A Partial Energy Budget for the Australian Crayfish *Cherax tenuimanus*

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Abstract

The freshwater crayfish *Cherax tenuimanus* (marron) has been attracting an increasing degree of attention for aquaculture due to its high growth rate and large harvest size. In this study some important parameters related to the physiological energetics of *C. tenuimanus* were defined in a series of independent experiments.

Food consumption by marron increased when fed a variety of foods, providing up to 29 joule/g dry wt crayfish per hour. Mean energy content of feces was 7,941 joule/g dry wt representing up to 17% of ingested food while excreted energy was not important in the overall budget. Metabolic requirements per hour were 5.4 joule/g dry wt. Gross conversion efficiency was up to 58% for the experimental diets. This ability gives the species a marked advantage for commercial culture over other related species with more subdued growth efficiencies.

The freshwater crayfish *Cherax tenuimanus* (marron) enjoys high consumer acceptability in Australia and its culture has been attracting an increasing degree of attention over the last decade due to its high growth rate and large harvest size. Momssy et al. (1986) and Villarreal (1988) reported that a large proportion of individuals over 40 grams can be obtained after one rearing season, confirming the growth potential of the species. However, in order to optimize culture conditions, it is desirable to understand the bioenergetic interactions of the species.

The bioenergetics of a heterotrophic organism (such as the crayfish) can be defined through the construction of a budget in which input nutrients are partitioned between growth and metabolism (Calow 1977). Metabolic responses to various feed ingredients are important determinants of the physiological processing of calories and nutrients and may provide an index of the efficiency of energy utilization and the growth promoting potential of a specific diet (Capuzzo 1983). In aquaculture, this knowledge will eventually lead to the optimization of least-cost rations which provide adequate levels of energy for the basic processes of the organism while permitting protein aggregation into tissue.

Among other investigators, Woodland (1967), Kossakowski (1975), Tcherkashina (1977), Jones and Momot (1983) and Sanguanruang (1988), have presented energy budgets for freshwater crayfish, emphasizing the need to further understand the pathways of energy uptake. In this study, a series of independent tests were conducted to construct a partial energy budget for *C. tenuimanus*, by estimating the rates of energy expenditure as a functional response of the organism (Brett and Groves 1979). This budget should provide an insight into some of the basic channels of energy utilization by the crayfish.

Materials and Methods

Diet Preparation

Three experimental semi-dried rations (Table 1) containing 17, 33 and 48% crude protein (CP) were prepared for evaluation by mixing the finely ground ingredients with vegetable oil in a food mixer. Tap water was incorporated until a stiff dough was formed before slow extrusion through a 1 mm hand
Table 1. Percentage composition and proximate analysis of experimental diets.

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Diet (% CP)</th>
<th>17</th>
<th>33</th>
<th>48</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish meal</td>
<td></td>
<td>2</td>
<td>31</td>
<td>60</td>
</tr>
<tr>
<td>Wheat meal</td>
<td></td>
<td>60</td>
<td>31</td>
<td>2</td>
</tr>
<tr>
<td>Soyabean meal</td>
<td></td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Corn meal</td>
<td></td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>Squid (Loligo sp.*)</td>
<td></td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Crayfish (C. cuspidatus*</td>
<td></td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Potato*</td>
<td></td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Carrot*</td>
<td></td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Vitamin and mineral mix*</td>
<td></td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Cholesterol</td>
<td></td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Vegetable oil</td>
<td></td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Gelatine (Binder)</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Proximate analysis (dry matter)

<table>
<thead>
<tr>
<th>Component</th>
<th>17</th>
<th>33</th>
<th>48</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein</td>
<td>16.6</td>
<td>32.7</td>
<td>47.5</td>
</tr>
<tr>
<td>Lipid</td>
<td>11.9</td>
<td>12.8</td>
<td>12.9</td>
</tr>
<tr>
<td>Carbohydrate</td>
<td>70.0</td>
<td>48.8</td>
<td>29.8</td>
</tr>
<tr>
<td>Ash</td>
<td>2.0</td>
<td>5.6</td>
<td>9.8</td>
</tr>
<tr>
<td>Moisture</td>
<td>24.1</td>
<td>26.3</td>
<td>23.1</td>
</tr>
</tbody>
</table>

\* Boiled 15 minutes in tap water; water and solubles were used to mix components.
\*\ Myadec Multivitamins and minerals (Parke Davis).

grill. The product was partially dried at 60 C in a convection oven for 3 hours and cut into 4–7 mm semi-dry pellets. Also tested was a combination (6:1 ratio) of a 15% CP commercial pellet (Golden Yolk Layer Pellets) and 7% CP decomposed organic matter collected from commercial growout ponds.

Protein content on the diets was determined using the Folin & Ciocalteu’s method described by Lowry et al. (1951) and modified by Hartee (1972). Lipids were determined by the sulphovanillin method described by Barnes and Blackstock (1973) and carbohydrates were determined by the colorimetric method of Kemp and Kits Van Heljningen (1954). Water content was taken as the loss in weight after oven-drying samples at 100 C for 24 h. Ash was determined by burning samples at 500 C for 15 h.

Growth

One hundred and twenty-six juvenile Cherax tenuimanus (mean wt = 3.8 ± 0.5 g) were starved for seven days in 18 aquaria (30 × 25 cm, area = 750 cm²) each containing four cylindrical shelters made of nylon shade-cloth. The crayfish were then fed ad libitum on one of the three semi-dried diets for seven days. Filtered water at 25.9 ± 1 C was recirculated at a rate of 250% per day and aerated (>80% oxygen saturation) using an air-compressor. After the acclimation period, the crayfish were weighed (precision = 0.01 g), measured with vernier callipers (0.01 cm) and marked with indelible ink on the carapace to make them recognizable. Seven crayfish were placed on each aquarium and fed one of the experimental rations 6 days/week at a rate of 4.7% of the total wet body weight/day for 57 days. Growth rates were monitored every two weeks and dead individuals were removed immediately after notice. Statistical differences were defined by analysis of variance and the Spearman’s rank correlation test (Sokal and Rohlf 1969).

Food Consumption and Egestion

Twenty-four crayfish (mean wt = 69.7 ± 8.8 g) were acclimated to one of the treatments for one week and were then starved for 24 h at 22 C before the trial. Experimental organisms were individually placed in 11.5 cm by 15.5 cm aquaria (area = 178 cm²) and allowed to feed for two hours either on a mixture (6:1 ratio) of the commercial 15% CP pellet and decomposed organic matter collected from the ponds, or one of the three experimental diets. After feeding, uneaten food was collected. The ingestion rate was determined by difference between food supplied (corrected for 2 hour leaching) and food remains after feeding. Twelve hours later feces were collected by means of a pipette, centrifuged at 2,500 rev/min for three min and oven dried at 100 C for 24 hours.

Excretion

The rate of ammonia excretion was determined after starving 24 marron (mean wt = 70.6 ± 5.2 g) for 24 hours at 22 C. The methods outlined above for feeding,
and feces collection were followed. An initial 50 ml water sample was taken at the time the animal was placed into the experimental chamber, and a second sample taken four hours after feeding was terminated. The level of ammonia was determined following the methods of Solorzano (1969).

**Metabolism**

Metabolism was calculated as energy of food assimilated, minus growth and excretion. It includes the energy demands of metabolic maintenance and behavioral activities (Capuzzo 1983).

**Energy Budget**

Assuming minimum entrophy, the first law of thermodynamics (enthalpy) leads to the energy budget equation:

\[ Q_c = Q_g + Q_u + Q_n + Q_r \]

(Capuzzo 1983; Brafield 1985)

where:

- \( Q_c \) = the energy content of food consumed;
- \( Q_g \) = energy retention as biomass (growth);
- \( Q_u \) = energy content of unassimilated matter (feces);
- \( Q_n \) = energy content of nitrogenous waste products; and
- \( Q_r \) = energy demands of metabolic maintenance.

Energy (joule/g dry wt crayfish/h) of food consumed \( Q_c \) was determined by using a Gallenkamp bomb calorimeter with benzoic acid as standard. Energy retention \( Q_g \) was determined from the growth study and an energy equivalent for \( C. \ tenuimanus \) tissue of 14,853 joule/g dry weight (Villarreal 1989). Crayfish used in this study were sexually immature, thus caloric utilization in gamete production was not included in the energy budget. Feces were diluted in caloric standard benzoic acid and the energy content determined by bomb calorimetry. Energy equivalents for waste excretion were obtained by multiplying recorded ammonia levels by 17 joule/mg NH\(_3\) (Smith 1971). From these results a partial energy budget was formulated.

Gross conversion efficiency \( (K_1) \) and net conversion efficiency \( (K_2) \) for the diets were calculated as follows (Jones and Momot 1983):

\[ K_1 = \frac{\text{growth energy retained}}{\text{food energy ingested}} \times 100 \]
\[ K_2 = \frac{\text{growth energy retained}}{\text{food energy ingested} - \text{fecal energy collected}} \times 100 \]

**Results**

**Growth**

There was considerable variation in individual size and growth. The size-frequency distributions tended to be positively skewed for all dietary treatments in aquaria. Table 2 presents mean initial and final weights, growth rates, food conversion ratios and survival for marron fed the semi-dried rations. Analysis of variance on growth rates and final weight showed that there were

<table>
<thead>
<tr>
<th>Dietary protein (%)</th>
<th>Initial number</th>
<th>Initial weight (g)</th>
<th>Final weight (g)</th>
<th>Growth rate (g/day)</th>
<th>FCR( ^a )</th>
<th>Survival (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>42</td>
<td>4.2 ± 2.1</td>
<td>7.1 ± 3.2</td>
<td>0.047 ± 0.012</td>
<td>17.3</td>
<td>31.0</td>
</tr>
<tr>
<td>33</td>
<td>42</td>
<td>4.2 ± 2.0</td>
<td>6.7 ± 3.4</td>
<td>0.042 ± 0.012</td>
<td>12.7</td>
<td>40.5</td>
</tr>
<tr>
<td>48</td>
<td>42</td>
<td>3.9 ± 2.3</td>
<td>8.3 ± 4.3</td>
<td>0.076 ± 0.015</td>
<td>13.2</td>
<td>28.6</td>
</tr>
</tbody>
</table>

\( ^a \) Apparent food conversion ratio.
Table 3. Fecal production (±SD), waste excretion (±SD) and energy equivalencies for Cherax tenuimanus fed diets with varying protein levels.

<table>
<thead>
<tr>
<th>Diet (%) CPb</th>
<th>Crayfish weight (g)</th>
<th>N</th>
<th>Feces Weight (mg/g/h)</th>
<th>Energya</th>
<th>Ammonia Excretion (mg/g/h)</th>
<th>Energya</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>72.2</td>
<td>6</td>
<td>0.28 ± 0.04</td>
<td>2.12</td>
<td>0.032 ± 0.004</td>
<td>0.55</td>
</tr>
<tr>
<td>33</td>
<td>65.2</td>
<td>6</td>
<td>0.33 ± 0.03</td>
<td>2.60</td>
<td>0.042 ± 0.007</td>
<td>0.72</td>
</tr>
<tr>
<td>48</td>
<td>80.8</td>
<td>6</td>
<td>0.34 ± 0.05</td>
<td>2.73</td>
<td>0.037 ± 0.006</td>
<td>0.63</td>
</tr>
<tr>
<td>Cc</td>
<td>60.8</td>
<td>6</td>
<td>0.53 ± 0.05</td>
<td>2.05</td>
<td>0.028 ± 0.005</td>
<td>0.48</td>
</tr>
</tbody>
</table>

a Joule/g crayfish/h.
b Crude protein.
c 6:1 ratio 15% CP commercial ration: 7% CP organic matter.

no statistical differences between treatments (P > 0.05).

Food Consumption and Egestion

Food consumption was equivalent to 2.1% b.w./day for the 17 and 33% CP diets and depended on weight (P < 0.05). A statistically different consumption (2.8% w.b.w./day) resulted from feeding the 48% CP diet (P < 0.05), and a higher level of ingested food (4.3% w.b.w./day) resulted from feeding a mixture of feeds (6:1 ratio 15% CP pellet: 7% CP organic matter).

The Spearman's rank correlation test showed that fecal production was related to crayfish size, ingested food and protein content of food consumed (P < 0.05), resulting in a fecal elimination rate of 0.318 ± 0.031 mg feces/g crayfish/h for the experimental rations (Table 3). Feeding a mixture of feeds to C. tenuimanus resulted in a fecal elimination equivalent to 7% of the ingested food.

Excretion

Crayfish appear to be ammoniotelic in freshwater (Sharma 1966); however, only small amounts of excreted ammonia were detected after the 4 hour trial (Table 3). There were no significant differences between treatments.

Energy Budget

Mean energy retention of crayfish for tissue production in the laboratory is shown in Table 4 where a partial energy budget for C. tenuimanus is presented. The energy diverted to growth for the 48% CP diet was 11.76 joule/g dry wt/h which was 1.6 times greater than that for the 17% CP diet or the 33% CP diet (P < 0.05). C. tenuimanus converted 41.8 to 57.5% of ingested energy (K₁) and 50.1 to 66.3% of digested energy (K₂).

Discussion

Growth in aquaria was restricted by the experimental time. Given a larger rearing time, final weight gain may have increased since the growth of juvenile crayfish behaves in an exponential, rather than linear, fashion over time (Morrissy et al. 1986). However, there is evidence that the performance of C. tenuimanus will fall below that

Table 4. A partial energy budget for Cherax tenuimanus juveniles (joule/g/h ± SD).

<table>
<thead>
<tr>
<th>Diet % CP</th>
<th>Food consumed</th>
<th>Feces eliminated</th>
<th>Food digested</th>
<th>Growth</th>
<th>Excretion</th>
<th>Metabolisma</th>
<th>K₁</th>
<th>K₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>15.10 ± 2.30</td>
<td>2.12 ± 0.30</td>
<td>12.98 ± 2.6</td>
<td>7.27 ± 1.86</td>
<td>0.55 ± 0.07</td>
<td>5.16 ± 0.77</td>
<td>48.15</td>
<td>56.01</td>
</tr>
<tr>
<td>33</td>
<td>15.57 ± 1.44</td>
<td>2.60 ± 0.24</td>
<td>12.97 ± 2.6</td>
<td>6.50 ± 1.86</td>
<td>0.72 ± 0.12</td>
<td>5.75 ± 0.86</td>
<td>41.75</td>
<td>50.12</td>
</tr>
<tr>
<td>48</td>
<td>20.46 ± 3.00</td>
<td>2.73 ± 0.40</td>
<td>17.73 ± 3.2</td>
<td>11.76 ± 2.32</td>
<td>0.63 ± 0.10</td>
<td>5.34 ± 0.80</td>
<td>57.48</td>
<td>66.33</td>
</tr>
<tr>
<td>Cb</td>
<td>29.38 ± 2.72</td>
<td>2.05 ± 0.19</td>
<td>27.33 ± 3.5</td>
<td>21.66 ± 3.91</td>
<td>0.48 ± 0.09</td>
<td>5.19 ± 0.78</td>
<td>73.72</td>
<td>79.25</td>
</tr>
</tbody>
</table>

a Metabolism was calculated as energy of food digested, minus growth and excretion.
b 6:1 ratio 15% CP commercial ration: 7% CP organic matter.
expected for commercial culture when pellets are the only source of nourishment (Morrissy 1984; Villarreal 1989).

Consumption rates for *C. tenuimanus* were higher than those reported by Bordner and Conklin (1981) for *Homarus americanus* (a slow, intermittent feeder), but about half the food consumption estimated by Kossakowski (1975) for *Orconectes limosus*. Nevertheless, ingested energy by marron in aquaria was similar to that obtained by the latter, and the values reported by Sanguanruang (1988) for *Procambarus* spp. It was also evident that food variety was more important than protein quantity for *C. tenuimanus*, with the superior growth reported for pond-reared individuals (Villarreal 1988), probably resulting from access to better habitat conditions, increased food consumption and an increased range of food substrates that probably included microorganisms and dead crayfish.

Crayfish are generally regarded as food selective (Momot et al. 1978; Cange et al. 1986; Capelli and Hamilton 1984; Hessen and Skurdal 1986). However, it is evident that *C. tenuimanus* is adaptable to a variety of feeds (Morrissy 1970a, 1970b, 1979, 1984; Villarreal 1988). From food consumption results in this study, it is apparent that there is an additive effect in marron, similar to that reported by Covich (1977) for *Procambarus acutus*, by which plant substrate ingestion encourages the consumption of more and different foods, providing a more appropriate substrate for increased assimilation efficiency (Calow 1977). Average assimilation efficiency was 85%, which is consistent with the level expected for an omnivore (Kossakowski 1975; Momot 1984). Newell (1966) and Odum and de la Cruz (1967) have indicated that omnivorous species usually improve their growth when feeding on mixed diets of plants and animals.

Marron used up to 57.5% of consumed energy for growth. This is consistent with the maximum gross efficiency estimated by Calow (1977) for poikilotherms (50%), with the difference probably resulting from underestimations of the fecal production (see below). *Cherax destructor* is also able to convert approximately 50% of the ingested energy to growth (Woodland 1967). This ability gives *Cherax* a bioenergetic advantage over other crayfish species with lower growth efficiencies (Mason 1975; Tcherkashina 1977).

Fecal elimination was equivalent to that reported by Jones and Momot (1983) for *Orconectes virilis*, Brown et al. (1986) for *Procambarus clarkii*, and Sanguanruang (1988) for *P. clarkii* and *P. acutus acutus*. However, the proportion of food digested was higher than the levels reported by Mo-shiri and Goldman (1969), Kossakowski (1975) and Mason (1975) for various crayfish species. Kleiber (1956), in a review of metabolic energy, claimed that the ratio of basal metabolism to maintenance ration is constant and independent of body weight, which implies that the conversion efficiency is also a weight-independent constant. Nevertheless, Calow (1977) in a more recent review indicated that, in general, gross efficiency alters in a systematic fashion with age and size during development. Thus, size differences between marron used in the independent tests in this study may have affected the overall energy budget by underestimating fecal production and, consequently, overestimating assimilation efficiency and metabolic requirements. Metabolism, calculated as the difference of assimilated energy minus growth and excretion, was slightly higher than that estimated by Villarreal (1990) from oxygen consumption recordings. However, it should be noted that some channels of energy expenditure which contribute to the metabolic cost were not considered in the budget. For example, the energy used for molting and the specific dynamic action (SDA) were incorporated, (but not estimated), in the partial energy budget. SDA may produce heat increments as high as 50% over the routine level (Hewitt 1984). On the other hand, the energy required for molting produced an energy cost
of 0.2–2.5 joule/g dry wt crayfish/h for Procambarus spp. (Sanguanruang 1988) and may divert up to 10% of ingested energy (Klein Breteler 1975; Logan and Epifanio 1978) in other decapods.

Ammonia is regarded as the main nitrogenous excretory product in crustaceans (Fellows and Hird 1979; Claybrook 1983) with levels of up to 95% of the total (Regnault 1987). Excretion rates by C. tenuimanus was similar to those obtained by Nelson et al. (1977) for Macrobrachium rosenbergii fed a variety of feedstuffs. Excretion was, however, noticeably higher than that reported by Sharma (1966) for Orconectes rusticus and about half of the ammonia produced by C. destructor when injected with amino acids (Fellows and Hird 1979). Overall, the level of ammonia excretion was of little importance in the general bioenergetic flow. However, the energy lost in excreted compounds had to be estimated directly, rather than calculated by difference from the other factors in the energy equation, to avoid incorporating a cumulative error.

A preliminary insight of the energy dynamics in culture conditions is also shown in Table 4. Villarreal (1988) reported a mean growth rate of 0.14 g/day for commercially reared marron fed a standard 15% CP commercial pellet. By incorporating this value to the bioenergetic equation with food consumption and fecal production for the commercial pellet-organic matter combination, gross conversion efficiency was 73.7% and net conversion efficiency 79.3%.

Momot (1984) concluded that species with lower metabolic requirements may use less food to complete their life cycles as a result of their superior growth rates, consequently sustaining high removal rates in energy-rich environments. There are strong indications that C. tenuimanus is highly efficient in terms of growth as indicated by the net conversion efficiency calculated for commercial culture conditions. Nevertheless, several channels of energy expenditure still have to be evaluated. Furthermore, it is important to identify the nutritional and environmental conditions that maximize energy utilization by crayfish. This, in turn, will benefit production in commercial ponds.

Acknowledgments

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