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Specific dynamic action and the metabolism of the brachyuran land crabs *Ocypode quadrata* (Fabricius, 1787), *Goniopsis cruentata* (Latreille, 1803) and *Cardisoma guanhumi* Latreille, 1825

Warren W. Burggren [a], Gloria S. Moreira [b] and Maria do Carmo F. Santos [b]

[a] *Department of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, Nevada, USA;* [b] *Instituto de Biociências and Centro de Biologia Marinha, Universidade de São Paulo, São Paulo, Brazil*

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Abstract: Oxygen uptake ($\dot{M}O_2$) was measured in the terrestrial crabs *Ocypode quadrata* (Fabricius, 1787), *Goniopsis cruentata* (Latreille, 1803) and *Cardisoma guanhumi* Latreille, 1825 as a function of digestive state to determine the magnitude and time course of specific dynamic action (SDA). Following 5 days of feeding ad libitum on fish flesh, "steady-state" $\dot{M}O_2$ was about 2.8, 1.0 and 1.6 $\mu m \cdot g^{-1} \cdot h^{-1}$ in *Ocypode* (29–31 °C), *Goniopsis* (23–25 °C) and *Cardisoma* (29–31 °C), respectively. After 5 days of fasting, "steady-state" $\dot{M}O_2$ was decreased greatly to 1.0 and 0.5 $\mu m \cdot g^{-1} \cdot h^{-1}$ in *Ocypode* and *Cardisoma*, respectively, but was not significantly changed from feeding values in *Goniopsis*. Time-course experiments indicated that the peak in $\dot{M}O_2$ following a single large meal occurred within 8 h in both *Ocypode* and *Cardisoma*. The apparent SDA persisted for longer than 50 h in *Cardisoma*, but less than 42 h in *Ocypode*. These data show that an apparent SDA of large magnitude and variable time course can occur in land crabs. However, the absence of any apparent SDA effect in *Goniopsis* indicates that it is not a necessary accompaniment to feeding in all terrestrial brachyurans, and must be verified on a species-by-species basis.

Key words: Crab; Feeding; Metabolism; Oxygen uptake; Specific dynamic action

Introduction

The stimulation of metabolism produced by food ingestion (specific dynamic action or SDA) was initially described in man, domesticated mammals and fishes, but in recent years this metabolic phenomenon has been documented in a variety of invertebrates including crustaceans (Newell et al., 1974; Aldrich, 1975; Hiller-Adams & Childress, 1983; Nelson et al., 1985; Carefoot, 1987, 1990) and mollusks (Thompson & Bayne, 1972; Bayne & Scullard, 197; Crisp et al., 1978; Kiörboe et al., 1985; Nelson et al., 1985; Gaffney & Diel, 1986). The observation of SDA in very divergent lineages within both vertebrates and invertebrates strongly suggests that metabolic effects of food ingestion, digestion and subsequent protein synthesis are general components of animal metabolism rather than specialized responses that have evolved only in certain taxa.

Correspondence address: W.W. Burggren, Department of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, NV 89154, USA.

The consequences of SDA are recognized by almost all researchers that measure metabolic rate, and so the condition of animals during the experiments (prandial, postprandial, etc.) is usually carefully controlled for and clearly stated. However, at least for the measurement of metabolic rates in crustaceans, there is no "standard" condition used in the literature. Some data are reported for animals allowed to feed ad libitum, while others are reported for animals starved for variable periods of time, which may or may not reflect a true "steady-state" metabolic rate. Since the magnitude and time course of SDA varies considerably between species in the Crustacea, the availability of food becomes a highly important variable in attempting to make intraspecific comparisons of metabolic rate. Moreover, SDA is only one component of the "apparent SDA" (Beamish, 1974), which includes the mechanical metabolic costs of feeding (transport of material through the gut, handling of food) and the increase of activity or excitement level during feeding as well as the actual stimulation of protein synthesis.

In recent reviews of the metabolic rate of terrestrial brachyuran crabs, neither McMahon & Burggren (1988) nor Herreid & Full (1988) could ascertain any clear difference in the metabolism of land crabs compared with marine crabs, in part because of considerable apparent variation in resting oxygen consumption between terrestrial species. Yet, respiratory and circulatory specializations in terms of the physiological processes that support metabolism are evident in land crabs. Either these specializations do not translate into clear differences in metabolic rate, or else the introduction of apparent SDA as an unintentional experimental variable has masked true metabolic differences between marine and terrestrial brachyurans. At present, this dilemma cannot be resolved because, to our knowledge, the magnitude and time course of apparent SDA in terrestrial brachyuran crabs has not been documented.

Consequently, the present study was designed to determine apparent SDA in 3 species of land crabs – the ghost crab *Ocypode quadrata* (Fabricius, 1787), the mangrove crab *Goniopsis cruentata* (Latreille, 1803), and the blue land crab *Cardisoma guanhumi* (Latreille, 1825). All 3 species are omnivorous and include some of the same food items in their natural diet. Resting, undisturbed individuals of all 3 species were alternatively fasted and fed the same protein-rich diet, while measurements of oxygen uptake were made. The magnitude and time course of the metabolic effects of feeding were determined using an identical experimental protocol, allowing an interspecific determination of apparent SDA.

MATERIALS AND METHODS

ANIMALS

Experiments were performed on 3 species of terrestrial crab: the ghost crab *Ocypode quadrata* ($n = 26$), the mangrove crab *Goniopsis cruentata* ($n = 17$) and the blue land crab,

Cardisoma guanhumi ($n = 12$). Adult intermolt crabs were collected at low tide in Saõ Paulo State, Brazil during the months of January and February, 1990, as described previously by Santos et al., 1989. *Ocypode quadrata* were collected at night from the intertidal zone of a fine sand shore, Guaecá Beach (23° 49′ S: 45° 27′ W). Air temperature during the time of collection varied from 28–33 °C; seawater salinity remained around 35‰. *Goniopsis cruentata* and *Cardisoma guanhumi* were collected in the mangrove area around Guaratuba Beach (23° 44′ S: 45° 54′ W). When active on the surface, *Cardisoma guanhumi* appears in more open areas of the mangrove exposed to more solar insolation (air temperatures above 30 °C). *Goniopsis cruentata* is found in the cool, shaded regions of the mangrove trees, where temperatures are about 25 °C and mangrove water salinities vary from 6 to 33‰ (Martinez, 1989; M.C.F. Santos, pers. obs.).

All crabs were transported to the laboratory (Centro de Biologia Marinha) in Saõ Sebastiaõ, S.P. and were maintained individually in separate containers containing 1–2 cm of 25% seawater (*Goniopsis* and *Cardisoma*) or were given free access to both 25% seawater and 100% seawater (*Ocypode*). Although water in the burrows of some land crabs is known to approach fresh water (see Greenaway, 1988), it was at least 50% seawater in all land crab burrows in the area in which the crabs used in this study were collected. All *Goniopsis* were maintained and measured at 22–25 °C, while all *Ocypode* and *Cardisoma* were maintained and measured at 29–31 °C. These temperatures approximated those measured in their natural environment at the time of capture while feeding on the surface. Burrow temperatures were not measured in this study, but have been found to be about 25 °C (Martinez, 1989).

Prior to beginning of the experimental protocol, crabs were fed fish daily, which was readily eaten by all 3 species. *Cardisoma* is often regarded as primarily a herbivore in Southern Florida (Herreid, 1963), but is frequently observed eating meat in Bermuda (Verrill, 1908) and at the site of collection in Brazil in the present study.

EXPERIMENTAL PROTOCOL

An identical experimental protocol was followed for all 3 species.

Oxygen consumption ($\dot{M}O_2$) and digestive state

While fasting is a necessary component of studies that investigate SDA, starvation over several days could lead to cumulative or long-term metabolic or biochemical changes that are not quickly reversed even by feeding, and which consequently could mask or otherwise alter the measurement of SDA. To control for any possible long-term effects of fasting, an experimental protocol was designed in which crabs of each species were divided into two separate experimental groups, Group 1 and Group 2, and were then fasted and fed in reverse order. Initially, Group 1 was fed fish ad libitum for a period of 5 days, while Group 2 was maintained under identical conditions except

that they were not fed. At the end of 5 days, all crabs from both groups were placed in respirometers (see below) and left undisturbed for 12–14 h. Small pieces of fish were placed in the respirometers for the crabs in Group 1, so that they could continue to feed during the period of acclimation to the experimental apparatus. Following the acclimation period, two sequential measurements of oxygen consumption ($\dot{M}O_2$) were made on both Group 1 and Group 2 as described below.

Following these first metabolic measurements, the conditions for Groups 1 and 2 were reversed, that is, food was withheld for 5 days from the crabs that previously comprised the fed group (Group 1), and the crabs that had been fasting were now fed fish ad libitum. At the end of 5 days of this new feeding/fasting regime, the crabs were placed once again in the respirometers and left undisturbed for 12–14 h, after which two sequential measurements of $\dot{M}O_2$ were made.

Thus, for each species, there were measurements of $\dot{M}O_2$ for two groups of crabs, both groups experiencing 5 days of feeding and 5 days of fasting, but in reverse order to the other group. This experimental design would reveal if fasting had any long-term effects on $\dot{M}O_2$ not reversible in the short term by feeding.

Time course of MO_2 changes associated with digestive state

A separate group of experiments was designed to determine the time course of changes in $\dot{M}O_2$ associated with feeding and fasting. A group of crabs from each of the 3 species was denied food for 5 days. At the end of this fasting period, all fasting crabs were placed individually in respirometers for 12–14 h to acclimate (crabs were not fed during this time). An initial measurement of $\dot{M}O_2$ was then made to determine the steady-state fasting rate. Small pieces of fresh fish were then gently introduced through a small port in the lid of the respirometer (see below). With few exceptions, the crabs immediately begin to feed voraciously within the respirometers. Fish was supplied ad libitum to the crabs until they were completely sated and all feeding behavior stopped, a process usually taking between 30 min and 1 h in all 3 species. Although the amount of fish was not quantified for every meal by every crab, preliminary experiments indicated that fasting *Cardisoma*, *Goniopsis* and *Ocypode* would eat about 2, 3 and 7%, respectively, of their body weight in fish following a 5-day fast. Following the fish meal, the respirometers were then sealed once again, and the $\dot{M}O_2$ measured at 2-h intervals for 24 h, then at 30, 42 and 50 h after the feeding bout.

MEASUREMENT OF OXYGEN CONSUMPTION

Oxygen consumption was measured using closed respirometry [for use with crabs, see for example Burggren & McMahon (1981), though descriptions abound]. Crabs were placed in glass chambers with gas-tight lids perforated by a pair of syringe needles. The volume of the chamber varied with species (*Cardisoma* = 1560 ml; *Goniopsis* = 480 ml; *Ocypode* = 265 ml). For each species, the size of the chamber al-

lowed considerable movement of the legs and chelae (feeding behavior within the respirometer appeared normal, for example) but was small enough to prevent the animal from walking or turning around. Each respirometer also contained a measured volume of either 25% seawater (*Goniopsis*, 50 ml; *Cardisoma*, 100 ml) or 100% seawater (*Ocypode*, 25 ml) to allow normal osmoregulation during the extended period of time in the respirometer. The effective gas volume of the chamber was calculated by subtracting the volume of water in the respirometer (which comprised approximately 6–10% of the total respirometer volume), and the volume of the crab from the total respirometer volume (which comprised approximately 5–15% of the total respirometer volume). The minute quantity of dissolved oxygen in the small volume of water in the respirometers was deemed insignificant, and was ignored in all calculations of $\dot{M}O_2$ (see below).

During the 12-h acclimation period and in the intervals between actual measurement periods, a gentle flow of air was maintained through the respirometers. Measurement periods began with the cessation of air flow through the respirometer chamber. A 1 ml gas sample was withdrawn from the respirometer into a glass syringe, and injected into a Beckman OM14 oxygen analyzer calibrated with humidified air between each injection. After 20 min, a second gas sample was withdrawn, and measured in the oxygen analyzer. After an additional 20 min, a third sample was drawn and measured. Thus, the reduction in fractional oxygen concentration of the gas within the respirometer (about 0.1–0.5% during 20 min) was calculated for two sequential time intervals. Following this period of gas sampling, a gentle flow of air through the analyzers was resumed until the next measurement period to prevent any depletion of oxygen within the respirometers.

At the conclusion of all measurements, each crab was removed from the respirometer, being careful to retain within the respirometer all water and any feces or unconsumed fish. Microbial $\dot{M}O_2$ (i.e. the "blank" measurement) was then determined over an ensuing 4-h period. In most cases, microbial oxygen consumption was just measurable within the resolution of the respirometer (e.g. a reduction of 0.05% over 4 h).

Oxygen consumption ($\dot{M}O_2$), expressed in μmol $O_2 \cdot kg^{-1} \cdot h^{-1}$, was calculated from the reduction in fractional O_2 concentration (corrected to account for any microbial respiration in the respirometer), the time interval over which this reduction occurred, the effective gas volume of the respirometer and the mass of the crab. No correction was made for the small amount of diffusion of oxygen into or out of the small amount of water in each respirometer – the water was assumed to be in equilibrium with the gas, and in any event the oxygen capacitance of the water accounted for less than 0.5 of 1% of the total oxygen of the gas in the respirometer. The mean of the two replications determined over a total 40-min period was used as the mean $\dot{M}O_2$ assigned to a given time. Thus, the designated $\dot{M}O_2$ for hour 2, for example, was the average of the $\dot{M}O_2$ measured in the 20 min before and following hour 2.

STATISTICAL ANALYSIS

All data are presented as means ± 1 SE. Differences in steady-state $\dot{M}O_2$ between fed and unfed populations of crabs were assessed with Student's-*t*-test for independent means. The significance of changes in $\dot{M}O_2$ measured in the 50 h following feeding in the time-course experiments were assessed by an ANOVA for repeated measures, followed by Student–Neuman–Keuls procedure to determine significant differences between measurement periods. A fiducial level of 0.05 was used for all analyses.

RESULTS

"Steady-state" $\dot{M}O_2$ in feeding crabs – comparison between species

Oxygen consumption measured in resting *Cardisoma guanhumi* (29–31 °C), *Ocypode quadrata* (29–31 °C), and *Goniopsis cruentata* (23–25 °C) feeding ad libitum for at least 5 days is indicated in Table I. Assuming a Q_{10} for metabolism of 2.6 for *Goniopsis*, based on the values reported for supratidal coenobitid crabs by Young (1973) and Burggren & McMahon (1981), then resting $\dot{M}O_2$ of *Goniopsis cruentata* at 30 °C is calculated to be about 1.4 $\mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$. Thus, at 30 °C resting $\dot{M}O_2$ during ad libitum feeding in these 3 species of supratidal crabs ranks is as follows: *Ocypode quadrata* > > *Cardisoma guanhumi* = *Goniopsis cruentata*.

"Steady-state" $\dot{M}O_2$ and digestive state

Changes in oxygen consumption associated with 5 days of either fasting and feeding in *Cardisoma*, *Ocypode* and *Goniopsis* are presented in Figs 1–3. Each figure shows the results of experiments on two separate populations – one group experiencing 5 days

TABLE I

Resting $\dot{M}O_2$ in *Cardisoma guanhumi*, *Ocypode quadrata* and *Goniopsis cruentata* provided with abundant food for 5 days. Mean values ± 1 SD are provided. ($\dot{M}O_2$ for *Goniopsis cruentata* at 30 °C was calculated assuming Q_{10} for $\dot{M}O_2$ of 2.6 – see text for further details.)

Species	*N*	Body mass (g)	Measurement Temperature (°C)	$\dot{M}O_2$ ($\mu mol \cdot O_2 \cdot g^{-1} \cdot h^{-1}$)
Cardisoma guanhumi	12	241.1 ± 17.1	29–31	1.49 ± 0.12
Ocypode quadrata	16	20.5 ± 1.8	29–31	2.57 ± 0.26
Goniopsis cruentata	15	61.4 ± 5.6	23–25	0.86 ± 0.05
			29–31	1.37 ± 0.08 (calculated)

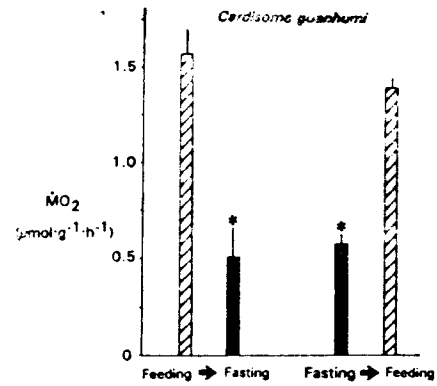

Fig. 1. $\dot{M}O_2$ following 5-day periods of normal feeding and fasting in *Cardisoma guanhumi* (29–31 °C). Crabs were divided into two groups, with the first group ($n = 6$) experiencing feeding and fasting in the reverse order from the second group ($n = 6$). Mean values ± 1 SE are presented. Asterisk (*, $p < 0.05$; **, $p < 0.01$) indicate that the $\dot{M}O_2$ during the second treatment in each group was significantly different from the first treatment.

with food followed by 5 days of fasting, the other group experiencing 5 days of fasting followed by 5 days with food.

Both *Cardisoma* and *Ocypode* showed large changes in oxygen consumption with digestive state. In both groups of *Cardisoma*, the difference between fasting and feeding crabs was highly significant ($p < 0.01$), and amounted to a 3-fold elevation of the feeding over the fasting rate (Fig. 1). There was no long-term effect on $\dot{M}O_2$ caused by fasting for 5 days, since there were no significant differences ($p > 0.1$) in $\dot{M}O_2$ between the two groups while feeding, even though in Group 2 the animals had earlier fasted for 5 days. Similarly, there were no significant differences ($p > 0.1$) between the

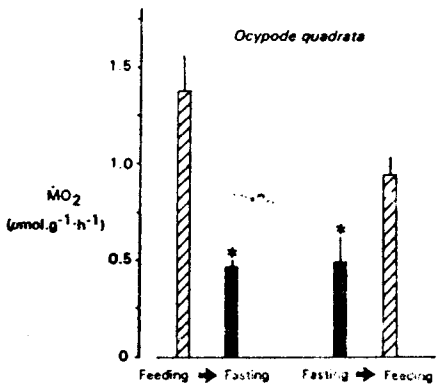

Fig. 2. $\dot{M}O_2$ following 5-day periods of normal feeding and fasting in *Ocypode quadrata* (29–31 °C). Feeding group, $n = 9$, fasting group, $n = 7$. See legend of Fig. 1 for explanation of presentation.

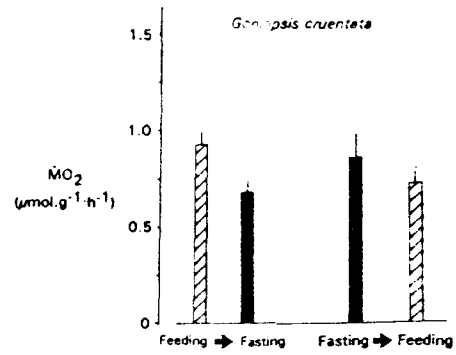

Fig. 3. $\dot{M}O_2$ following 5-day periods of normal feeding and fasting in *Goniopsis cruentata* (23–25 °C). Feeding group, $n = 10$, fasting group, $n = 7$. See legend of Fig. 1 for explanation of presentation.

fasting values for the two groups. Thus, the metabolic effects of 5 days of fasting were completely reversible in *Cardisoma*.

As for *Cardisoma*, the oxygen consumption in *Ocypode quadrata* was significantly reduced ($p < 0.01$) to 1/3 following 5 days of fasting in the first group of crabs (Fig. 2). The fasting rate of $\dot{M}O_2$ in Group 2 was not significantly different ($p > 0.1$) from the fasting rate in the first group. The $\dot{M}O_2$ in Group 2 following 5 days of feeding was nearly double the rate recorded earlier during fasting, but was still significantly less than in Group 1 during feeding. Thus, while the general pattern of change in $\dot{M}O_2$ with digestive state in *Ocypode* was the same as in *Cardisoma*, the results for *Ocypode* Group 1 and Group 2 were not mirror images of each other, as for *Cardisoma*.

Digestive state in *Goniopsis*, unlike in *Cardisoma* and *Ocypode*, did not influence $\dot{M}O_2$ (Fig. 3). Even though all of the *Goniopsis* in both Group 1 and Group 2 were observed to eat during the feeding phase of the experiments, there were no significant differences ($p > 0.1$) in $\dot{M}O_2$ in any condition or group in *Goniopsis*. This lack of a significant difference in *Goniopsis* could not be attributable simply to increased intraspecific variability in *Goniopsis*, as the variability in $\dot{M}O_2$ under all measurement conditions was similar in each species.

Time course of $\dot{M}O_2$ changes associated with digestive state

The time course of changes in $\dot{M}O_2$ in *Cardisoma*, *Ocypode* and *Goniopsis* associated with a single episode of feeding are shown in Fig. 4.

In *Cardisoma*, the fasting rate of $\dot{M}O_2$ measured at the beginning of the time-course experiment (i.e. the "control" value) was not statistically different from that measured in fasting Group 1 and Group 2 crabs shown in Fig. 1. $\dot{M}O_2$ in *Cardisoma* increased significantly ($p < 0.01$, SNK) within 30 min of the end of a single bout of feeding to satiation (Fig. 4). Postprandial $\dot{M}O_2$ peaked at about 1.4 $\mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$ between 4

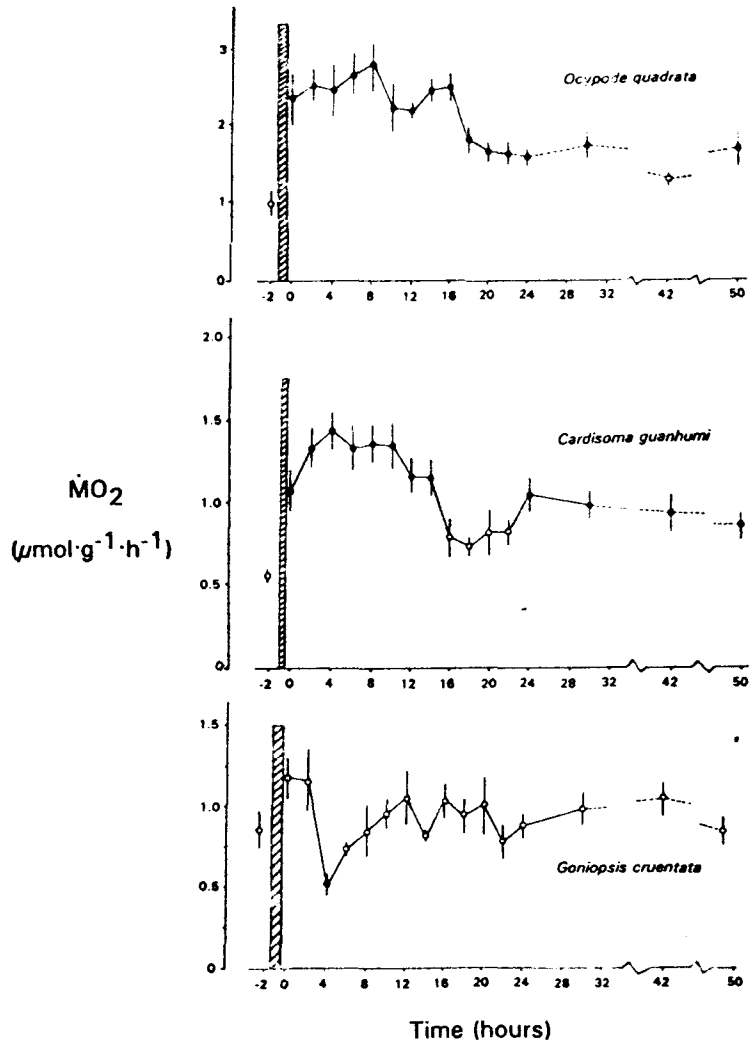

Fig. 4. $\dot{M}O_2$ at the end of 5 days of fasting and during a 50-h period following feeding in *Ocypode quadrata* (29–31 °C), *Cardisoma guanhumi* (29–31 °C) and *Goniopsis cruentata* (23–25 °C). Animals were actually fed during the period ending at $t = 0$, indicated by the hatched bar. Mean values ± 1 SE are presented. The numbers of animals examined are as follows: *Ocypode quadrata*, $n = 10$; *Cardisoma guanhumi*, $n = 6$; *Goniopsis cruentata*, $n = 10$. A solid symbol following the point of feeding indicates that the $\dot{M}O_2$ is significantly different ($p < 0.05$) from the value measured immediately before feeding. An open symbol following the point of feeding indicates that the $\dot{M}O_2$ is not significantly different from the value measured immediately before feeding.

and 10 h following feeding. This peak $\dot{M}O_2$ was not significantly different ($p < 0.01$, *t*-test) from the $\dot{M}O_2$ values measured during feeding in Group 1 and Group 2 *Cardisoma* shown in Fig. 1. From its peak values between 4 and 10 h, $\dot{M}O_2$ began to de-

crease 16 h following feeding. Although dipping towards control (fasting) values between hours 16 and 20, $\dot{M}O_2$ was still significantly elevated above the initial, fasting (control) value 50 h after feeding.

In *Ocypode*, the fasting rate of $\dot{M}O_2$ measured in this time-course experiment was not statistically different ($p > 0.1$) from that measured in fasting Group 1 and Group 2 crabs shown in Fig. 2. $\dot{M}O_2$ in *Ocypode quadrata*, as in *Cardisoma*, increased significantly ($p < 0.1$, SNK test) immediately after feeding. For the first 16 h, $\dot{M}O_2$ remained elevated at levels comparable to the oxygen consumption values of fed Group 1 and Group 2 *Ocypode*. After 16 h, postprandial $\dot{M}O_2$ began to decline, but did not return to values not significantly different from the fasting values prior to feeding until hour 42.

Changes in $\dot{M}O_2$ associated with digestive state in *Goniopsis cruentata* were significant, but this was due to only a single depressed point at 4 h. $\dot{M}O_2$ at all other times during the measured time course were not significantly different from the fasting value at time = −2 h. This confirms the lack of an effect of digestive state on $\dot{M}O_2$ shown earlier for this species in Fig. 3. Values for $\dot{M}O_2$ measured throughout these experiments were comparable to those measured for Group 1 and Group 2 animals during both fasting and feeding.

The differing absolute levels of $\dot{M}O_2$ after 5 days of fasting (the "control" value) between *Cardisoma*, *Ocypode* and *Goniopsis* complicate the comparison of the time course of the effects of feeding. Thus, Fig. 5 presents the normalized $\dot{M}O_2$, in which $\dot{M}O_2$ is expressed as a unitless value relative to a value of 1.0 for the fasting (control)

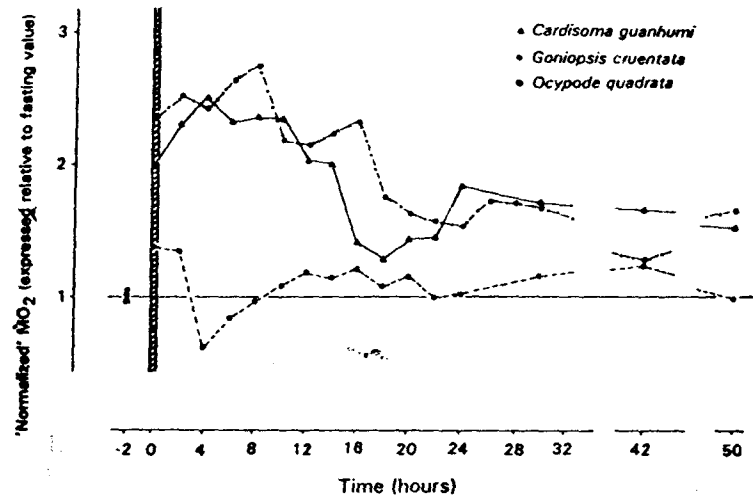

Fig. 5. Normalized values for $\dot{M}O_2$ at the end of 5 days of fasting and during a 50-h period following feeding in *Ocypode quadrata* (29–31 °C), *Cardisoma guanhumi* (29–31 °C) and *Goniopsis cruentata* (23–25 °C). Values plotted, the $\dot{M}O_2$ at a given time following feeding divided by the fasting $\dot{M}O_2$ for that animal, are derived directly from data presented in Fig. 4.

value. Essentially, both *Cardisoma* and *Ocypode* show a similar time course for post-feeding stimulation of $\dot{M}O_2$, with $\dot{M}O_2$ peaking in the first 12 h at about 2.5 times the fasting value. *Goniopsis* shows only small oscillations about the normalized fasting value.

Discussion

$\dot{M}O_2$ in feeding crabs – comparison between species

"Steady-state" measurements of $\dot{M}O_2$ in resting crabs with free access to fish indicated that *Cardisoma guanhumi* had a similar $\dot{M}O_2$ to that of *Goniopsis cruentata* (corrected for measurement temperature differences), both of which had a $\dot{M}O_2$ approximately one-half that of *Ocypode*. *Ocypode quadrata* is an extremely active crab in its natural habitat, and shows a relatively high aerobic scope for activity (see Herreid & Full, 1988; Weinstein & Full, 1992). Although the present measurements were made on undisturbed animals, a greater level of routine activity by *O. quadrata* within the respirometers probably accounted for the higher $\dot{M}O_2$ of this species under all measurement conditions.

The present measurements of "steady-state" $\dot{M}O_2$ in feeding *Ocypode quadrata* ($2.6\ \mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$ at 29–31 °C) are in good agreement with that of $2.3\ \mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$ at 25 °C measured for this species in air by Burnett (1979). However, the present values of $\dot{M}O_2$ for *Cardisoma* at 29–31 °C ($1.5\ \mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$) are lower than the literature values for *Cardisoma* measured at a 5 °C lower temperature ($2.0–2.6\ \mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$) (see McMahon & Burggren, 1988 for references). On the other hand, our values for *Goniopsis cruentata* are higher than the value of $0.46\ \mu m \cdot O_2 \cdot g^{-1} \cdot h^{-1}$ reported for this species by Young (1973). Differences in $\dot{M}O_2$ between studies could easily be accounted for by small differences in spontaneous activity in supposedly resting animals, or as mentioned in the Introduction, from differences between studies in the fasting or feeding state of the animals.

"Steady-state" $\dot{M}O_2$ and digestive state

This study documents that a postprandial elevation of oxygen consumption occurs in terrestrial brachyurans. In this respect, these specialized crabs resemble their marine counterparts. In the shore crab *Carcinus maenas*, for example, $\dot{M}O_2$ at 15 °C rises nearly 3-fold with 2–4 h of consuming a meal of *Mytilus* tissue amounting to 1.4% of the crab's body mass. Other crustaceans such as the supralittoral isopod *Ligia pallasii* (Carefoot, 1990) show an apparent SDA of similar magnitude, with a peak increase in $\dot{M}O_2$ of 100–200%. However, a much smaller increase was reported in the terrestrial woodlouse *Porcellio scaber* (Newell et al., 1974).

Although a large apparent SDA was observed in both *Ocypode* and *Cardisoma*, none

was found in *Goniopsis*. This enigmatic response is difficult to explain. Certainly *Goniopsis* within the respirometers consumed (with great relish) amounts of fish equivalent to those consumed by the other two species, so all of the components of apparent SDA, including mechanical costs of transport, feeding behavior, and an amino acid stimulus to protein synthesis, would seemingly be present in these experiments. SDA effects might be partially masked if they were superimposed on a high metabolism due to activity, for example. Yet, as indicated above, *Goniopsis* exhibited a very low, rather than high, $\dot{M}O_2$ during both the time-course and steady-state experiments. Experiments on *Goniopsis* involving actual measurement of protein synthesis, such as carried out by Houhlihan et al. (1990) for *Carcinus maenas*, would reveal to what extent (if any) a fish meal stimulates metabolic changes independent of large increases in $\dot{M}O_2$.

The protocol of the present experiment, involving 5 days of fasting followed by 5 days of feeding (or the reverse sequence), allows determination of a "steady-state" $\dot{M}O_2$ for both the fasting and feeding condition, as distinct from the $\dot{M}O_2$ response elicited by a single meal followed immediately by a second fasting session coincident with the postprandial period. The determination of $\dot{M}O_2$ during a prolonged experimental period characterized by frequent (at least daily) feeding may in fact accurately reflect the foraging excursions and feeding bouts that occur several times daily in many terrestrial crabs (Dunham & Gilchrist, 1988). Yet, in both *Ocypode* and *Cardisoma* the peak $\dot{M}O_2$ measured in the postprandial hours following a single meal was equivalent to the "steady-state" $\dot{M}O_2$ recorded in crabs allowed to feed ad libitum. This indicates that the steady-state $\dot{M}O_2$ in continuously feeding crabs is not reflecting a cumulative effect or summation on metabolism stimulated by several meals. Rather, a single meal apparently creates enough of a stimulus to produce a complete apparent SDA response.

Time course of $\dot{M}O_2$ changes associated with digestive state

The time-course experiments indicate that the apparent SDA effect in both *Ocypode* and *Cardisoma* begins within an hour of food ingestion, and lasts for at least 24 h. Factors that can influence the time course of SDA include the rate of mechanical and chemical digestion within the gut, the rate of amino acid uptake, and the transit time of ingested nutrients through the gut. These factors are probably strongly influenced by temperature. Consequently, the time course (as well as the magnitude) of SDA profiles in tropical species might be expected to differ from those of cold water, temperate species. Yet, the time profile of apparent SDA measured in the present study in *Cardisoma* and *Ocypode* at 29–31 °C generally matches that measured in other crustaceans at 15 °C, e.g. the shore crab *Carcinus maenas* (Houlihan et al., 1990) and the supralittoral isopod *Ligia pallasii* (Carefoot, 1990). Experiments explicitly designed to consider the temperature dependence of apparent SDA in crustaceans would be very useful in further interpreting these similarities in pattern between diverse crustacean lineages.

Aldrich (1975) indicates that factors other than apparent SDA, such as tidal or other biological rhythms, may exert a powerful influence on $\dot{M}O_2$ in *Cancer pagurus* and *Maia squinado*, greatly complicating analysis of the effects of feeding and starvation on metabolic rate by introducing large variability between individuals. The present experiments revealed great differences in fasting and fed $\dot{M}O_2$ with relatively little individual variability in *Cardisoma* and *Ocypode*. *Goniopsis*, which showed no apparent SDA effect, showed individual variability comparable to the other two species, suggesting that biological rhythms were not masking SDA effects. However, the fall and subsequent rise in $\dot{M}O_2$ between hours 14 and 24 in *Cardisoma*, which was not evident in *Ocypode*, could have represented an interaction between the long-term stimulating effect of SDA and a temporary downturn in $\dot{M}O_2$ associated with a biological rhythm.

In conclusion, an apparent SDA has been clearly documented in *Cardisoma guanhumi* and *Ocypode quadrata*, but was absent in *Goniopsis cruentata*. The magnitude (more than a doubling in $\dot{M}O_2$) and the duration (at least 24 h) of the apparent SDA effect indicate that nutritional status must form an integral part of an experimental protocol including $\dot{M}O_2$ measurements of terrestrial brachyurans. The lack of an apparent SDA in *Goniopsis*, despite an identical experimental protocol, suggests that generalized assumptions about the magnitude and duration of SDA may not be valid. Consequently, apparent SDA effects must be verified for each species of land crab.

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