EXERCISE IN THE TERRESTRIAL CHRISTMAS ISLAND RED CRAB GECARCOIDEA NATALIS

II. ENERGETICS OF LOCOMOTION

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Summary

The respiratory and circulatory physiology of exercising Christmas Island red crabs Gecarcoidea natalis were investigated with respect to their annual breeding migration. Red crabs were allowed to walk for up to 45 min. During this exercise period, the functioning of the circulatory system in gas transport and the energy status of the red crabs were quantified.

Energy production during exercise required both aerobic and anaerobic contributions. The aerobic scope of G. natalis was low, with only a doubling of the resting rate of oxygen consumption (resting $M\dot{O}_2=95\pm15 \mu mol \ kg^{-1} \ min^{-1}$). Maximal $O_2$ consumption was attained within the first 5 min of exercise and the level remained stable thereafter. The anaerobic contribution to energy production was directly related to the speed of locomotion. $l$-lactate levels in blood and leg muscle were similar throughout the exercise period; blood lactate concentration was 33.39±2.29 mmol l$^{-1}$ after 45 min of exercise. Heart rate in resting animals was 56±7 beats min$^{-1}$. At the onset of exercise, heart rate also doubled, but without a significant increase in cardiac output. Increased $O_2$ delivery was facilitated by increased extraction from the blood.

During the 45 min of exercise, glucose levels increased rapidly in the muscle tissue (from 2.30±0.54 to 8.78±1.20 mmol l$^{-1}$) and subsequently in the blood (from 1.22±0.26 to 2.12±0.17 mmol l$^{-1}$), fuelling increased glycolysis during locomotion. The energy production from stored glucose/glycogen was sufficient to support the energetic needs of locomotion, since the energy charge remained stable at 0.82.

Haemolymph $l$-lactate levels in crabs sampled in the field after migration were high compared with levels in many crustacean species but equivalent to $l$-lactate levels in laboratory animals exercised for less than 10 min. During their migration, therefore, the red crabs avoid exceptional $l$-lactate build-up in the blood by either walking very slowly or intermittently. However, G. natalis are exceptionally well adapted to cope with exhaustive locomotion and the resultant severe metabolic acidosis.

Introduction

The Christmas Island red crab Gecarcoidea natalis must, like many other land crabs,

Key words: land crab, Gecarcoidea natalis, muscle, exercise, oxygen, anaerobiosis, locomotion.
complete an annual breeding migration to the ocean. The red crab may need to walk for several kilometres (Hicks et al. 1990; Hicks, 1985). Birds and mammals rely on aerobic metabolism to fuel locomotion during migration (reviewed by Bennett, 1978). Studies on the energetics of locomotion in crustaceans have concentrated on particular aspects of the respiratory physiology and have thus been limited in their conclusions. Many of these investigations have concentrated on O$_2$ consumption, with little consideration of anaerobic energy production (e.g. Herreid et al. 1983; Full and Herreid, 1983; Houlihan et al. 1985; Houlihan and Innes, 1984; Full, 1987). Similarly, heart rate has been used as an index of O$_2$ delivery to the tissues (Herreid et al. 1983) despite the fact that heart rate is often poorly correlated with cardiac output (McMahon, 1981; Booth et al. 1982; Hamilton and Houlihan, 1992). Furthermore, some workers have concentrated on measuring the extraction of O$_2$ per volume of air/water (Batteron and Cameron, 1978; Herreid et al. 1983; O’Mahoney and Full, 1984) without any specific consideration of O$_2$ use by the tissues.

Several aspects of locomotion in crustaceans have, however, been well established. Endurance capacity has been shown to decrease with speed of locomotion (Wood and Randall, 1981; Houlihan et al. 1984), and anaerobic metabolism contributes to energy production during exercise in most species (Booth et al. 1982; Greenaway et al. 1988; Forster et al. 1989; Hamilton and Houlihan, 1992). Heart rate generally increases in response to exercise, and the cardiac pauses characteristic of rested animals cease with the onset of locomotion (Smatresk and Cameron, 1981; Herreid et al. 1983; Morris and Taylor, 1984, 1985).

The contributions of respiration and anaerobiosis are determined by the limitations of the gas-exchange organs and the circulatory system in delivering O$_2$ to the tissues or by limitations on O$_2$ diffusion into the tissues. Examples are few, but in the terrestrial Birgus latro, locomotion is limited by the diffusion of O$_2$ into the tissues (Morris et al. 1987, 1988; Greenaway et al. 1988). However, in the aquatic Calinectes sapidus, anaerobiosis appears to be important only during the initial few minutes of activity (Booth and McMahon, 1985, 1992).

Glycogen is the primary fuel source in exercising crustaceans (Herreid and Full, 1988). Although glucose is the major carbohydrate constituent in the haemolymph (Telford, 1968a), its concentration varies greatly between species and individuals (Telford, 1968b; Chang and O’Connor, 1983). Brief bursts of activity such as an ‘escape responses’ may be fuelled initially by arginine phosphate, while sustained exercise must be fuelled by tissue ATP stores (Herreid and Full, 1988).

There are no data available on the changes in high-energy phosphate levels in crustaceans during locomotion. This study investigates metabolic substrate utilisation and energy production in G. natalis, the contribution of aerobic and anaerobic energy production, the function of the circulatory system during exercise and the ability of G. natalis to maintain levels of high-energy phosphates during sustained locomotion. Some of the possible limitations on energy production were considered and the data were interpreted with respect to information on blood function and acid–base status (Adamczewska and Morris, 1994) and with reference to the ecology and ethology of the red crabs.
Materials and methods

*Gecarcoidea natalis* were collected under Australia Nature Conservation Agency (ANCA) permit from Christmas Island and maintained as described previously (Adamczewska and Morris, 1994). Prior to experiments, animals were isolated overnight in darkened respiratory chambers supplied with water-saturated air, with no access to food or water. Resting animals were sampled directly from the chambers whereas exercised animals were allowed to walk at the speed of their own choosing in an arena, marked with a grid, for 5, 10, 20 or 45 min before sampling. Simple tactile stimulation was sufficient to encourage the crabs to continue walking during prolonged exercise periods. Locomotion was recorded with a video camera (Sony, CCD-AU230) and subsequently analyzed to determine actual walking speed.

Aerobic metabolism

Oxygen consumption rates (\(M_{O_2}\)) were measured using flow-through respirometry at 20 ml min\(^{-1}\) for rested animals and 60 ml min\(^{-1}\) for exercised animals. Animals were placed in cylindrical respiratory chambers (diameter 10 cm and length 15 cm) placed in an incubator thermostatted at 25±0.2 °C, supplied with humidified air (95–100 % relative humidity). Steady-state oxygen uptake, \(M_{O_2}\), sampled every second, was recorded using an Applied Electrochemistry O\(_2\) analyser (Amatek) and DATACAN V data-logging software (Sable Systems).

Humidified room air was passed through the respiratory chambers and sampled once per second with a precision of 0.01 % O\(_2\). For control purposes, the background oxygen consumption (\(M_{O_2}\)) of the respirometer was determined by comparing the air from the respirometer with that of an empty unused chamber after the measurement of O\(_2\) consumption of the quiescent animals. Washout time of the chamber (the time required for the air in the chamber to be completely exchanged) was determined by injecting a 30 s nitrogen pulse. Recordings for the exercised animals were transformed to provide ‘instantaneous’ \(M_{O_2}\) measurements (Bartholemew *et al.* 1981).

Heart rate

Heart rate was measured using an impedance method previously used for crustaceans (Morris and Taylor, 1984). Ten animals were used and each animal was exercised for 45 min. For the purpose of statistical analysis, two animals were randomly assigned to each sample time to ensure that the data were independent.

Cardiac output

Cardiac output was estimated to provide rate of blood flow around the body according to the Fick principle:

\[
\dot{Q} = \frac{M_{O_2}}{([O_2]_a - [O_2]_v)},
\]

where \(\dot{Q}\) is cardiac output (ml kg\(^{-1}\) min\(^{-1}\)), \(M_{O_2}\) is oxygen uptake rate (\(\mu\)mol kg\(^{-1}\) min\(^{-1}\)), [O\(_2\)]\(_a\) is the oxygen content of pericardial blood (mmol l\(^{-1}\)) and [O\(_2\)]\(_v\) is the oxygen content of venous blood (mmol l\(^{-1}\)) using the O\(_2\) contents of arterial and venous blood from Adamczewska and Morris (1994), together with mass-specific mean.
O₂ values (sampling animals in respirometers would introduce a further disturbance factor to $M_\text{O}_2$).

**Anaerobic metabolism – lactate production**

Haemolymph for L-lactate analysis was mixed with an equal volume of 6% perchloric acid and then $K_2CO_3$ (2.5 mol$^{-1}$) was added in the ratio of 2.5. The tubes were then frozen until analysis. The L-lactate content of the blood and leg muscle homogenate (see below for tissue preparation) was measured using a test kit (Boehringer Mannheim, no. 139 084) and an ultraviolet/visible spectrophotometer (Pharmacia LKB Ultraspec III) interfaced with an 80826 computer system running BIOCHROM kinetics software.

**Tissue acquisition and preparation**

Six animals were exercised at each of 0, 5, 10, 20 and 45 min (total $N$=36). After the allotted time, each animal was encouraged to autotomise one leg. The flesh separated from the exoskeleton was wrapped in prelabelled aluminium foil and then immediately frozen in liquid nitrogen and stored at $-70^\circ C$. The time from removal of the leg to freezing in liquid nitrogen was always less than 120 s.

Each muscle sample collected was analyzed in duplicate for the following: (1) ATP; (2) ADP and AMP; (3) muscle L-lactate; (4) glycogen; (5) muscle glucose. Absorbances for all assays were measured using the Ultraspec III spectrophotometer.

Frozen tissue was powdered in a ceramic mortar with liquid nitrogen, homogenised with $HClO_4$ and neutralised with $K_2CO_3$ as specified in Bergmeyer (1985a). The ATP content was determined using the Sigma ATP test kit (no. 366 UV). All solutions used in assays for determination of ADP and AMP were obtained from Boehringer Mannheim and the assay procedure used was as described in Bergmeyer (1985a).

Glucoamylase was used to hydrolyse muscle homogenates, which were then analysed for total glucose content. Background glucose of the homogenate was also measured in every sample prior to glucoamylase digestion using the techniques described in Bergmeyer (1985b). Blood glucose levels were measured using a glucose test kit (Sigma Diagnostics, no. 510).

**Field haemolymph L-lactate measurements**

Blood samples from pre-migratory animals resting in their burrows were obtained for measurement of L-lactate. In addition, red crabs were sampled for blood lactate at two sites near the coast after they had completed the journey from the forest. All samples for L-lactate determination were immediately deproteinised in the field.

**Results**

**Oxygen consumption**

The rate of O₂ consumption in resting animals was $95.4\pm15.6 \mu\text{mol kg}^{-1} \text{ min}^{-1}$ and increased significantly to $211.6\pm34.6 \mu\text{mol kg}^{-1} \text{ min}^{-1}$ (ANOVA, $F_{4,28}=6.498$) at the onset of exercise. There were no further significant increases during the entire subsequent exercise period (Fig. 1).
Heart rate

Heart rate also increased significantly (ANOVA, $F_{4.5}=29.08$) from a mean of 56 beats min$^{-1}$ in the resting animals to 120 beats min$^{-1}$ at the onset of exercise. Heart rate also remained relatively constant during the exercise period (Fig. 2). The heart rate of quiescent animals showed periods of pronounced bradycardia and even complete cessation of beating (Fig. 3A) in some individuals. Heart beat in exercised animals was always continuous (Fig. 3B).

Cardiac output

Calculated cardiac output increased from 466.8±76.4 ml kg$^{-1}$ min$^{-1}$ in the resting...
animals to 595.4±71.1 ml kg\(^{-1}\) min\(^{-1}\) in animals exercised for 20 min (Fig. 4), but never became significantly elevated above initial rates (\(P=0.2\)).

**L-Lactate**

The haemolymph \(l\)-lactate concentration increased significantly after 5 min of exercise (ANOVA, \(F_{4,32}=36.181\)). \(l\)-Lactate level continued to increase during the exercise period.
from 0.79±0.14 mmol l$^{-1}$ in resting animals to 33.39±2.29 mmol l$^{-1}$ after 45 min of exercise (Fig. 5).

Muscle L-lactate concentration in the resting animals was 6.05 mmol kg$^{-1}$ tissue (Fig. 5). Muscle lactate levels increased steadily during the exercise period, becoming significantly elevated compared with the initial resting state (ANOVA, $F_{4,25}=10.26$) at 10 min, with a further significant increase after 20 min. Maximum recorded L-lactate levels were achieved at 45 min, reaching 37.37±5.73 mmol kg$^{-1}$.

**Metabolic substrates**

Blood glucose content remained relatively stable during the first 20 min of exercise, ranging from 1.08 to 1.22 mmol l$^{-1}$, but increased significantly (ANOVA, $F_{4,54}=5.541$) to 2.12±0.17 mmol l$^{-1}$ after 45 min of exercise (Fig. 6).

Resting muscle glucose content was 2.30±0.54 mmol kg$^{-1}$ and increased significantly after 10 min of exercise to 5.15±1.45 mmol kg$^{-1}$, and again after 20 min, reaching a concentration of 9.5 mmol kg$^{-1}$ (ANOVA, $F_{4,25}=9.24$) (Fig. 6). In contrast, the glycogen content (measured in glycosyl units) showed no significant change during the exercise period (Fig. 7). The mean glycogen levels varied from 230.4±34.7 mmol kg$^{-1}$ in quiescent red crabs to 265.3±60.5 mmol kg$^{-1}$ in crabs exercised for 10 min and decreased gradually to 200.4±24.9 mmol kg$^{-1}$ after 45 min of exercise.

**Walking speed**

Initial walking speeds were relatively high (mean 0.48±0.04 km h$^{-1}$) (Fig. 8), but decreased rapidly (ANOVA, $F_{4,25}=42.49$, $P<0.05$) during the first 5 min of exercise to 0.22±0.02 km h$^{-1}$, and then more slowly to 0.14±0.01 km h$^{-1}$ after 45 min of exercise (significant at $P=0.08$).

**Field values**

Blood lactate content of the red crabs in their natural environment showed similar
trends to those of the laboratory study. Blood L-lactate levels of rested pre-migratory crabs were significantly lower than those in animals that had just arrived at the coast (ANOVA, $F_{2,25}=20.69$) (Fig. 9). Furthermore, animals sampled at site A had significantly higher L-lactate concentrations than the animals sampled at site B ($P<0.05$). The two sampling sites differed in the amount of vegetation cover. Site A was very exposed and the animals had to travel a much longer distance in direct sunlight than at site B.
The ATP levels in the walking muscle were the highest of all the adenylates measured, averaging 2.06 mmol g$^{-1}$ tissue, and remained constant during 45 min of exercise (Fig. 10). The mean ADP concentration was approximately half that of ATP. After 10 min, the ADP content increased significantly to 1.31±0.12 mmol g$^{-1}$ compared with the resting value of 0.95±0.07 mmol g$^{-1}$ (ANOVA, $F_{4,25}=3.366$). The AMP levels were

**Adenylate content and energy charge**

Fig. 8. Voluntary walking speed (km h$^{-1}$) in *Gecarcoidea natalis* during a 45 min exercise period ($N=6$).

Fig. 9. Field data. Blood l-lactate concentration in *Gecarcoidea natalis* prior to migration at two different sites after migrating to the coast (sites A and B) and in resting pre-migratory conditions, while the crabs were in their burrows. Site A had less vegetation cover than site B; consequently, the crabs had to traverse more exposed area in direct sunlight and at a lower humidity ($N=8$).
comparatively very low, reaching a maximum of $0.10 \pm 0.03$ mmol g$^{-1}$ tissue after 20 min of exercise, which was significantly greater than the resting value of $0.01 \pm 0.00$ mmol g$^{-1}$ (ANOVA, $F_{4,25} = 3.11$). These differences in the individual adenylates, however, were not reflected in the ‘energy charge’, which remained stable between 0.80$\pm$0.02 and 0.84$\pm$0.01 during the entire exercise period. The total adenylate concentration (calculated as the sum of ATP, ADP and AMP concentrations for each animal) was uniform in all groups of animals, except for the group after 10 min of exercise, which had a significantly higher adenylate content (ANOVA, $F_{4,25} = 3.94$).

**Discussion**

**Aerobic energy production**

Sustained locomotion, such as a migration, must be fuelled by aerobic metabolism, since anaerobic metabolism imposes an $O_2$ debt that must be repaid. A rapid increase in $M_O\text{O}_2$ to a new steady state is characteristic of primarily aerobic energy production in terrestrial crustaceans, vertebrates and insects (e.g. Herreid, 1981; Full, 1987; van Aardt, 1991).

Factorial aerobic scope (FAS) is equal to maximal $M_O\text{O}_2$/resting $M_O\text{O}_2$ and may be as high as 12 in some crustaceans such as ghost crabs, *Ocypode quadrata* (Full and Herreid, 1987).
Full, 1987). Available data for a range of crabs suggest that larger air-breathing crabs have a greater FAS (Fig. 11) and thus migrating *G. natalis* might be expected to exhibit a high FAS. However, *G. natalis* utilised anaerobiosis in addition to respiration from the onset of exercise and the elevated $\dot{M}O_2$ stabilised within the first 5 min of exercise (Fig. 1) with an FAS of only 2. This is low even for crustaceans, the majority of which tend to have low aerobic scopes (FAS=3–5) and to supplement anaerobic energy production during exercise (Full and Herreid, 1984; Booth and McMahon, 1985; Greenaway et al. 1992). Interestingly, low FAS has been previously associated with an absence of a steady-state $\dot{M}O_2$ in *Uca pugilator* (Full and Herreid, 1984), *Cardisoma guanhumi* (Herreid et al. 1979) and *Gecarcinus lateralis* (Herreid et al. 1983).

The resting $M_O_2$ (5.72 $\mu$mol g$^{-1}$ h$^{-1}$) of *G. natalis* was relatively high compared with that of other species of air-breathing decapods, but after exercise it was similar to the $M_O_2$ of other exercised crabs (Fig. 11). Thus, the low FAS of 2 in *G. natalis* compared with a ‘mean’ FAS of 6.1 for a 250 g air-breathing crab (derived from Fig. 11) appears to be the result of a high resting metabolic rate. The quiescent laboratory animals exhibited exactly the same venous $P_O_2$ as animals sampled in their burrows on Christmas Island.
Heart rate and cardiac output

Active crustaceans generally exhibit higher heart rates and/or stroke volumes as well as increased ventilation rates (Cameron and Mecklenburg, 1973; reviewed by Wilkens, 1981; Wood and Randall, 1981; Booth et al. 1982). In G. natalis, heart rate doubled in response to exercise but without a clear increase in cardiac output, possibly as a result of incomplete diastolic filling at higher heart rates (reviewed by Wilkens, 1981). The relatively constant cardiac output contrasts with previous studies on a variety of crustaceans (McMahon et al. 1979; Booth et al. 1982; Hamilton and Houlihan, 1992) and, therefore, in exercising G. natalis increased $\dot{M}O_2$ appears to be exclusively facilitated by increased O$_2$ uptake from the blood during passage through the tissues (Adamczewska and Morris, 1994). Tissue perfusion rate is an obvious limitation to the aerobic capacity in red crabs, and the apparent inability of G. natalis to increase the rate significantly requires further more detailed study.

Energetics of locomotion

Despite a low adenylate pool in the leg muscle of G. natalis compared with that of other species (e.g. Beis and Newsholme, 1975), the relatively constant levels of ATP, ADP and AMP indicate that ATP synthesis satisfied energy demand during the 45 min exercise period. The energy charge (0.82) was comparable to that found in fish experiencing environmental hypoxia (Pelster, 1985; Pelster et al. 1988).

Anaerobiosis made an important contribution in exercising red crabs and haemolymph L-lactate concentrations after 45 min were among the highest reported for any crustacean.
(mean 33.4 mmol l\(^{-1}\)). Haemolymph \(\text{L-lactate}\) concentrations in post-exercise crabs have usually been near 10 mmol l\(^{-1}\) or less (McMahon, 1981; Booth and McMahon, 1985; Hamilton and Houlihan, 1992; Greenaway et al. 1992). However, high blood \(\text{L-lactate}\) concentrations exceeding 25 mmol l\(^{-1}\) have been reported for \(B. \text{latro}\) after 30 min of exercise (Greenaway et al. 1988) and values of 20 and 44 mmol l\(^{-1}\) have been reported in the haemolymph and levator muscles, respectively, of \(\text{Callinectes sapidus}\) (Milligan et al. 1988). Anaerobiosis is relatively inefficient and requires proportionally more metabolic fuel. Glucose is the major component of circulating carbohydrates in crustaceans, but its concentration varies markedly between species (Chang and O’Connor, 1983). No measurements of glucose levels during controlled exercise in crustaceans are available, but blood glucose levels have been shown to increase in response to stress in \(\text{Homarus americanus}\) from 0.59 to 0.71 mmol l\(^{-1}\) (Telford, 1968a) and in \(\text{Palaemon}\) in response to environmental hypoxia (Taylor and Spicer, 1987). Muscle glucose levels in \(G. \text{natalis}\) increased in response to increased metabolic demand. Thus, the red crabs appear to be adapted to sustaining anaerobiosis to the point of severe acidification.

Glycogen stores have been identified in several tissues of crustaceans, including gonads, abdominal muscle, gills, integumentary tissue and muscles (Keller and Andrew, 1973; Herreid and Full, 1988). Glucose from any of these stores could fuel metabolism during locomotion, but an increase in tissue glucose levels prior to an increase in blood glucose level (Fig. 6) implicates muscle glycogen mobilisation.

The proportion of energy produced by aerobic and anaerobic metabolism can be calculated by examining the consequences of glycolysis with and without \(O_2\) as a terminal acceptor in the electron transport chain.

\[
\text{Aerobic} \quad 6O_2 + C_6H_{12}O_6 \rightarrow 6CO_2 + 6H_2O + 38\text{ATP},
\]

\[
\text{Anaerobic} \quad C_6H_{12}O_6 \rightarrow 2\text{L-lactate} + 2\text{ATP}.
\]

Using the measured oxygen consumption rates and the amount of lactate produced, it is possible to calculate the rate of ATP production. If glycogen is the fuel source, then 1 mole of \(O_2\) consumed results in the production of 6.33 moles of ATP, and every mole of \(\text{L-lactate}\) is accompanied by the production of 1.5 moles of ATP (Full and Herreid, 1984). Despite its inefficiency, anaerobic metabolism supplements energy production in many crustaceans (reviewed by Herreid, 1981; Herreid and Full, 1988).

The rate of \(\text{L-lactate}\) efflux from the muscles in \(G. \text{natalis}\) was such that the haemolymph and tissue concentrations were similar throughout the exercise period. Red crabs could not be killed in order to measure whole-body lactate and therefore \(\text{L-lactate}\) concentrations were extrapolated to total body tissue concentrations and used to estimate anaerobic energy production. During the first 10 min of exercise, anaerobic metabolism contributed most of the ATP (Fig. 12). However, after 20 min of exercise, the rate of ATP production stabilised and anaerobiosis contributed less than half of the total ATP (Fig. 12).

The extent of anaerobiosis in \(G. \text{natalis}\) appears to be related to the speed of locomotion, in contrast to previous studies where \(M_\text{O2}\) increased with speed of locomotion in crabs travelling at speeds of 0.13–0.28 km h\(^{-1}\) (Full and Herreid, 1983).
Thus, it appears that aerobic metabolism in red crabs was limited by the rate of O\textsubscript{2} diffusion from the blood into the tissues. The stabilised rate of ATP turnover between 20 and 45 min of exercise was a product of constant rates of anaerobiosis and respiration. However, three variables indicated that after 45 min of exercise the red crabs had become fatigued. After 45 min, the rate of anaerobic ATP turnover increased slightly, accompanied by a slight decrease in the aerobic ATP turnover (Fig. 12). At the same time, the arterial–venous O\textsubscript{2} difference declined slightly, indicating reduced O\textsubscript{2} extraction by the tissues (Adamczewska and Morris, 1994).

The endurance capacity of crustaceans is variable, as is the contribution of aerobic and anaerobic energy production during locomotion (Full and Herreid, 1984; Full et al. 1985). Furthermore, the speed of locomotion is inversely related to endurance (Wood and Randall, 1981; Full and Herreid, 1984; Houlihan et al. 1984), and therefore it is difficult to make direct comparisons between crabs exercised on treadmills (where the speed of locomotion is fixed and thus somewhat unnatural) and the results obtained in this study, in which the red crabs were allowed to walk at their chosen speed (speed variable but greater than 1.3 km h\textsuperscript{-1}). G. natalis appears to be unusual in exhibiting relatively high endurance capacities but low aerobic scope (Fig. 11), supplemented by high anaerobic capacity. Booth and McMahon (1992) found that exercising Callinectes sapidus exhibited an FAS of between 4 and 5 with only transient anaerobiosis at the onset of exercise, suggesting that this FAS is clearly adequate for Callinectes.

Although there are no estimates for migrating crabs, the slow walking speeds (<0.07 km h\textsuperscript{-1}) observed in the field (A. M. Adamczewska and S. Morris, personal observations) for non-migrating red crabs, together with the lactate levels (post-migratory \(\leq 5\) mmol l\textsuperscript{-1}), indicate that the laboratory exercise regime to which G. natalis was subjected may be more indicative of the response to interactions with predators or conspecifics but may not be directly representative of migratory locomotion. However, the strenuous exercise regime did test the locomotor capacity of red crabs. Thus, it seems likely that migrating red crabs either walk at speeds less than 1.3 km h\textsuperscript{-1} or travel intermittently during their migration, for periods of less than 10 min, followed by periods of rest when the O\textsubscript{2} debt is repaid. Intermittent locomotion has been reported to increase distance capacity in ghost crabs (Weinstein and Full, 1991).

Cost of migration

During their annual migration, the red crabs must walk several kilometres to reach the shore (maximum 8 km). To walk a distance of 4 km at an average speed of 0.14 km h\textsuperscript{-1} the crabs would have to walk for just over 28 h. Using the formula for complete glucose combustion (see above) and the rate of O\textsubscript{2} consumption (Fig. 1), the amount of glucose consumed aerobically during 1 h of walking by a red crab is estimated to be 2.2 mmol kg\textsuperscript{-1}, therefore, in 28.6 h, 63 mmol kg\textsuperscript{-1} of glucose would be consumed. If anaerobiosis proceeded at the stabilised rate achieved between 20 and 45 min of exercise (0.73 mmol ATP kg\textsuperscript{-1} min\textsuperscript{-1}) (Fig. 12), the anaerobic contribution to metabolism would require a further 636 mmol kg\textsuperscript{-1} glucose. A total of approximately 700 mmol kg\textsuperscript{-1} would be required for the migration, which is 2–3 times the amount of glucose found in the muscle glycogen reserves of red crabs.
Obviously L-lactate does not continue to accumulate in the body indefinitely and it is eventually reoxidised to pyruvate and utilised in respiration. A closer approximation of the cost of the migration would, therefore, be obtained by examining the amount of glucose that would be consumed, assuming that all the energy was produced aerobically. The stabilised rate of ATP production between 20 and 45 min of exercise (2.16 mmol kg\(^{-1}\) min\(^{-1}\)) would result in 3.71 mol kg\(^{-1}\) ATP being produced during a 28.6 h migration at the speed of 1.4 km h\(^{-1}\). If this ATP were produced aerobically, 481 mmol kg\(^{-1}\) O\(_2\) and 80 mmol kg\(^{-1}\) glucose would be consumed in the process. This is substantially less than the 700 mmol kg\(^{-1}\) estimated using the aerobic and anaerobic contributions to energy production. Therefore, the glycogen stores in the muscle of G. natalis are a substantial energy reserve for the migration and the associated breeding activities. This has obvious implications for resource use during the migration, especially the need to feed. G. natalis have been observed to feed during their migration on vegetable matter as well as scavenging on dead comrades.

Although the glycogen stores measured in the muscle are obviously not representative of values in the other body tissues, the muscle stores are probably sufficient to fuel the energy needs during the migration. Aside from the actual cost of migration, the red crabs face the costs associated with reproduction, such as mating, male combat, burrow defence and egg production and brooding as well as the return journey to the forest after the mating season (Hicks, 1985; Hicks et al. 1990). The red crabs appear to be well equipped in energy stores for their migration, considering that glycogen reserves are not their sole energy source during their migration.

In summary, anaerobic energy production during exercise in G. natalis causes significant haemolymph acidosis. Substrate mobilisation and ATP turnover (anaerobic and aerobic) were increased to meet the energy needs of the crabs during walking. An apparent limitation to the locomotory capacity of G. natalis is the inability to increase cardiac output, limiting O\(_2\) delivery to the tissues. Field data suggest that G. natalis attempt to minimise metabolic acidosis, although L-lactate level does rise to 5 mmol l\(^{-1}\). The migration must occur at a slow pace and the crabs appear to travel intermittently. Field work on these animals, although difficult, is imperative. Human activities on Christmas Island have resulted in clearing of the rainforest and red crabs travelling to and from the ocean also face the danger of debilitating dehydration. The role of hydration state and environmental humidity in controlling the activity of these animals also requires detailed study. More work is required in determining the limitation of aerobic metabolism in G. natalis. Furthermore, recovery from exercise must be investigated as well as intermittent locomotion with respect to endurance and distance capacity.

This study currently provides, however, the most complete investigation of the functions and interactions of the respiratory and circulatory systems and the limitations placed on the locomotor ability of a crustacean.

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References


