Energy Balance Of White Amur Fed Egeria

JON G. STANLEY

Fisheries Biologist (Research)
Bureau of Sport Fisheries & Wildlife
Fish Farming Experimental Station
Stuttgart, Arkansas 72160

ABSTRACT

A study of energy balance revealed that 1-kg white amur (Ctenopharyngodon idella Val.) inefficiently assimilated egeria (Egeria densa Planch.) but that a low metabolic rate allowed efficient conversion of assimilated food into fish biomass. Food intake (96 kcal) minus egestion (40 kcal) balanced within experimental error the sum of respiration (8 kcal) and growth (74 kcal). Although food contained largely carbohydrates, metabolism of protein accounted for 63% of the respiration, whereas carbohydrates were converted largely to fat.

INTRODUCTION

The white amur is an unusual fish which as an adult feeds almost exclusively on aquatic macrophytes. In a discussion of food efficiencies, Welch (22) generalizes that
carnivores have high digestive efficiencies but expend a large amount of energy in assimilation (digestion and absorption) and respiration, whereas herbivores digest less of the ration but expend low amounts of energy in metabolic processes. The white amur seems to conform to the typical herbivore pattern. About half the vegetation consumed is assimilated (8, 20), and the respiratory rate (5) is lower than for most fish. However, the conversion of ingested vegetation into fish biomass is less than 4% for energy (18, 19), and 2 to 6% for dry weight (10).

The objective of this study was to resolve the inconsistency of how a herbivore that assimilates half its food could have a conversion ratio of food into flesh of less than 4%. The rates of feeding (ingestion), fecal elimination (egestion), ammonium excretion, respiration, and growth were measured under laboratory conditions and each was expressed in terms of energy values. The objective was to construct a balance sheet for energy metabolism in the white amur.

**METHODS AND MATERIALS**

The routine care of the fish is described in detail elsewhere (16). Initially, the 12 fish used in this study weighed between 0.89 and 1.30 kg but gained approximately 0.2 kg each during the 5 weeks of the study. They were fed egeria which contained about 5 g of snails per kg of wet weight of which the snails were 90% Gyrulus sp. and 10% Physa sp. The experiments were conducted in 400-liter fiberglass tanks with two fish per tank. Photoperiod was 13 hr light and 11 hr dark in February and March, 1972. Water temperature was maintained at 22.1 to 23.7°C with a thermostatically controlled heater.

Each of six pairs of white amur was presented daily with 1 kg of egeria for 1 week to establish consistent feeding. An experiment to quantitate ingested food, fecal wastes, and ammonium excretion then was begun. An initial water sample was taken to establish a baseline value for organic matter and nitrogenous wastes already present in the water. Then 1.0 kg of egeria was added to each of the six tanks. After 24 hr the experiment was terminated and the fish were temporarily removed and weighed. Fecal material (solid waste) was allowed to settle for 1 hr, siphoned off, then filtered through 0.7-mm mesh screen. The filtrate was returned to each tank, and the water mixed. A sample was taken to determine ammonium and fecal material suspended in the water. The quantity of snails was estimated from the weight of snails initially on egeria and the amount remaining after the egeria was consumed. The fish then were returned to the tanks.

Dry and ash weights were determined on samples of egeria, snails, water, and solid wastes. Ingestion was considered equal to the intake of egeria plus snails; egestion was the sum of solid wastes siphoned from the bottom plus the increase in organics in the water. Assimilation was the difference between ingestion and egestion.

Kjeldahl nitrogen was determined for egeria, snails, solid wastes, and water samples and converted to crude protein by multiplying by 6.25 (13). Protein ingestion was the product of protein content times the daily rate of food consumption. Protein egestion was the product of crude protein content times egestion. Ammonium excretion was determined by direct Nesslerization of water samples (and subtracted from Kjeldahl nitrogen of water samples). Ammonium nitrogen multiplied by 6.25 gave the quantity of protein burnt in respiration.

Fat metabolism was not measured. Aquatic plants are low in lipid which can be ignored except for the most precise calculations. Fat content of egeria was taken as 3.27% dry weight (5) of the food consumed. One fish was killed and five samples of fat removed from the body cavity were dried at 105°C for 10 hr to determine dry weight of adipose tissue.

Carbohydrate ingestion from egeria was the difference between the intake of ash-free dry weight and the combined intake of protein and fat. Protein only was subtracted from the ash-free dry weight of snails. Carbohydrate egestion was calculated by subtracting the respective protein excretion rates from ash-free dry weights of suspended wastes and solid wastes. Carbohydrate assimilated was the difference between intake and egestion.

Caloric values were calculated by multiplying ingestion and egestion of protein by 5.65 kcal per g, carbohydrate by 4.15 kcal per g, and fat by 9.4 kcal per g (15).

Growth rates were estimated for these fish. Two fish were placed in each tank and fed for 1 week, then starved for 30 hr to allow emptying of the digestive tract. They then were anesthetized in a 30-mg per liter solution of quinaldine (2-methylquinoline) and weighed to the nearest gram. Egeria weighing 1 kg was added daily to each tank, then after 8 days the fish again were starved for 30 hr, anesthetized, and re-weighed. The daily growth rate was calculated from the increase in weight divided by the 8 days during which they fed.

The rate of oxygen consumption was determined individually for the 11 remaining fish by a water exchange system modified from Krogh (11). The fish were fed 1 kg of egeria per day for 1 week to allow recovery from previous handling. They then were introduced into respirometers and oxygen determinations were made after 2, 4, 10, and 22 hr. The fish fed until the time of their introduction into the respirometers, hence sampling times also represent time elapsed since the last meal. Respirometers contained 40 liters each and had an exchange rate of 0.66 to 1.40 liters per min. Oxygen concentrations within the respirometers were maintained between 5.2 and 7.2 mg per liter with inflowing water. Oxygen concentrations of the inflowing and outflowing water were determined with an oxygen meter, and the exchange rate was measured by collecting the outflow in a graduated cylinder. Oxygen consumption of each of the 11 fish was computed by the difference in oxygen concentration between the inflow and outflow multiplied by the exchange rate, divided by the body weight of the fish. Oxygen consumption as measured here is equivalent to routine metabolic rate (6).

The oxygen required to burn protein was obtained by multiplying by 966 ml per g protein (5). The oxygen needed for metabolizing carbohydrates represented the difference
between total oxygen consumption and the amount needed to burn protein. The caloric equivalent for burning carbohydrate was 5.0 kcal per liter (23). Subtracting the calories of carbohydrate burned from that assimilated gave the carbohydrate energy available for growth. This plus the calories from lipids gave the total energy available for growth. This has probably resulted in an overestimation since no allowance was made for fat excretion.

Growth was the daily increase in body weight, which was assumed to be entirely fat because these fish were in negative nitrogen balance. Correcting for 3.5% water of depot fat gave dry weight which was multiplied by the caloric value of fat to give the daily energy needed for growth.

All values are reported in this paper as the mean, plus or minus the standard error. The regression equation describing the relationship between body weight on oxygen uptake was calculated by the least squares method with data obtained in this study and values taken from the literature.

RESULTS

Data obtained on food consumption, egestion, growth, and respiration were suitable for calculation of an energy budget for white amur.

An average 1-kg fish daily consumed 24 g of food (dry weight), of which 50% was egested and 33% converted to fish biomass (dry weight) (Table 1). The remainder was presumed to have been burnt in respiration. Ingested food included 0.66 g protein, 0.77 g fat, and 20.4 g of carbohydrate. Egested material included 0.65 g protein, and 8.7 g carbohydrate.

The daily increment in body weight of 0.8% for these fish is similar to growth rates previously reported for this species (1, 17). Growth might have been greater had the fish been fed ad lib. The increase in body weight was thought to consist entirely of lipid deposition since these fish were in negative nitrogen balance (16). The quantity of protein consumed each day approximated that egested indicating that no net assimilation of protein occurred. In addition, 142 mg ammonium nitrogen was excreted, representing metabolism of 0.89 g protein.

The oxygen consumption of white amur varied from 0.5 to 1.8 liters per kg fish per day (Figure 1). The high rate of oxygen consumption observed immediately after the fish were placed in the respirometers probably was due to excitement from handling. The values from 4 to 10 hr represent oxygen consumption of fish with food in their digestive tracts. Because white amur in habitats with abundant vegetation are seldom without food, the value of 1.44±0.16 liters per kg per day is taken as the respiration rate for fish averaging 1.2 kg in weight and at 22.8 °C. The oxygen consumption was considerably less at 22 hr, and perhaps can be attributed to the fish being in a post-absorptive state. Although confinement in an enclosed chamber may have reduced the metabolic rate, the white amur normally is a quiet fish that likes to stay among aquatic plants without moving (2).

Of the 96 kcal ingested by 1 kg white amur, 42% was egested (Figure 2). Thus, the white amur does not efficiently digest its food, a conclusion also reached by Stroganov (20) and Hickling (8). However, because of a low rate of respiration (8 kcal) more than half the food consumed was available for growth (48 kcal).

DISCUSSION

The white amur exhibited unusual characteristics in the items of its energy budget.

White amur on a diet of mature egeria were unable to remain in nitrogen balance. Some of the plant protein was no doubt assimilated but this was offset by loss of an equal

![Figure 1. Oxygen consumption by the white amur. The fish fed until introduced into the respirometer, hence time represents hours elapsed since the last meal.](image)

### Table 1. Daily Ingestion And Egestion Of White Amur Fed Egeria.

<table>
<thead>
<tr>
<th></th>
<th>Wet wt. (g)</th>
<th>Dry wt. (g)</th>
<th>Ash-free (g)</th>
<th>Protein (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ingestion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Egeria</em></td>
<td>265 ± 15</td>
<td>23.7 ± 1.3</td>
<td>21.7 ± 1.2</td>
<td>643 ± 38</td>
</tr>
<tr>
<td><em>Snails</em></td>
<td>0.9 ± 0.1</td>
<td>0.3 ± 0.03</td>
<td>0.1 ± 0.02</td>
<td>17 ± 2</td>
</tr>
<tr>
<td><strong>Total Ingestion</strong></td>
<td>266 ± 15</td>
<td>24.0 ± 1.3</td>
<td>21.8 ± 1.2</td>
<td>662 ± 38</td>
</tr>
<tr>
<td><strong>Egestion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Suspensions</em></td>
<td>N.D.a</td>
<td>6.5 ± 1.2</td>
<td>5.2 ± 1.0</td>
<td>462 ± 106</td>
</tr>
<tr>
<td><em>Solids</em></td>
<td>78 ± 6</td>
<td>5.5 ± 0.6</td>
<td>4.2 ± 0.5</td>
<td>190 ± 15</td>
</tr>
<tr>
<td><strong>Total Egestion</strong></td>
<td>82 ± 22</td>
<td>8.0 ± 1.4</td>
<td>5.4 ± 1.0</td>
<td>652 ± 112</td>
</tr>
</tbody>
</table>

*a N.D. = not determined
Figure 2. Daily energy balance in kcal per kg body weight for white amur fed egeria.

quantity in digestive enzymes and mucoprotein. Nitrogen imbalance occurred because the fish daily metabolized 0.89 g protein per kg body weight. The energy derived daily from burning protein was 5.0 kcal per kg, which represents 63% of the total energy expenditure. Fischer (5) found daily protein metabolism of 4.3 kcal per kg which supplied 28% of the energy in 35 g fish. Thus, the white amur burns a considerable quantity of protein which in nature must be obtained from high-protein foods such as growing shoots, filamentous algae, or animals.

No measurements were made of lipid metabolism. A part of dietary lipid was probably digested and absorbed since lipase occurs in the intestinal tract of the white amur (8).

A comparison of ingestion to egestion suggests assimilation of about 57% of the carbohydrate. Only 6% of the carbohydrate assimilated was burned in respiration. Most was stored, probably in the form of fat since fish store relatively little glycogen (14).

The respiratory rate of the 11 white amur was low compared to rates observed in other species. Such comparisons may lack validity since the various investigators used fish which differed in their acclimation times, degree of confinement, nutritional state, excitability, weight, temperature, and oxygen levels. Winberg (23) devised procedures for correcting to a standard temperature of 20 C and to account for differences in body weight. He reported expected oxygen uptake values for fishes weighing 1 kg: 105 ml per hr for sturgeons (Family Acipenseridae), 95 for salmonid fishes (Family Salmonidae), 122 for carp (Cyprinus carpio L.), and 54 for tench (Tinca tinca (L.)). Oxygen uptake in 1 kg white amur, also corrected to 20 C, was 38 ml per hr. The white amur may thus fit a model suggested by Welch (22) which indicated that herbivores have relatively low respiration rates. Tench have a low respiratory rate and along with common carp are considered to be euryphagous (7). Whether the low rate of respiration in tench is related to diet remains speculative. Likewise, the low respiratory rate of white amur may be fortuitous and unrelated to the herbivorous diet since 65% of the energy needs are met by burning of protein. I tentatively conclude, based on measurements by Fischer (5) on white amur of about 35 g and my own measurements of 1.2 kg fish, that this species has a low respiratory rate compared to other fishes.

Chen and Shi (4) measured oxygen consumption of white amur but at 27 to 30 C, including two fish weighing about 1 kg. These fish had respiratory rates about three times higher than the white amur in my study, possibly due to the higher temperature. Yeh (25) measured oxygen consumption of two small specimens. Using data from these sources and from my study, corrected to 20 C using Winberg’s (23) equation, I calculated a regression equation, oxygen uptake Q, in ml per hr against body weight W in grams, for fish ranging in weight from 1.1 to 1300 g. This equation, Q = 0.220 W^0.76, fits published oxygen uptake data and provisionally replaces the equations of Winberg (23) and Fischer (5) for this species.

The items in the energy budget correspond to the variables in the basic equation of Q = Q_e + Q_o given by Warren and Davis (21) where Q_e equals the energy value of the food consumed, Q_w is the energy value of all waste products in feces and urine and those lost through the gills and skin, Q_o is the change in the energy value of the materials of the body, and Q_t is the energy released in metabolism in all ways and for all purposes. Of the variables, growth was determined least precisely in this study, due to variations between individual fish. Also, because these fish were in negative nitrogen balance when fed egeria it was assumed that the weight increment was fat, which was equated to calories of energy by multiplying by 4.4 kcal per g. If the weight increase had included protein, the conversion ratio would have been closer to that for protein, 5.65 kcal per g. Although routine metabolism only approximates Q_w, even a 100% error would not change the energy balance significantly.

Although some uncertainty exists for each parameter of energy metabolism, the ingestion of 96 kcal less egestion of 40 kcal approaches (within experimental error) the sum of respiration and growth which is 82 kcal. This lends support to the conclusion that the white amur has a low efficiency of assimilation, but that the small expenditure of energy in respiration allows for an excellent over-all conversion of vegetation to fish biomass.

One reason for the high energy efficiency reported here is that the conversion of carbohydrates to lipids is quite efficient (9). It was calculated that of the 85 kcal carbohydrates ingested, 49 kcal was assimilated and 3 kcal burned in metabolism, leaving 46 kcal for conversion to lipid. The efficiency reported here is better than those previously published for white amur. Less than 4% of the food energy in lettuce (Lactuca sativa L.) or Elodea canadensis Michx. was converted to white amur flesh (18, 19) and a conversion of 2 to 6% of dry weight was reported by I-kuei et al. (10).

The discrepancy between results reported here and data from the literature might be accounted for by differences in the sizes of fish used and in the conditions of the experiment. Small fish used in other studies might have lower assimilation efficiencies and greater expenditures of energy. Oxygen levels less than 5 mg per liter in the study by I-kuei et al. (10) and temperatures less than
20 C in the investigations of Stott and his co-workers (18, 19) also may have influenced their results. Temperatures used in my study were near the optimum for conversion of pelleted feed by white amur (12).

ACKNOWLEDGEMENT

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LITERATURE CITED