A ROTATING RESPIROMETER TO MONITOR VOLUNTARY ACTIVITY AND ASSOCIATED EXCHANGE OF RESPIRATORY GASES IN THE LAND HERMIT CRAB (*COENOBITA COMPRESSUS*)

BY MICHÈLE G. WHEATLY

*Department of Zoology, University of Florida, Gainesville, FL 32611,
U.S.A.*

BRIAN R. McMAHON

*Department of Biology, University of Calgary, 2500 University Drive
NW, Calgary, Alberta, T2N 1N4 Canada*

WARREN W. BURGGREN AND ALAN W. PINDER

*Zoology Department, University of Massachusetts, Amherst, MA 01003,
U.S.A.*

SUMMARY

A rotating respirometer was designed which enabled respiratory gas exchange in the land hermit crab *Coenobita compressus* to be correlated with voluntary submaximal sustained pedestrian activity. In the laboratory, crabs remained spontaneously active for up to 150 min, maintaining velocities of $0.6 \, \text{cm s}^{-1}$. Comparable activity patterns were observed in the field. Quiescent O_2 uptake (M_{O_2}) increased logarithmically as a function of load rating of the adopted molluscan shell. Steady-state M_{O_2} and M_{CO_2} were measured after 30 min of spontaneous activity and both increased linearly with velocity. There was good correspondence between Y-intercept values and those measured in inactive crabs. At the mean locomotory speed, M_{O_2} and M_{CO_2} were increased 3.4-fold and 2.6-fold respectively above settled rates. Minimum and gross energetic cost of transport were estimated and compared with values in the literature. M_{O_2} and M_{CO_2} returned to settled levels within the first hour of recovery. The activity profile and concomitant changes in gas exchange are discussed in the context of acquisition of the shell-dwelling habit.

INTRODUCTION

In recent years much interest has focused on the physiological changes which accompany exercise in decapod crustaceans (see review articles by Herreid, 1981; McMahon, 1981; McMahon & Wilkens, 1983). In many of the original studies (e.g. McDonald, McMahon & Wood, 1979; McMahon, McDonald & Wood, 1979;

Rutledge, 1980) distance, speed and force of locomotion were not quantified; animals were simply exercised to exhaustion which generally occurs within 10 min. This has made a comparison with the literature on ectothermic vertebrates difficult (reviewed by Brett, 1972; Bennett, 1978). Some of the more recent investigations on the land crabs *Cardisoma* (Wood & Randall, 1981*a,b*; Herreid, O'Mahoney & Full, 1983), *Birgus* (Smatresk & Cameron, 1981), *Ocypode* (Full & Herreid, 1983) and *Uca* (Full & Herreid, 1984) have quantified speed of enforced locomotion using classical tread-mill techniques. The focus however has remained on 10- to 20-min bursts of exhausting activity (speeds of around 10 cm s^{-1}). While bursts of sprinting activity are important in escaping predators, submaximal but sustained locomotion may be far more typical of the natural behavioural repertoire. The only existing study on maintained activity is on the blue crab, *Callinectes sapidus*, (Booth, McMahon & Pinder, 1982) which can be forced to swim for up to 1 h.

Treadmill studies in all animals are somewhat questionable since speed is generally preset by the investigator, frequently unsupported by measurements of field activity. Furthermore, recent studies in humans have demonstrated that even trained treadmill runners experience balance problems which are not associated with ground running (Woolley & Winter, 1980). Thus treadmill exercise is undoubtedly more stressful than voluntary activity.

At night, on beaches in Panama, we were impressed by the sustained pedestrian locomotion of a local terrestrial hermit crab (*Coenobita compressus* H. Milne Edwards). Previous studies of short bursts of forced activity of this species have been made using a treadmill (C. F. Herreid & R. J. Full, unpublished). Hermit crabs are interesting from an energetic viewpoint due to the additive locomotor costs associated with carriage of the adopted molluscan shell which is frequently equivalent to body mass (Wheatly, 1984). As such, they provide a unique opportunity to assess the natural effects of loading in an invertebrate species. Furthermore, hermit crabs provide an interesting comparison with other decapods since they do not use sideways octapedal locomotion but move in a forwards direction using the chelipeds, second and third pairs of legs for walking. The fourth and fifth pairs of legs are reduced and modified to assist in shell retention.

The present paper describes observations we made in the field on natural locomotory patterns in *Coenobita*. We subsequently developed a rotating respirometer to study the energetics of voluntary activity in this species. This apparatus enabled us to correlate exercise performance with exchange of respiratory gases.

MATERIALS AND METHODS
Study site and experimental animals

The study was conducted on land hermit crabs *Coenobita compressus* (H. Milne Edwards – identified by reference to Ball & Haig, 1973) which were collected at Boy Scouts' Beach on Naos Island, off the Pacific coast of Panama in April and May of 1983. In this population, crabs had a mean body mass of 10.5 ± 1.1 g ($N = 29$) and most frequently inhabited *Nerita scabricosta* shells (identified from Keen, 1971) with a mean weight association index (WI = mollusc shell mass/crab body mass; Wheatly,
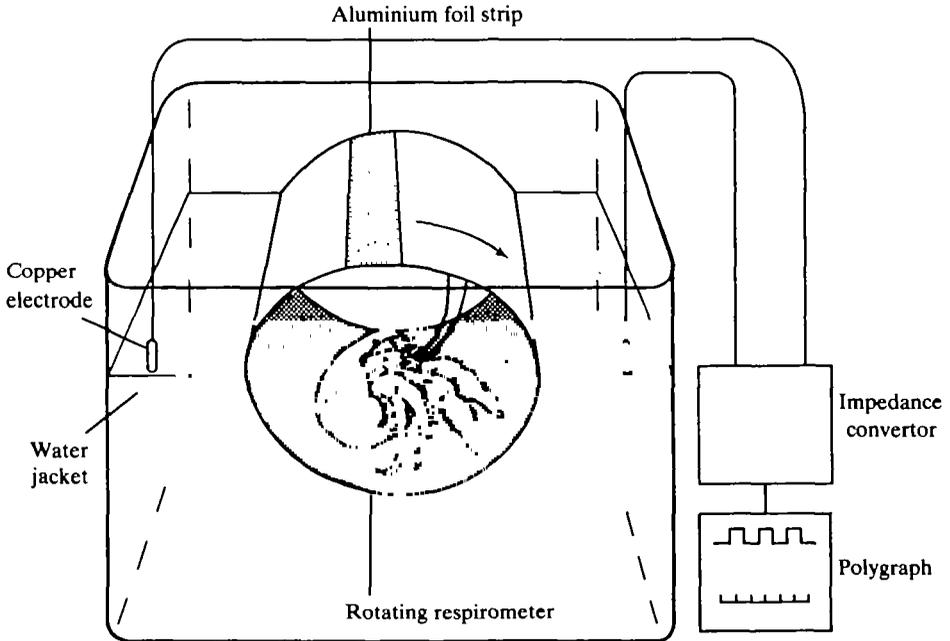
Fig. 1. Experimental apparatus. Operational details are given in the text.

1984) of 0.96 ± 0.06 ($N = 22$). Less frequently *Coenobita* were found inside shells of *Muricanthus, Polinices, Thais, Nattica, Northia* and *Opeatostoma* providing WI ratios ranging up to 1.45. Activity patterns were observed in the natural environment. For physiological investigation, animals were transported to the nearby Naos Laboratory of the Smithsonian Tropical Research Institute where they were maintained under ambient conditions (i.e. air temperature $\simeq 30 \pm 4\,°C$; humidity $\simeq 70 \pm 10\,\%$) in glass terraria ($60 \times 30 \times 45$ cm) for 1 week prior to experimentation. During this period they had free access to $10\,\%$ sea water and fruit. A scaffolding of ceramic tiles was erected inside the terrarium to provide shelter and internal geography.

Field transect survey

On the evening of 27th April 1983, a day which had experienced tropical weather typical of the season (i.e. brief but heavy rainfall around 10.00 h), a transect survey was run on the central portion of Boy Scouts' Beach ($8\,°54·8'\,N-79\,°31·9'\,W$). We had previously observed that crabs spent daylight hours sheltering in a patch of rocks high up on the beach. A 6-m wide transect was marked off in 2-m grids from these rocks down to the water line – a total distance of 30 m. Numbers of crabs in each grid were recorded at hourly intervals from 19.00 h until midnight.

Experimental apparatus – the rotating respirometer

Locomotory activity and associated changes in gas exchange were studied in a closed respirometer (Fig. 1) which the crab could rotate at will by walking along the inside inclined surface. The apparatus was fashioned after a system used by Jensen

& Holm-Jensen (1980). The respirometer was a 316 ml glass storage jar (i.d. 85 mm), with a counterbalanced lid, which would float sideways and approximately 50 % submerged in a surrounding water jacket. The dimensions of the outer container only marginally exceeded the depth and external diameter of the respirometer so that movements other than rotational were eliminated. A plastic meshwork was glued onto the inside wall of the jar to provide traction for the crab's walking movements. The water jacket was heated with a small aquarium filament heater to maintain air temperature inside the respirometer at the experimental temperature which was $30 \pm 2\,°C$. A hole drilled through the lid of the jar was sealed with dental dam serving as a sampling port for respirometer gas.

A 3-cm strip of aluminium foil was glued along the outside of the jar in parallel with the axis of rotation so that it was immersed in the surrounding water during half of each complete revolution. Two large flattened copper electrodes were positioned at right angles to this strip and led *via* an impedance convertor (UFI Model 2991, Morrobay, CA) to a Gilson biscriptual polygraph (ICT-SH). Complete revolutions were detected as changes in the impedance of the water each time the foil strip was immersed and were recorded as positive square-based deflections in the polygraph trace. Distance covered, duration and velocity of *voluntary* locomotion could, in this way, be quantified.

Protocol and analytical procedures

Based on preliminary field observations (see Results), animals were placed in the respirometer in the early morning and allowed to acclimate to the experimental chamber during a period of the day when they were normally inactive. Pre-exercised (control) rates of O_2 consumption ($\dot{M}_{O_2}$) and CO_2 production ($\dot{M}_{CO_2}$) were estimated 3 h later by analysing the gas content of samples sequentially removed from the inside of the respirometer. 'Steady-state' active or recovered levels of $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ (as defined by Stainsby & Barclay, 1970) were measured over the two time periods $0.5–1.0$ and $1.0–1.5$ h from the start or end of spontaneous activity. Trials were performed on loaded and unloaded crabs. In the case of loaded crabs, animals were removed from their shells for determination of body mass only upon completion of measurements.

Gas samples (50–100 µl) were removed from the respirometer using gas-tight Hamilton syringes. Contents of O_2 and CO_2 were measured using Applied Electrochemistry analysers (S-3A O_2 sensor N-37M and CD 3A CO_2 sensor P61B, Sunnyvale, CA) electrically interfaced with a two-channel Linear Instruments Model 595 flat bed chart recorder. Flow of gas through the analysers was generated by two suction pump/flow meter systems (R/2a Applied Electrochemistry) which were set to have identical flows of 12.5 ml min^{-1}. These two systems effectively operated in parallel. One drew dehumidified room air first through a CO_2 analyser and then through channel 2 of a differential O_2 analyser. The second meanwhile drew dehumidified room air directly through the reference channel (1) of the O_2 analyser. The O_2 analyser was set to display the differential between the two channels. A diagram of this arrangement is given by McMahon & Burggren (1985).

The two-analyser system was first calibrated using a standard gas which was 3 % CO_2 in N_2. Different volumes (10, 20, 30, 40, 50 µl) were injected as a discrete

bolus into the gas inflow at an injection port. Since all tubing was small bore, the gas passed through the analysers as a bolus and appeared on the chart as peaks of higher CO_2 and lower O_2 concentration (as compared with room air). The CO_2 analyser system could be calibrated relatively simply since the area beneath CO_2 peak was directly proportional to the CO_2 content of the injected gas.

The O_2 analyser was also calibrated using unitary injections of 3 % CO_2 in N_2 since this was the only certified gas mixture available to us in the field. The negative peak on the O_2 differential trace effectively represented displacement of O_2 from room air (termed O_2 'deficit'). This was again calibrated by integrating the area beneath the curve. In calculating O_2 consumption inside the respirometer it was important to remember that O_2 'deficit' was attributable to CO_2 addition as well as O_2 removal by the crab. In calculating that part of the deficit which was due to O_2 removal it was necessary to know proportional changes in CO_2 content of respirometer gas and the total amount of CO_2 which had been evolved.

Contents of O_2 and CO_2 in gas samples removed from the respirometer were thus measured in μmol and were subsequently used to calculate $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ knowing the volume of the respirometer, elapsed time and animal mass.

Statistical treatment of data

All data are expressed as mean ± 1 s.e. (number of observations). Samples were tested for homogeneity of variance (F test) and means compared by Student's two-tailed t-test (paired or unpaired design) using $P = 0.05$ as the fiducial limit. Linear regression was performed by the least squares method. Slopes from different treatments were compared using an analysis of covariance (Zar, 1974). In cases where regression lines were parallel, coincidence was tested by comparing elevations using the Newman-Keuls multiple comparison procedure (Newman, 1939; Keuls, 1952).

RESULTS
Spontaneous activity

Field observations

Fig. 2 illustrates the distribution of hermit crabs on the experimental grid from 19.00 h to midnight on a typical evening in the tropics. At 19.00 h no crabs were present. Over the next hour 35 animals emerged and occupied transects anywhere up to 21 m from the rocks. To establish this position it was necessary for them to move at a speed of $0.58 \mathrm{~cm~s}^{-1}$. The mean weighted distance travelled however was 3·86 m which equates to an average velocity of $0.11 \mathrm{~cm~s}^{-1}$. Over the next 2 h the weighted mean distance increased to 6·20 m and then decreased to 3·30 m by midnight as the nightly excursion came to a close. From the difference in weighted mean distances covered per unit time, minimum running speeds of 0·09, 0·05 and $0.04 \mathrm{~cm~s}^{-1}$ were calculated for successive hourly intervals between 21.00 h and midnight. These are probably conservative estimates of running speed since the movement of animals during the first hour of activity clearly indicates that individuals were capable of greater velocities. An in-depth survey would demand that individual crabs be marked and followed. Visual inspection did reveal however that the population as a whole
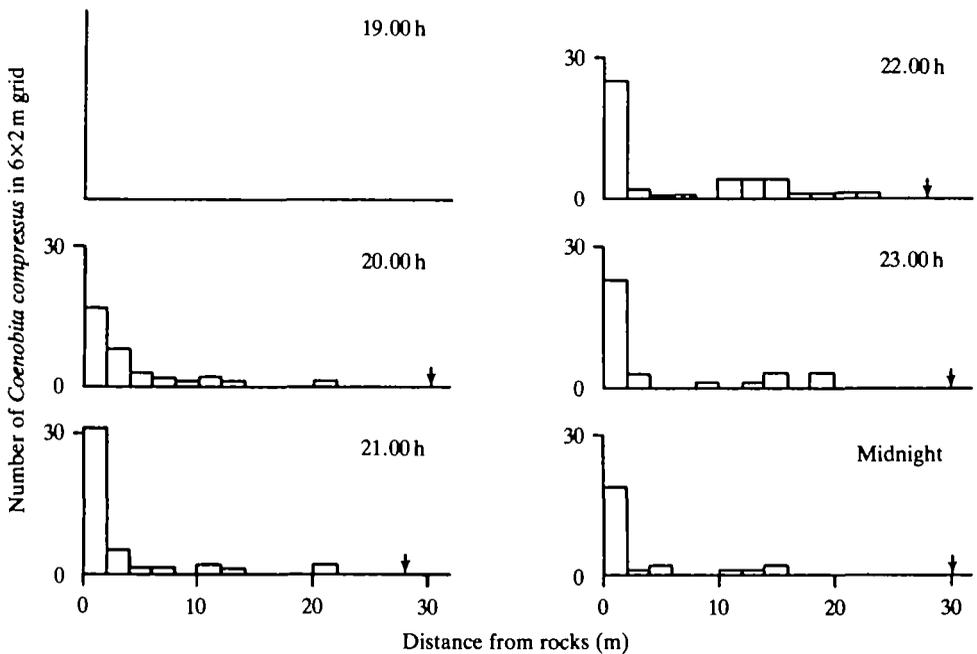
Fig. 2. Frequency distribution of *Coenobita compressus* from 19.00 h to midnight (27 April 1983) in 2-m grids of a 6-m wide transect laid from rocks at high tide level (0 distance) to water line (marked by downward pointing arrow) on Boy Scouts' Beach, Balboa, Panama.

remained active for a number of hours and so sustained submaximal exercise is a prominent feature of the normal activity pattern.

Voluntary activity in the rotating respirometer

In the laboratory hermit crabs exhibited forward pedestrian locomotion using the chelae as levers for propulsion in addition to the second and third pairs of legs. Animals were virtually 100 % successful in rotating the respirometer and entire actograph traces were obtained from 32 individual trials. Activity spontaneously commenced in the late afternoon and continued uninterrupted for an average of 148 ± 13 min. During this time crabs covered $52\cdot9 \pm 7\cdot3$ m at an average velocity of $0\cdot6$ cm or $0\cdot2$ BL (body lengths) s^{-1} where BL is taken as the tip of the chelae to the projection of the shell apex.

As in the field, individual crabs were variable in their exercise performance. The maximum values observed for speed, distance covered and duration of spontaneous activity were respectively $2\cdot5$ cm s^{-1} ($0\cdot7$ BL s^{-1}), 150 m and 300 min. Crabs were divided arbitrarily into high and low performers based on their ability to cover distances 2 standard errors in excess of the mean value. An analysis of velocity with time during the exercise bout (Fig. 3) revealed that high performers maintained a velocity of $0\cdot81$ cm s^{-1} throughout the entire 221 min of activity whereas low performers exhibited a progressive decrease in running speed which became significantly reduced prior to cessation of activity at 119 min.
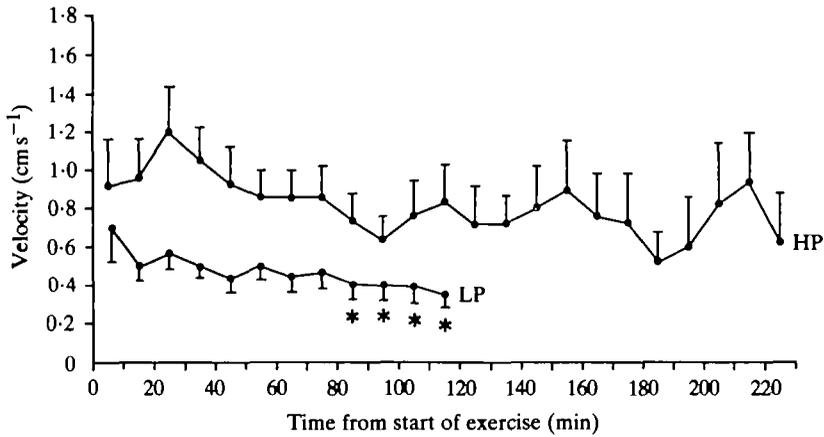
Fig. 3. Mean velocity (± S.E.M.) with time after start of exercise in two groups of land hermit crabs. High (HP; $N = 9$) and low performers (LP; $N = 19$) covered distances exceeding or less than 70 m respectively. Asterisks denote significant change in velocity compared to initial rate.
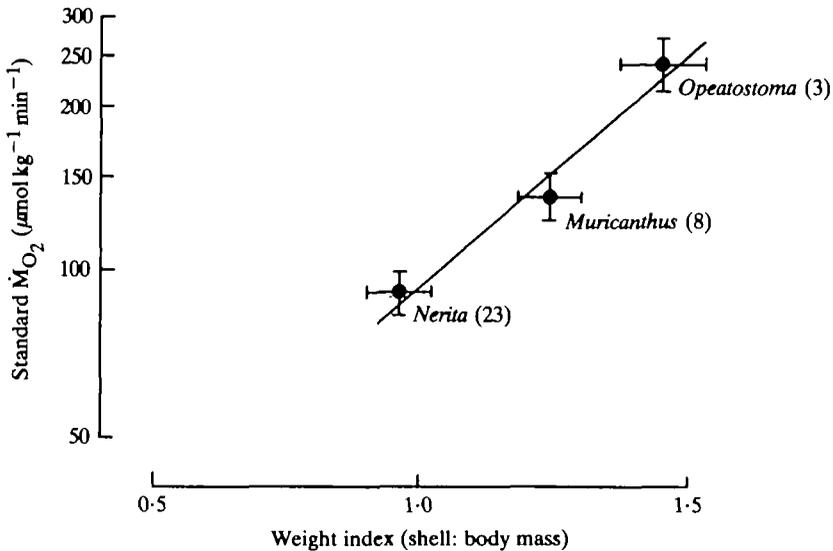

Fig. 4. Standard $\dot{M}_{O_2}$ (note log scale) *versus* weight index (mass of shell: mass of crab) for *Coenobita compressus* inhabiting three different species of molluscan shell. Linear regression analysis (on log $\dot{M}_{O_2}$ values): $\log \dot{M}_{O_2} = 1.11 + 0.86WI$ ($r = 0.985$, $N = 3$).

Respiratory gas exchange

Pre-exercised

Standard $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ in inactive *C. compressus* occupying *Nerita* shells at 30 °C were respectively 91·4 ± 8·9 (23) and 41·6 ± 4·4 (22) μmol kg^{-1} min^{-1} producing an *r* value of 0·5. When removed from their shells, these same crabs maintained $\dot{M}_{O_2}$ at 92·8 ± 9·7 μmol kg^{-1} min^{-1} but $\dot{M}_{CO_2}$ declined to 27·2 ±2·9 μmol kg^{-1} min^{-1}. Quiescent $\dot{M}_{O_2}$ increased logarithmically by a factor of 0·86 with WI (shell:body mass ratio) (Fig. 4). Habitation of the mollusc shells *Muricanthus*

and *Opeatostoma* significantly increased the load rating (WI) to $1 \cdot 24 \pm 0 \cdot 06$ ($N = 8$, $P = 0 \cdot 013$) and $1 \cdot 45 \pm 0 \cdot 08$ ($N = 3$, $P = 0 \cdot 007$) respectively when compared with *Nerita* associations. Quiescent $\dot{M}_{O_2}$ increased correspondingly to 138 ± 13 (8) and 245 ± 24 (3) μmol kg^{-1} min^{-1}. Both increases were highly significant compared to crabs inside *Nerita* shells ($P = 9 \cdot 9 \times 10^{-3}$, $3 \cdot 6 \times 10^{-5}$ respectively).

Active

To remove gas samples, it was necessary to stop the rotation of the respirometer momentarily. Although momentum was instantly re-established, sampling was restricted to 30-min intervals to minimize any possible disturbing effect on the locomotory patterns. The $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ values for the initial half hour of activity were discounted since lactic acid accumulated at the start of exercise (see M. G. Wheatly, B. R. McMahon, W. W. Burggren & A. W. Pinder, in preparation) and we were
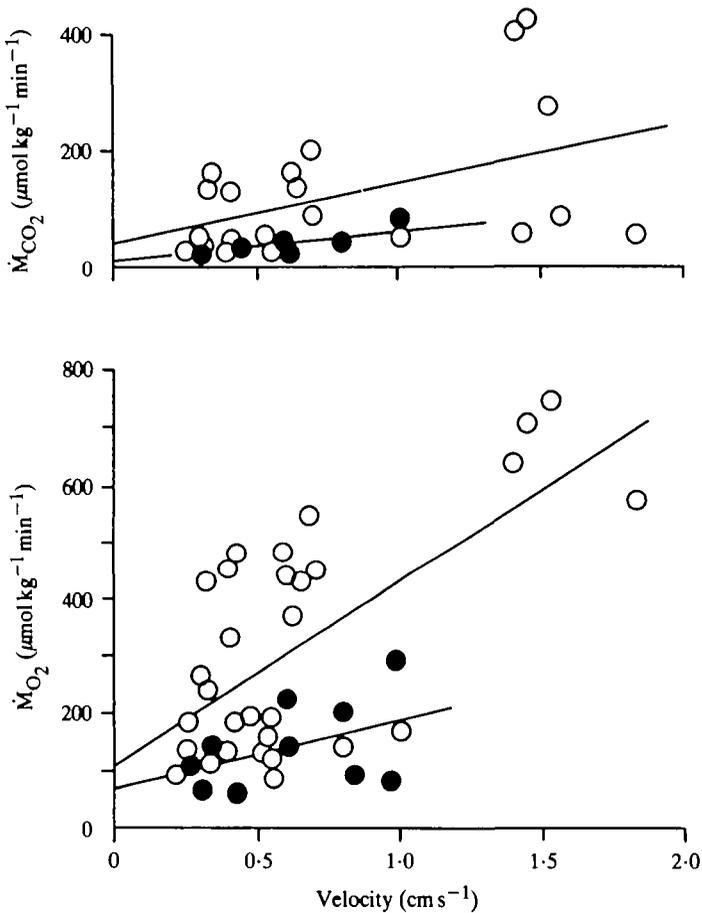

Fig. 5. $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ of *Coenobita compressus* as a function of running velocity. Open and closed symbols in each case are animals with and without *Nerita* shells. Regression equations are: with shells: $\dot{M}_{O_2} = 111 \cdot 7 + 331 \cdot 5$ (vel) ($r = 0 \cdot 674, N = 30$), $\dot{M}_{CO_2} = 45 \cdot 4 + 102 \cdot 3$ (vel) ($r = 0 \cdot 440, N = 21$), without shells: $\dot{M}_{O_2} = 68 \cdot 4 + 123 \cdot 6$ (vel) ($r = 0 \cdot 442, N = 10$), $\dot{M}_{CO_2} = 4 \cdot 8 + 63 \cdot 4$ (vel) ($r = 0 \cdot 820, N = 7$).

Table 1. *Y-intercept (zero velocity) and M_{run} (minimum cost of transport in terms of $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$) in* Coenobita compressus *running in a rotating respirometer with and without* Nerita *shells*

	$\dot{M}_{O_2}$		$\dot{M}_{CO_2}$	
	Y-intercept (μmol kg^{-1} min^{-1})	M_{run} (mmol g^{-1} km^{-1})	Y-intercept (μmol kg^{-1} min^{-1})	M_{run} (mmol g^{-1} km^{-1})
With shells	111·7	0·552	45·4	0·171
Without shells	68·4	0·206	4·8	0·106

Data taken from Fig. 3.

uncertain of the extent to which anaerobic ATP production fuelled locomotion at this time. However, the increase in lactate was not cumulative and so the values of $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ recorded in the two subsequent time periods are representative of a 'steady state' and have been used to assess the total energy required to run at a given velocity. The mean values reported therefore correspond to measurements taken 45 min into the exercise bout and are plotted as a function of velocity in Fig. 5 for loaded and unloaded crabs. Velocity was calculated from the polygraph trace as revolutions per minute multiplied by the internal circumference of the jar.

$\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ both increased linearly with velocity which is diagnostic of a number of birds, mammals and reptiles (Taylor, 1973). Crabs running with shells exhibited running speeds anywhere from 0·2–2·0 cm s^{-1}. Unloaded crabs displayed velocities at the lower end of this range. The gradient of this line is termed M_{run} (minimum cost of transport) and is commonly used to assess the energetic cost of locomotion (Taylor, Schmidt-Nielsen & Raab, 1970; Taylor, Heglund & Maloiy, 1982) since it is independent of an animal's resting $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ and range of running velocities. As such, this index allows comparison of widely differing species. M_{run} represents the total amount of energy required to locomote at a given velocity and assumes that steady-state $\dot{M}_{O_2}$ has been reached (Seeherman, Taylor, Maloiy & Armstrong, 1981; Rome, 1982). Both requirements were fulfilled in the present study.

In the case of O_2 uptake, M_{run} increased significantly from 0·21–0·55 mmol g^{-1} km^{-1} as a result of shell carriage or loading. When regression coefficients for animals with and without shells were tested for homogeneity *via* analysis of covariance, the slopes were found to be significantly different ($F_{(1), 1,36} = 9·14$; $0·005 < P < 0·0025$). The null hypothesis could not be rejected for $\dot{M}_{CO_2}$ *vs* velocity however ($F_{(1), 1,24} = 1·22$; $P > 0·25$) and a common weighted regression coefficient of 134·1 was computed. Statistically however, these two lines do not coincide, since their elevations are different ($F_{(1), 1,25} = 13·9$; $P = 0·001$).

The Y-intercept values (corresponding to zero velocity) extrapolated from these regression equations (Table 1) show good agreement with values measured in inactive animals (see above). $\dot{M}_{O_2}$ measured in unloaded crabs was somewhat higher than predicted indicating that removal from the shell had traumatized the animal. In this same group Y-intercept $\dot{M}_{CO_2}$ values were very low suggesting that it is not advisable to extrapolate outside the measured range.

Interpolation of the mean locomotory velocity of 0·6 cm s^{-1} onto the regression
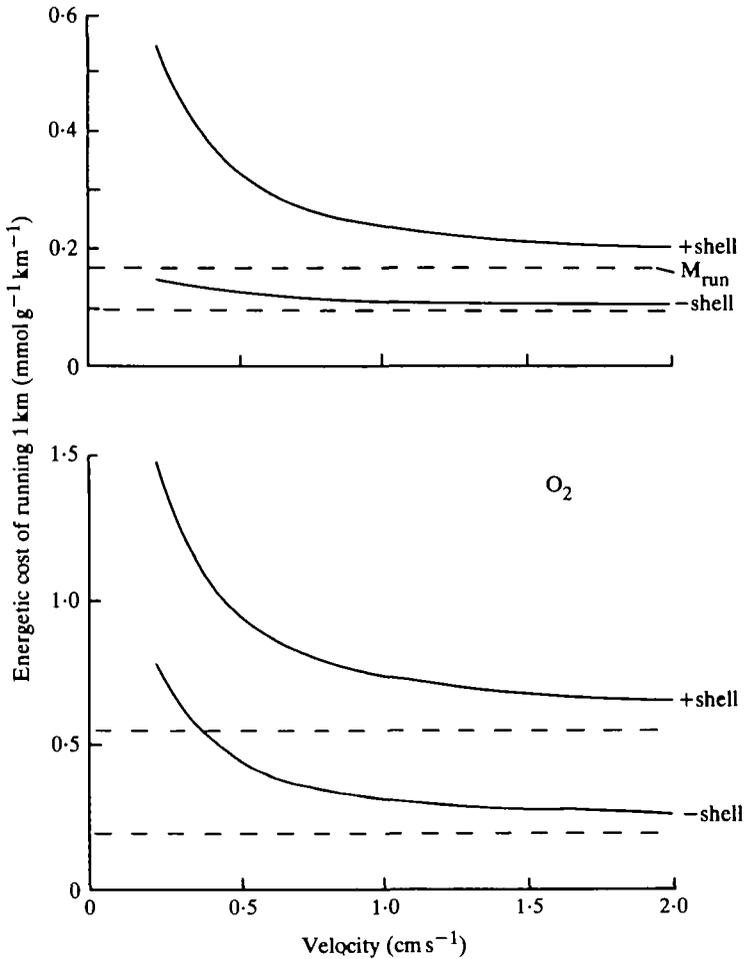
Fig. 6. Energetic cost per gram (in terms of O_2 uptake and CO_2 production) of running 1 km as a function of speed (data taken from Fig. 3) in *Coenobita compressus* running with and without shells. M_{run} indicates minimum cost of transport. The equations describing these lines are: CO_2: + shells $y = 0 \cdot 172x^2 - 0 \cdot 523x + 0.586$ $(r = 0 \cdot 897)$, − shells $y = 0 \cdot 185x^2 - 0 \cdot 603x + 0 \cdot 155$ $(r = 0 \cdot 917)$; O_2: + shells $y = 0 \cdot 418x^2 - 0 \cdot 126x + 0 \cdot 157$ $(r = 0 \cdot 895)$, − shells $y = 0 \cdot 189x^2 - 0 \cdot 602x + 0 \cdot 735$ $(r = 0 \cdot 950)$.

equations for crabs carrying shells produced mean active $\dot{M}O_2$ and $\dot{M}CO_2$ values of 310·6 and 106·8 μmol kg^{-1} min^{-1}. These represent respectively 3·4 and 2·6 factorial increases above inactive values. Corresponding values for crabs removed from their shells were 142·6 and 42·8 μmol kg^{-1} min^{-1}, both of which constitute a 1·6-fold increase over resting rates.

The gross energetic cost of transport was calculated (in mmol g^{-1} km^{-1}) from these regression lines by dividing $\dot{M}O_2$ or $\dot{M}CO_2$ by velocity (see Herreid, 1981). This index exhibited an exponential decay which could be fitted, with greater than 90% confidence, by a second order polynomial for all four treatments (Fig. 6.). The asymptote was in all cases close to the value for M_{run}. At high velocity the gradient of this line for all treatments was consistently 1·39 mmol g^{-1} km^{-2} h^{-1}. As velocity decreased, the gradient increased to as much as 26·4. The first significant departure from the

asymptote was arbitrarily defined as the velocity at which the gradient doubled. This so-called 'critical velocity' was $1{\cdot}0\,\mathrm{cm\,s^{-1}}$ for animals carrying shells ($1{\cdot}1\,\mathrm{cm\,s^{-1}}$ for $\dot{M}_{O_2}$; $0{\cdot}9\,\mathrm{cm\,s^{-1}}$ for $\dot{M}_{CO_2}$) which is fairly close to the mean velocity observed during spontaneous locomotion ($0{\cdot}6\,\mathrm{cm\,s^{-1}}$) suggesting that animals voluntarily minimize energetic expenditure. Interestingly the critical value was lower when animals were removed from their shells ($0{\cdot}9\,\mathrm{cm\,s^{-1}}$ for $\dot{M}_{O_2}$; $0{\cdot}3\,\mathrm{cm\,s^{-1}}$ for $\dot{M}_{CO_2}$) which may explain why this group voluntarily ran at a lower speed.

Recovered

$\dot{M}_{O_2}$ recorded between 30 min and 1 h after activity ceased was $65{\cdot}3 \pm 9{\cdot}3$ (13) $\mu\mathrm{mol\,kg^{-1}\,min^{-1}}$ which was not significantly different from the pre-exercised rate ($P = 0{\cdot}06$). In some experiments, 20 ml of 10 % sea water was introduced into the respirometer by injection through the lid at the start of the recovery period (see M. G. Wheatly, B. R. McMahon, W. W. Burggen & A. W. Pinder, in preparation). Under these circumstances $\dot{M}_{O_2}$ declined to $165{\cdot}9 \pm 39{\cdot}4$ (7) $\mu\mathrm{mol\,kg^{-1}\,min^{-1}}$ which was half the active rate. However, this rate was significantly higher than the pre-exercised level ($P = 8{\cdot}7 \times 10^{-7}$). $\dot{M}_{CO_2}$ was $18{\cdot}8 \pm 2{\cdot}6$ (13) $\mu\mathrm{mol\,kg^{-1}\,min^{-1}}$ in crabs recovering without water which was a significant reduction below settled values ($P = 4{\cdot}95 \times 10^{-5}$). When crabs had access to water at this time the $\dot{M}_{CO_2}$ measured in the gas phase decreased further to $12{\cdot}9 \pm 1{\cdot}0$ (7) $\mu\mathrm{mol\,kg^{-1}\,min^{-1}}$. This reduction was significant compared to settled levels ($P = 7{\cdot}17 \times 10^{-4}$) but not compared to $\dot{M}_{CO_2}$ during recovery without water ($P = 0{\cdot}12$).

DISCUSSION

This investigation presents an innovative approach to the study of exercise physiology in decapod crustaceans. Its most unique feature is that, by virtue of the design of the apparatus, the activity studied in the hermit crab *C. compressus* was entirely voluntary and not dictated by the experimentor. Furthermore an attempt was made to relate the laboratory exercise performance to activity patterns observed in the field.

The shell-dwelling habit creates an important distinction between the land hermit crab and other terrestrial crabs since it affords a built-in protection mechanism against adverse environmental stimuli or predators. If disturbed, crabs will withdraw into the shell using the major chela in addition to other flattened ambulatories to obstruct the aperture (Harms, 1929). The success of this species in the terrestrial environment is largely attributed to retention of the mollusc shell for purposes of concealment (Reese, 1969). For this reason terrestrial hermit crabs can avoid bursts of high speed pedestrian activity which are observed in other species such as *Uca* (Full & Herreid, 1984) or *Cardisoma* (Wood & Randall, 1981a,b; Herreid *et al.* 1983) and are short-lived since they are fuelled predominantly anaerobically (see review article by McMahon, 1981). This field has focused in the past on short periods of exhaustive activity (McDonald *et al.* 1979; Rutledge, 1980) since it is often difficult accurately to quantify exercise performance without sophisticated instrumentation.

Sustained submaximal pedestrian activity has not previously been studied since most species exhibit erratic movements when running at low speeds on treadmills (Full & Herreid, 1984). Marathon swimming activity has however been studied in the

blue crab (*Callinectes sapidus*) which naturally undertakes long-distance migrations (Judy & Dudley, 1970). Booth *et al.* (1982) examined 1 h of forced swimming in this species. Their study revealed some important differences in the physiological responses to submaximal *versus* exhaustive activity and these have been further documented in the present study for pedestrian locomotion.

Their rapid and effective method of withdrawal from hostile conditions has enabled hermit crabs to colonize extensively the terrestrial environment. While their activity lacks the urgency of other terrestrial species, it is no less impressive especially considering the imposed load which they support in the form of the adopted molluscan shell. The conspicuous regimented motion of this particular species across beaches in the tropics has earned them the local name of 'soldachi' – 'soldiers' in translation. The nocturnal activity pattern presently reported confirms original observations made by Ball (1972) who reported that *C. compressus* became active at night in arid areas.

Activity

The rotating respirometer used in this study afforded us the unique ability to quantify voluntary locomotion in terms of time active, distance covered and running speed. There was a strong similarity between activity profiles in the laboratory and field. In the field at night, crabs were found as far as 24 m from their daytime retreat (Fig. 2), suggesting an upper limit of 48 m for a nightly excursion. The mean distance covered in laboratory trials was 53 m. Conservative estimates from transect data suggest that crabs moved at speeds anywhere from $0 \cdot 11 – 0 \cdot 58 \, \mathrm{cm \, s^{-1}}$. Mean speeds observed in the laboratory ($0 \cdot 6 \, \mathrm{cm \, s^{-1}}$) were at the upper end if this range. Compared to other terrestrial species these are moderate speeds. The fastest documented land crab is the ghost crab *Ocypode gaudichaudii* (Full & Herreid, 1983) which has a body mass of $2 \cdot 5 \, \mathrm{g}$ and can attain speeds of $21 \cdot 1 \, \mathrm{cm \, s^{-1}}$. Larger species such as *Gecarcinus lateralis* ($50 \, \mathrm{g}$) and *Cardisoma guanhumi* ($150 \, \mathrm{g}$) display running speeds around $4 \cdot 7 \, \mathrm{cm \, s^{-1}}$ (Herreid, Lee & Shah, 1979; Herreid *et al.* 1983). Full & Herreid (1984) attribute decreases in speed and endurance time to increase in body mass. While *C. compressus* has a mean body mass of $10 \cdot 5 \, \mathrm{g}$, the total mass transported is $20 \, \mathrm{g}$ due to the additional mass of the shell. Nonetheless the average speed reported is still comparatively low. Body length is another size criterion used in comparing exercise performance of different species. Based on the classification of Wood & Randall (1981*a*) a velocity of $0 \cdot 2 \, \mathrm{BL \, s^{-1}}$ in *Coenobita* would equate to 'moderate' exercise for *Cardisoma carnifex*. However, again work performed is not a simple function of BL in hermit crabs due to the load of the shell.

Crabs which fell into our category of 'high performers' (Fig. 3) maintained velocity throughout 3 h of activity. Based on physiological parameters which we subsequently measured (M. G. Wheatly, B. R. McMahon, W. W. Burggren & A. W. Pinder, in preparation) it is our opinion that exercise terminated in the laboratory as a consequence of natural activity patterns and not in response to any physiological limitation.

Respiratory gas exchange

Standard

Standard $\dot{M}_{O_2}$ agreed with values reported in other decapods at comparable

acclimation temperatures (see McMahon & Wilkens, 1983). The discovery that standard $\dot{M}_{O_2}$ correlated with WI (Fig. 4) was not altogether unexpected except that it was not a simple function of load rating. On transferring from a *Nerita* to an *Opeatostoma* shell, *Coenobita* increased the total load supported by only 25 % yet $\dot{M}_{O_2}$ increased by 2·6-fold. Most animals which carry shells are physically attached to them. In hermit crabs, the shell is held in various ways. The left uropod is enlarged and modified for hooking on to the columella of the shell. Contraction of the longitudinal abdominal muscles presses the surface of the abdomen against the inner wall of the shell and the last two pairs of legs are pushed against the wall of the shell opening. All of these gripping mechanisms are energetically expensive which means that there is a postural cost of shell habitation even when the animal is stationary. The increased cost of supporting visually larger or heavier shells is offset by the advantage afforded in territorial conflict (Hazlett, 1970).

Inactive $\dot{M}_{CO_2}$ has been reported in two other species of land crab (Herreid *et al.* 1979; Wood & Randall, 1981*a*). In both cases the respiratory quotient (RQ) measured in the gas phase was significantly less than unity, agreeing with the present findings. One major deficiency acknowledged in respiratory studies in land crabs is the extent to which branchial water is retained and subsequently used for CO_2 elimination. Based on low settled blood CO_2 tensions measured in another study (see M. G. Wheatly, B. R. McMahon, W. W. Burggren & A. W. Pinder, in preparation), the aquatic route could be a major pathway for CO_2 excretion in *Coenobita compressus*, and this would explain the spuriously low RQ values obtained in the gas phase. The problem may be exacerbated in hermit crabs since they have a greater volume of water at their disposal on account of the reservoir contained inside the whorls of the molluscan shell (see McMahon & Burggren, 1979; Wheatly, Burggren & McMahon, 1984). This being true, it is surprising that gaseous $\dot{M}_{CO_2}$ did not increase when crabs were removed from their shells. However animals were considerably traumatized in the process and so unloaded crabs were not truly quiescent. Wood & Randall (1981*a*) attribute the low RQ to retention of respiratory CO_2 for carapace information.

Active

Since our protocol involved intermittent sampling of a closed respirometer, it was not our original intention to determine the kinetics of gas exchange. However, the values we obtained at 30 min after the start of exercise did not increase significantly in the remaining two sampling periods and so 'steady-state' rates must have been attained within that time. Since we know that lactate did not accumulate appreciably (see M. G. Wheatly, B. R. McMahon, W. W. Burggren & A. W. Pinder, in preparation), the aerobic response to exercise was relatively fast. A rapid increase in $\dot{M}_{O_2}$ has been reported in response to submaximal exercise regimes in mammals (Cerretelli, Pendergast, Paganelli & Rennie, 1979), cockroaches (Herreid, Prawel & Full, 1981) and blue crabs (Booth *et al.* 1982). By comparison, the terrestrial crabs *Cardisoma* and *Gecarcinus* (Herreid *et al.* 1979, 1983) display sluggish and reduced aerobic responses. Booth *et al.* (1982) were able to demonstrate the rapidity of the response in *Callinectes* by recording scaphognathite and heart rates and O_2 extraction. Physiological recordings were made on 50-g hermit crabs by McMahon & Burggren (1979). However, reducing the tubing diameter in order to fit a 10-g crab with a

respiratory mask would undoubtedly increase resistance as well as being an energetic encumbrance. In the present investigation we therefore sacrificed this information in favour of obtaining reliable settled gas exchange data (see below and arguments raised by Herreid, 1981).

In *Coenobita* $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ were both proportional to velocity (Fig. 5) agreeing with a variety of other invertebrates (Herreid, 1981) and higher vertebrates (Taylor *et al.* 1970; Taylor, 1973; Fedak, Pinshow & Schmidt-Nielsen, 1974). Changes in gait can frequently explain a switch to a curvilinear relationship (Margaria, Cerretelli, Aghemo & Sassi, 1963). Minimum cost of transport (M_{run}) was calculated from the gradient of this line (Table 1) for all treatments. Expressed in terms of O_2 uptake, M_{run} has previously been determined for two other species of land crab – *Uca* (Full & Herreid, 1984) and *Ocypode* (Full & Herreid, 1983). Both species have a body mass around 2.5 g and an M_{run} value of 0.08 mmol $O_2 g^{-1} km^{-1}$ ($= 1.9$ ml $O_2 g^{-1} km^{-1}$). Since M_{run} characteristically decreases with body mass on a double log plot, it is surprising that the M_{run} values for *Uca* and *Ocypode* are less than half the values presently measured in unloaded *Coenobita* and must reflect some fundamental differences in muscular efficiency which makes the smaller crabs more agile.

Based on the original equation of Taylor *et al.* (1970) relating M_{run} (in ml $O_2 g^{-1}$ km^{-1}) to body weight (W in g) (i.e. $M_{run} = 8.64 W^{-0.4}$), a hermit crab of average mass 10.5 g should have an M_{run} value of 3.31 ml $O_2 g^{-1} km^{-1}$ ($= 0.131$ mmol $O_2 g^{-1} km^{-1}$). The value measured was 5.19 ml $O_2 g^{-1} km^{-1}$ ($= 0.206$ mmol $g^{-1} km^{-1}$), which is slightly higher than the value predicted from the empirical equation. This may relate to the unorthodox gait they exhibit. Careful observation revealed that hermit crabs brace the chelipeds in the substrate and drag the shell along in a fashion analogous to the use of handpoles by a skier. This mode of transport will increase frictional resistance and thereby energy expenditure (Denny, 1980). Together with data from Jensen & Holm-Jensen (1980) and Full & Herreid (1984), the present findings suggest that Taylor's original equation for vertebrates is applicable to a range of invertebrates. If M_{run} is a direct function of mass supported, then carriage of a 10-g shell should theoretically increase M_{run} to 6.62 ml $O_2 g^{-1} km^{-1}$ ($= 0.262$ mmol $O_2 g^{-1} km^{-1}$). The value measured in loaded hermit crabs was double this which suggests that it requires more energy to carry each gram of an imposed load than an equivalent unit of body mass (cf. Taylor, Heglund, McMahon & Looney, 1980).

The fact that extrapolated Y-intercept values for $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ showed good agreement with values measured in inactive crabs suggests that the voluntary exercise regime we employed did not unduly stress the animals. Classical treadmill techniques customarily report Y-intercept values 1.7-fold in excess of settled rates (Taylor *et al.* 1970; Herreid *et al.* 1979). This discrepancy may be attributed to problems with balance when speeds are involuntarily imposed in addition to elevation in basal metabolic rates by the use of respiratory masks and recording electrodes, etc.

When running at an average speed of 0.6 cm s^{-1}, loaded crabs increased $\dot{M}_{O_2}$ by 3.4-fold producing an aerobic metabolic scope (AMS) of 219μmol $O_2 kg^{-1} min^{-1}$. The majority of decapods studied have an aerobic factorial scope of 2.5–5.0 (see Table 1; McMahon, 1981) although Full & Herreid (1983) report a 12-fold increase in *Ocypode* which is more in line with exercising fish (Brett, 1972) and mammals (Taylor *et al.* 1980). Carbon dioxide flux in loaded crabs did not increase correspondingly (2.6

factorial) which had a profound effect on acid-base balance. This aspect of the study is further examined in another paper (M. G. Wheatly, B. R. McMahon, W. W. Burggren & A. W. Pinder, in preparation). The factorial scope would appear to be a function of loading since values of 1·6 × were obtained in unloaded crabs. Furthermore, $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ changed concomitantly in this group suggesting that the inequality in $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ in loaded crabs relates to the presence of the shell water.

Gross cost of transport decreased with velocity to an asymptote of M_{run} (Fig. 6) which is thus largely hypothetical since it is only ever approached at high speed. Interestingly it transpired that M_{run} was first attained at around $1·0\ cm\ s^{-1}$ which is close to the average velocity observed in the laboratory and in the field. Therefore crabs voluntarily elect to run at speeds which are least energetically expensive. Unloaded crabs could achieve the same energy economy at lower speeds which was exactly what we observed in laboratory trials (cf. Fig. 5).

Recovered

$\dot{M}_{O_2}$ recovered rapidly after the exercise bout as one would predict in the absence of an appreciable O_2 deficit. When water was made available during the recovery period it was used to replenish the branchial/shell reservoir and correct acid-base balance (see M. G. Wheatly, B. R. McMahon, W. W. Burggren & A. W. Pinder, in preparation). The intense period of exchange which ensued raised $\dot{M}_{O_2}$ but not to exercised levels. The presence of water during recovery facilitated CO_2 excretion so that $\dot{M}_{CO_2}$ recorded in the gas phase was reduced.

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