Bioenergetics of Nile Tilapia, *Oreochromis niloticus*: Effects of Food Ration Size on Metabolic Rate

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Abstract

The metabolic rate of Nile tilapia (*Oreochromis niloticus*) was determined at 30°C in relatively large respirometers. Fish were fed at five ration levels (2, 4, 6, 8 and 10% body weight per day). The weight of fish ranged from 5.0 to 7.9 g. Both total and feeding (total minus fasting) metabolic rates increased linearly with increased rate of food consumption. As ration increased from 2 to 10%, the proportion of food energy spent in feeding metabolism decreased from 32.33 to 16.43%, and that spent in total metabolism decreased from 61.80 to 23.19%.
Introduction

In fish bioenergetics, the energy channeled into metabolism can be divided into three components, standard metabolic rate ($R_s$), specific dynamic action (SDA) and activity metabolic rate ($R_a$) (Warren and Davis 1967; Brett and Groves 1979). $R_s$ is defined as an approximation of the minimum rate for the intact organism, and is preferably determined as the value at zero activity in the postabsorptive state (Fry 1971); SDA is the energy cost of biochemical processing of food following ingestion of a meal; and $R_a$ is the metabolic cost of locomotor activity. SDA is usually determined by measuring the post-prandial increase in metabolic rate, and is usually linearly related to ration size (Hamada and Maeda 1983; Hamada et al. 1985). In most studies, SDA expressed as a percentage of food energy was 10-20% (Muir and Niimi 1972; Beamish 1974; Yarzhombek et al. 1983; Ross et al. 1992).

SDA and activity metabolism in feeding fish are usually difficult to separate technically because fish may exhibit activity following feeding. Technical difficulties also exist in the measurement of standard metabolism, as fish are rarely completely inactive and often display spontaneous activities, which are
difficult to quantify. Thus, several terms are used to express approximations of Rs, e.g., routine metabolism, lower routine metabolism, resting metabolism and fasting metabolism (Jobling 1994). In this paper, we used the concept of From and Rasmussen (1984) and divided total metabolism into fasting and feeding metabolism. Fasting metabolism is defined as the metabolic rate of fasting, undisturbed fish, and any post-prandial increase over the fasting level is feeding metabolism. In most studies, it was assumed or found that SDA (or more properly, feeding metabolism, in studies where activity cost was not separated) is a constant proportion of food energy (Muir and Niimi 1972; Beamish 1974; Miura et al. 1976; Jobling 1981; Yarzhombek et al. 1983). Several studies have shown that feeding metabolism increases with increased ration level (Brett 1976; Hogendoorn 1983; From and Rasmussen 1984).

Tilapia is a widely cultured fish, and numerous reports on its metabolism or oxygen consumption have been published (Ahmed and Magid 1969; Farmer and Beamish 1969; Magid and Babiker 1975; Zhang et al. 1982; Ross and Ross 1983; De Silva et al. 1986; Meyer-Burgodoff et al. 1989; Becker and Fishelson 1990; Yamamoto 1992; Fernandes and Rantin 1994). Most of these reports studied metabolism in relation to body size, swimming speed and salinity, etc.; and many studied fasting metabolism. Almost all were carried out in relatively small respirometers or channel respirometers. Only one study (Meyer-Burgodoff et al. 1989) dealt with metabolism at different ration levels, using only narrow ranges of rations (around the maintenance level). No data was available for feeding metabolism or SDA at feeding level from starvation to satiation or next to satiation. In a previous study, the proportion of food energy spent in feeding metabolism was shown to be lowest at an intermediate ration level, and to increase at lower and higher rations (Xie et al., in press). However, metabolism was indirectly calculated from energy budget. Most studies on the metabolic rates of different fish have confined fish in relatively small respirometers, and the rates thus determined may not be representative of the level in aquarium conditions. This experiment examined the effects of ration level on the metabolic rate of Nile tilapia (Oreochromis niloticus) determined using relatively large respirometers to simulate aquarium conditions.

Materials and Methods

Semi-closed respirometers were used. Each respirometer had a 20-l volume, and was of clear plexiglass with an opening on top, which could be sealed. The respirometers were immersed in a water bath of 30°C and could be flushed with well-oxygenated water from a reservoir pre-heated to 30°C. Dechlorinated tap-water was used.

A practical-type diet was used, whose formulation and nutrient composition are shown in Table 1. The diet was prepared by pelleting, and stored at 4°C before use.

Chemical analysis was done on the feed. Dry matter was determined after the sample was oven-dried to constant weight at 105°C. Crude protein was
Table 1. Formulation and nutrient composition of the experimental diet (g·100 g⁻¹).

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fishmeal</td>
<td>10</td>
</tr>
<tr>
<td>Rapeseed meal</td>
<td>25</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>25</td>
</tr>
<tr>
<td>Wheat</td>
<td>31</td>
</tr>
<tr>
<td>Plant oil</td>
<td>2</td>
</tr>
<tr>
<td>Vitamin premix¹</td>
<td>1</td>
</tr>
<tr>
<td>Mineral premix²</td>
<td>5</td>
</tr>
<tr>
<td>CMC</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein³</td>
<td>34.4</td>
</tr>
<tr>
<td>Crude fat</td>
<td>3.2</td>
</tr>
<tr>
<td>Ash</td>
<td>9.1</td>
</tr>
<tr>
<td>Fiber</td>
<td>6.6</td>
</tr>
<tr>
<td>Dry matter</td>
<td>84.3</td>
</tr>
<tr>
<td>Gross energy (J mg⁻¹)</td>
<td>17.4</td>
</tr>
</tbody>
</table>

¹Vitamin premix (mg kg⁻¹): B1, 10; B2, 20; B6, 10; B12, 2; A, 4; D3, 0.4; K3, 80; folic acid, 5; cadmium pantothenic, 40; inositol, 400; niacin, 150; E, 60; choline, 6000; C, 500; wheat powder, 218.6.

²Mineral premix (g kg⁻¹): NaCl, 0.25; MgSO₄, 3.75; KH₂PO₄, 8; Ca(H₂PO₄), 5; FeSO₄, 0.72; (CH₃CH₂COOH)₂Ca·SH₂O, 0.88; ZnSO₄·7H₂O, 0.088; MnSO₄·4H₂O, 0.040; CuSO₄·5H₂O, 0.008; CoCl₂·6H₂O, 0.00025; KIO₃·6H₂O, 0.00075; Wheat powder, 0.112.

³All nutrient composition were determined and expressed as g 100g⁻¹ on a dry-matter basis.

by 3 d starvation. On the feeding day, fish were fed once a day for low ration sizes (2, 4 and 6%) and twice a day for high ration sizes (8 and 10%). Oxygen consumption was measured on day 3 (the last feeding day) and 6 (the last fasting day). BOD was measured on day 7 after the fish were removed. On days when oxygen consumption was not measured, the respirometer was unsealed and aerated. On the day of measurement, the respirometer was sealed for 24 h. Water was completely changed every 12 (at lower rations of 2, 4, 6 and 8%) or 8 h (at the higher ration of 10%) by flushing with fresh, aerated water of three times its volume. The oxygen concentration of the respirometer water was measured before and after each flushing using Winkler’s method (APHA 1975). The difference in dissolved oxygen before and after each period was 3-5 mg·L⁻¹, and the minimum oxygen level recorded was 4 mg·L⁻¹. On day 7, after the fish were removed, the respirometer was sealed for another 24 h and oxygen consumption by bacteria (BOD) was determined. BOD was found to be significant (0.038-0.061 mgO₂·L⁻¹·h⁻¹) and was subtracted from oxygen

Tilapia were collected from a fish farm in Hubei, China, about one month before the experiment. The fish were raised in the laboratory at 30°C. This temperature was also used throughout the acclimatization and experimental period. One week before the start of each experiment, one fish was placed into each respirometer. The weight of the fish averaged 6.3 g with a range of 5.0-7.9 g. The fish were fed to satiation twice daily during the acclimatization period.

Six fish were tested at each of five ration levels: 2, 4, 6, 8 and 10% body weight per day. Metabolic measurement followed a 7-d procedure. Each fish was fed the prescribed ration for 3 d, followed...
consumption by the fish. Metabolic rate in oxygen consumption was calculated as:

Total metabolism = oxygen consumption on feeding day - BOD
Fasting metabolism = oxygen consumption on fasting day - BOD
Feeding metabolism = total metabolism - fasting metabolism

Metabolic rates in terms of oxygen consumption were converted into energy using the oxy-calorific coefficient of 13.54 J·mg⁻¹ O₂ (Elliott and Davison 1975).

Least-squares regression was used to develop relationships between metabolic rates and rate of food consumption. Analysis of variance was used to analyze the differences among ration groups. The Newman-Keuls test was used for multiple comparison of means.

Results

Fasting metabolic rate (Rfa) per unit weight was not significantly different among ration groups (Table 2). Total metabolic rate (R), feeding metabolic rate (Rfe) and the R/Rfa ratio increased linearly with increased feeding rate, while the proportions of food energy spent in total and feeding metabolism decreased with increased feeding rate. Regression analysis showed the following relationships between metabolic parameters and feeding rate (C: J g⁻¹ d⁻¹) (Figs. 1 and 2):

Total metabolism (J g⁻¹ d⁻¹):
\[ R = 134.60 + 0.14C \quad (r^2 = 0.82) \]

Feeding metabolism (J g⁻¹ d⁻¹):
\[ R_{fe} = 53.2 + 0.13C \quad (r^2 = 0.89) \]

Ration level significantly affected the proportions of food energy spent in total and feeding metabolism. As ration increased from 2 to 10%, the proportion of food energy spent in total metabolism decreased from 61.8 to 23.2%, and that spent in feeding metabolism decreased from 32.3 to 16.4% (Table 2).

Table 2. Effects of ration level on metabolic rates of tilapia¹,².

<table>
<thead>
<tr>
<th>Ration level (g×100g BW⁻¹·d⁻¹)</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>C (J.g⁻¹.d⁻¹)</td>
<td>293.5</td>
<td>587.0</td>
<td>880.5</td>
<td>1174.0</td>
<td>1467.5</td>
<td></td>
</tr>
<tr>
<td>Rfa (J.g⁻¹.d⁻¹)</td>
<td>86.49±6.73</td>
<td>89.74±5.35</td>
<td>84.11±12.85</td>
<td>98.27±3.28</td>
<td>99.28±1.90</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Rfe/C (%)</td>
<td>32.3±2.37</td>
<td>21.8±1.26</td>
<td>17.3±1.08</td>
<td>17.9±0.48</td>
<td>16.4±0.64</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>R/C (%)</td>
<td>61.8±1.30</td>
<td>37.1±1.16</td>
<td>26.9±2.35</td>
<td>26.3±0.25</td>
<td>23.1±0.70</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>R/Rfa</td>
<td>2.1±0.19</td>
<td>2.4±0.16</td>
<td>2.9±0.20</td>
<td>5.1±0.30</td>
<td>3.4±0.09</td>
<td>P&lt;0.05</td>
</tr>
</tbody>
</table>

¹Mean ± SE.
²C: food consumption; Rfa: fasting metabolism; Rfe: feeding metabolism; R: total metabolism.
**Fig. 1.** Relationship between total metabolic rate (R: J g⁻¹ d⁻¹) and ration level (C: J g⁻¹ d⁻¹).
The line shows the regression relationship, and the open circles the values by the measurements.

**Fig. 2.** Relationship between feeding metabolic rate (Rᶠ: J g⁻¹ d⁻¹) and ration level (C: J g⁻¹ d⁻¹).
The line shows the regression relationship, and the open circles the values by the measurements.

**Discussion**

With the increases in the rate of food consumption, both total and feeding metabolism increased linearly. The result is the same as reported in most other studies (Brett 1976; From and Rasmussen 1984; Muir and Niimi 1972; Soofiani and Hawkins 1982).

In this study, the proportion of food energy used for feeding metabolism varied from 16.42 to 32.53%. The values are higher than for *Lepomis*
macrochirus (7.5-32.3%, Schalles and Wissing 1976) and Pleuronectes platessa (16%, Jobling and Davies 1980), but lower than for six teleosts reported by Cui and Liu (1990). Besides species differences, the method of metabolic measurement may also contribute to the differences. In the studies of Schalles and Wissing (1976) and Jobling and Davies (1980), flow-through respirometers with relatively small volumes were used. Cui and Liu (1990) indirectly estimated metabolism from energy budget in long-term growth trials. In the present study, large semi-closed respirometers were used, providing relatively natural conditions similar to aquarium situations. The feeding-induced activity level in the present study may be higher than in Schalles and Wissing (1976) and Jobling and Davies (1980).

In many studies on SDA, activity level was not measured or controlled (Muir and Niimi 1972; Yarzhombek et al. 1983; Ross et al. 1992); the SDA determined also included the cost of any feeding-induced increases in activity and should be equivalent to the feeding metabolism determined in the present study. In most of these studies, SDA (or feeding metabolism by definition of the present study) was found to be a constant proportion of food energy (Muir and Niimi 1972; Beamish 1974; Miura et al. 1976; Jobling 1981; Yarzhombek et al. 1983). The present results show that the proportion of food energy spent in feeding metabolism decrease with increased ration size. There may be two possible reasons for this: (1) the SDA/food energy ratio decreased with increased ration; and (2) the activity metabolism/food energy ratio decreased with increased ration. Future studies should investigate the activity-ration relationship for tilapia.

Results of the present study also contradict those from a previous study on Nile tilapia (8.56-11.0 g) at 30°C (Xie et al., in press), in which metabolic rate was indirectly calculated from the energy budget equation using data from a long-term growth trial. This previous study showed that the proportion of food energy spent in feeding metabolism was lowest at an intermediate ration level, and increased at lower or higher levels. Discrepancies in fasting metabolism also exist between the two studies. Fasting metabolic rate in the present study was 86.46-99.28 J g⁻¹ d⁻¹, much higher than the 50.45-63.58 J g⁻¹ d⁻¹ calculated from the growth trial (Xie et al., in press). It is possible that metabolic rate measured over a short period of time (24 h) in the present study was different from that during long-term growth. Several studies have shown that fasting metabolic rate of fish may continue to decline during prolonged starvation (Livingston 1968; Marias 1978; Du Preez et al. 1988). There has been no study on the variations in feeding metabolism during long-term growth. Direct measurements of metabolic rate during long-term growth are necessary in future studies of metabolism-ration relationship for fish.

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References


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