J. (1946). Notes on the behavior of the ghost crab. *Am. Nat.* **80**, 362–380.
- MULLER, U. AND CLARAC, F. (1990a). Dactyl sensory influences on rock lobster locomotion. I. Intrasegmental and intersegmental leg reflexes during standing and walking. *J. exp. Biol.* **148**, 89–112.
- MULLER, U. AND CLARAC, F. (1990b). Dactyl sensory influences on rock lobster locomotion. II. Role in interleg coordination. *J. exp. Biol.* **148**, 113–128.
- POND, C. M. (1975). The role of the 'walking legs' in aquatic and terrestrial locomotion of the crayfish *Austropotamobius pallipes* (Lereboullet). *J. exp. Biol.* **62**, 447–454.
- SCHULTZ, J. W. (1987). Walking and surface film locomotion in terrestrial and semi-aquatic spiders. *J. exp. Biol.* **128**, 427–444.
- VOGEL, S. (1981). *Life in Moving Fluids. The Physical Biology of Flow*. 352pp. Boston: Willard Grant Press.
- WARD, T. M. AND HUMPHREYS, W. F. (1981). The effect of filming speed on the interpretation of arthropod locomotion. *J. exp. Biol.* **92**, 323–331.
- WEIHS, D. (1974). Energetic advantages of burst swimming of fish. *J. theor. Biol.* **48**, 215–229.
- WILSON, D. M. (1966). Insect walking. *A. Rev. Ent.* **11**, 103–122.

