ARE THERE ANY PHYSIOLOGICAL DIFFERENCES BETWEEN THE MALE MORPHOTYPES OF THE FRESHWATER SHRIMP *MACROBRACHIUM AMAZONICUM* (HELLER, 1862) (CARIDEA: PALAEMONIDAE)?

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**ABSTRACT**

A comparison was made of the metabolism, nitrogenous excretion, growth, oxidized energy substrate, ingestion rate, and fecal production of the males of three morphotypes (CC, GC1, and GC2) of the palaemonid shrimp *Macrobrachium amazonicum* (Heller, 1862). The proportion of these morphotypes in the population is fixed, and individuals can change from one type to another (TC to CC, CC to GC1, and GC1 to GC2) to maintain this proportion. The three morphotypes were evaluated for 30 days, during which individuals were fed daily with commercial food. Food debris, feces, and exuviae were collected daily. Oxygen consumption was measured in a closed respirometer, and ammonia excretion was measured by colorimetry. The atomic ratio O:N was used to indicate the predominant energy substrate oxidized.

The existence of morphotypes among males that occupy the same ecological niche has been described in other species of freshwater palaemonid shrimps such as *Macrobrachium rosenbergii* (De Man, 1879) (Ra’anan and Cohen, 1985; Kuris et al., 1987), *M. dayanum* (Henderson, 1893) (Langer et al., 2002), and *M. grandimanus* (Randall, 1840) (Wortham et al., 2012). These morphotypes perform distinct functions in the population and are characterized by their morphological differences (size, color, number of spines) and reproductive and behavioral patterns. The proportion of these morphotypes in the population is fixed and species-specific, and individuals can change from one type to another (TC to CC, CC to GC1, and GC1 to GC2) to maintain this proportion. Males of different morphotypes but of the same age can be descendants of the same female. According to Moraes and Valenti (2004), the passage from one morphotype to another may occur through a single molt or through a gradual process. Passage through all phases may

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**KEY WORDS:** excretion, fecal production, growth, metabolism, physiology, sex differences

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**INTRODUCTION**

The neotropical palaemonid shrimp *Macrobrachium amazonicum* (Heller, 1862) has a wide distribution, occurring in the Orinoco, Amazon, São Francisco, Paraná, and Paraguay rivers and in coastal regions of northern and northeastern South America, including the Paraguay River and the Miranda, Negro, and Taboco rivers (Maciel and Valenti, 2009). There is a geographical separation and, as a consequence, genetic isolation between different populations of *M. amazonicum* in the northern (including the Atlantic and Caribbean coasts) and southern (La Plata River system) regions of Brazil. This wide geographical distribution results in distinct physiological, reproductive, behavioral, and ecological patterns between many individuals of the populations. *Macrobrachium amazonicum* is of particular interest because males show distinctive morphotypes (TC, CC, GC1, and GC2) as a result of its wide distribution (Moraes-Riodades and Valenti, 2004).

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not be obligatory, and retrocess may occur. Ra’an and Cohen (1985) and Kuris et al. (1987) identified three morphotypes in populations of *M. rosenbergii* (SM, BC, and OC), which were characterized by morphological, reproductive, and behavioural differences. Genetic characterization of the males of the different *M. rosenbergii* morphotypes showed that there are significant differences at the molecular level between the morphotypes (Ranjeeet, 2010). Moraes-Rioidades and Valenti (2004) demonstrated the existence of four groups of males from a population of *M. amazonicum* in northeastern Pará State, northern Brazil: Translucent Claw (TC), Cinnamon Claw (CC), Green Claw 1 (GC1) and Green Claw 2 (GC2).

The TC morphotype originates from undifferentiated juveniles and comprises small and agile animals (approximately 5.5 cm postorbital length) that present some juvenile characteristics. The CC morphotype consists of slightly larger individuals than TC (approximately 6.3 cm) and with a higher ratio between the size of the chela and the rest of the body. The GC1 and GC2 morphotypes are larger (approximately 8.7 cm) with highly differentiated chelae; GC1 presents low reproductive activity, whereas GC2 is sedentary and is the morphotype with the highest reproductive activity in the population. The presence of males of different sizes in the population of shrimps of the genus *Macrobrachium* is evidence of the existence of a social hierarchy (Karplus et al., 1992). The adaptive value of a hierarchy among males is mainly related to the reproductive success of the species and protection against predation.

Papa (2007) observed the presence of a functional reproductive system in all *M. amazonicum* morphotypes, but they did not verify differences in the growth of the hepatopancreas, body weight, or chela length between GC1 and GC2, which suggested the existence of only three morphotypes in the population. Santos et al. (2014) detected differences in proteolytic activities among farmed morphotypes but not among wild individuals.

A clear definition of the morphotypes of caridean shrimps is extremely important both for understanding their adaptive value in the population and for aquaculture because once species such as *M. amazonicum* and *M. rosenbergii* are farmed, their rearing in fattening hatcheries must account for the heterogeneous growth of males to maximize production. In *M. rosenbergii*, some researchers have successfully developed a rearing method compatible with the growth characteristics of the morphotypes (Karplus et al., 2000; Tidwell et al., 2001).

We compared the physiological characteristics of three morphotypes (CC, GC1 and GC2) of *M. amazonicum* fed with commercial food by evaluating the metabolism, nitrogenous excretion, growth, energy substrate (proteins, carbohydrates or lipids) predominantly oxidized, ingestion, fecal production and energy expenditure from molting. These same physiological characteristics have already been described by Augusto and Masui (2014) for the TC morphotype and will be used for comparative purposes with the other morphotypes studied here.

**Materials and Methods**

Collection and Acclimation of Laboratory Animals

Male *M. amazonicum* at the inter-molt stage were collected in hatcheries from the Aquaculture Center of UNESP (CAUNESP), Jaboticabal, São Paulo State, Brazil. These individuals came from a population in northeastern Pará State, Brazil (01°14′30″S, 48°19′52″W), and have been kept in hatcheries since 2001. All individuals collected were at the inter-molt stage. After collection, shrimp were maintained for 7 d in the Carciniculture Laboratory of the Aquaculture Center of UNESP (CAUNESP) to acclimate them to laboratory conditions. During this period, they were kept in individual tanks containing fresh water with constant aeration, a temperature of 30°C, and a photoperiod of 12 h light and 12 h of darkness. Approximately 50% of the water in tanks was changed every two days. Animals were fed daily with commercial shrimp food (Poli-Nutri®) in an amount corresponding to 7% of their body mass. Food was offered at 1800 h (6 pm) because a pilot experiment found that individuals kept in the laboratory feed mainly in the evening.

All experimental groups (CC, GC1, and GC2) consisted of at least seven individuals. The shrimp, which were at the pre-molt or post-molt stage at the end of the experiment, were discarded once their elevated hydration would alter the measurements of mass gain.

Experimental Procedures for the Evaluation of Physiological Parameters

The shrimp were weighed (Marte balance AS 2000C) after acclimatization to laboratory conditions and transferred to individual aquaria containing fresh water for the evaluation of daily ingestion and excretion rates and weekly growth rate for 30 d. Laboratory animals were kept as indicated above. At the end of this period, the individuals were used to evaluate oxygen consumption and ammonia excretion.

Evaluation of the Ingestion (C) and Egestion (F) Rates

Ingestion rate was calculated as the difference between the mass of the food offered and the mass of the food left in the tanks. Unconsumed food was removed from the aquaria in the morning daily by siphoning, dried in filter paper, weighed (wet mass), oven dried at 60°C for 48 h and weighed again to 1 μg (Mettler Toledo). Control samples of food were weighed, placed in tanks that were kept under the same experimental conditions, but without animals, stored in Eppendorf tubes, and kept in a freezer for further energy content analysis. Food energy content was determined by the wet combustion of samples from 8 to 12 mg dry weight (Karzinkin and Tarkovskaya, 1964). This method is based on the oxidation of organic matter with potassium iodate in the presence of sulfuric acid and using sodium thiosulfate as a titrant.

Egestion was measured by taking feces from the tanks every day in the morning using a plastic pipette, dried at 60°C for 48 h, and weighed as in unconsumed food.

**Growth (P)**

Males were weighed weekly for a period of 30 days. On the last day of the experiment, after oxygen consumption and ammonia excretion were evaluated, animals were killed by freezing, oven dried at 60°C for 48 h, and weighed again. Energy content was determined using a calorimetric pump (Parr, 6300). Samples of at least 1 g were macerated and burned with sodium thiosulfate as a titrant.

Energy content was obtained by calculating the ratio between the heat released and the heating of the water around the pump. An increase of 1°C per kilogram of water is equivalent to 1 kcal of energy. Exuviae (Ew)

Samples of exuviae were collected from tanks during the 30 day experimental period. Exuviae were dried with absorbent paper and weighed as indicated above. They were then oven dried at 60°C for 48 h and weighed again. Food energy content was determined by wet combustion of samples ranging from 8 to 12 mg dry weight (Karzinkin and Tarkovskaya, 1964).

Oxygen Consumption, Ammonia Excretion, and O:N Ratio

Oxygen consumption and ammonia excretion were measured on the last day of the experimental period (day 30). Shrimp were kept for 24 h without food to avoid the calorigenic effect of food and their gut content was observed with the purpose of verifying the absence of food (Rosas et al., 1999; Lemos and Phan, 2001). After this period, animals were placed in individual conical respirometric chambers containing 440 ml of filtered water and maintained in trays with water and an electrical heater at
30°C (Augusto and Masui, 2014). Individuals were kept in respirometric chambers for 30 min with aeration to acclimatize them and reduce the stress caused by manipulation. Aeration was then removed and the oxygen concentration within the chamber was measured using a dissolved oxygen meter (monitor and probe, YSI, Yellow Spring, OH, USA, models 53 and 5905, respectively). The oxygen concentration was measured again after 60 min. Control chambers without animals were kept under the same experimental conditions.

Variations in oxygen concentration were calculated as the difference between the values obtained in samples and controls (no animals). After incubation, shrimp were killed by freezing, oven dried at 60°C for 48 h and weighed (Marte balance AS 2000C). Ammonia excretion was measured in samples of 5 ml of water obtained from the respirometer chambers at the beginning and end of the experiment to measure oxygen consumption. The ammonia concentration in water samples was determined in triplicate by colorimetry (Koroleff, 1983). The O:N ratio was calculated by dividing the ammonia concentration in water samples and controls (no animals). After 60 min. Control chambers without animals were kept under the same experimental conditions.

Ammonia excretion was different among all morphotypes, varied between the morphotypes (Table 1). Oxygen consumption and individual ammonia excretion were higher in GC2 than in the other two morphotypes investigated. The variation in oxygen concentration was calculated as the difference between the values obtained in samples and controls (no animals). After 60 min. Control chambers without animals were kept under the same experimental conditions.

The atomic ratio of O:N was lower than 7 in GC2, which suggests the use of proteins as an energy substrate, whereas the results obtained for CC and GC1 indicated a mixture of proteins and carbohydrates.

The energy content of food was 13.8 ± 0.2 kJ (g MS)−1 and 7.9 ± 0.2 kJ (g MS)−1 for exuviae, which corresponds to approximately 40% of the energy value of the whole bodies of shrimp (Table 1).

The specific dry-mass oxygen consumption was similar for all morphotypes (Fig. 1). Ammonia excretion was approximately 180% higher in GC2 than in the other two morphotypes evaluated (Fig. 2).

**DISCUSSION**

Results from this investigation suggest that the male morphotypes of *M. amazonicum* exhibit not only morphological differences but physiological differences as well. These differences, especially between CC and GC1 (and GC2; Augusto and Masui, 2014) in relation to GC2, may be related to the physiological differences that characterize every morphotype, such as an unequal pattern of activity, growth, function in the population, and reproductive behavior. Because morphotypes were evaluated in isolation from the others, these differential responses may also be related to the physiological processes that precede the transformation of morphotypes. Some experiments, such as those outlined here, cannot be conducted with all morphotypes kept together in the same aquarium due to the impossibility of identifying the food ingested or the feces produced by each. Nevertheless, it is important that, whenever possible, future studies that investigate aspects of the biology of the different morphotypes are done with them kept together such that the studies will not miss the effects of social interactions.

The physiological aspects of *M. amazonicum* male morphotypes investigated suggest differences mainly between the CC and GC1 male morphotypes compared to GC2 morphotypes regarding mass gain, nitrogenous excretion, and oxidized energy substrate.

**Growth**

Heterogeneous growth in crustaceans often leads to the establishments of social hierarchies in a population (Barki et al., 1992; Silva and Arruda, 2015). Such development,
could be advantageous if fights among individuals of the same species end in death when the fighting is between individuals of the same size. We have verified that mass gain was higher in the CC and GC1 morphotypes and that GC2 had almost no gain (Table 1). These data show that CC and GC1 represent morphotypes with an elevated growth rate, whereas GC2 must use its ingested energy in other pathways, such as reproduction. According to Moraes-Riodades and Valenti (2004), GC2 is the morphotype with the largest overall size and with the largest chelae, and is dominant in the population. Augusto and Masui (2014) verified that the TC morphotype gains approximately 15 mg WW$^{-1}$ day$^{-1}$, which corresponds to a gain of 22% of its initial wet weight after 30 days. These results suggest that the TC morphotype invests a great portion of the energy ingested in growth, as do the CC and GC1 morphotypes. The elevated growth rates observed in CC and GC1 (present work) and in TC (Augusto and Masui, 2014) are consistent because these morphotypes are smaller and are expected to require a significant investment in growth. GC1 males, however, have not yet developed large chelae that could serve both as a sex attractant and in agonistic behaviour. The three morphotypes of *M. rosenbergii* also present different growth patterns but the growth rate of males of the OC (orange claw) morphotype is higher than in the SM (small claw) and BC (blue claw; male dominant in population) morphotypes (Ra’an and Cohen, 1985).

Despite the elevated growth rate observed in the CC and GC1 morphotypes, the growth of several other aquatic animals can vary in nature due to factors such as social interaction, diet, and available space (Michaels et al., 2015; da Costa et al., 2016; Hellmann et al., 2016). For example, in fishes such as *Centropomus parallelus* (Poey, 1860) (Lemos et al., 2006), the presence of other individuals may reduce stress through social interactions, stimulating appetite and growth. Therefore, given the complex hierarchy that exists among species of *Macrobrachium* (Ra’an and Cohen, 1985; Moraes-Riodades and Valenti, 2004; Ibrahim,
The data set presented suggests that GC2 may be channeling a great portion of ingested energy and nutrients into reproduction. This morphotype nevertheless showed a high ammonia excretion rate (approximately 15% higher than the other morphotypes). The ammonia excretion of crustaceans can be altered by physiological factors such as molting cycle, size, diet, and environmental factors such as temperature, salinity, pH, dissolved oxygen and ammonia (Hayd et al., 2010; Augusto and Masui, 2014). It is possible that whereas TC, CC, and GC1 use amino acids in tissue growth, GC2 uses amino acids as an energy source. In addition, the food might have had an unbalanced composition in terms of free amino acids for the GC2 morphotype, or shrimp may have been fed in excess. The percentage of feces eliminated by the morphotypes, however, was always proportional to the ingestion rate (approximately 2%), thus suggesting a similar utilization in terms of absorption of nutrients among the morphotypes.

The O:N ratio is associated with the availability of energy reserves and the use of body protein (Mayzaud and Conover, 1988). Several factors may influence the use of the three different energy substrates (protein, carbohydrates, and lipids) by crustaceans, including diet (Pascual et al., 2004; Hayd et al., 2010; Rocha et al., 2013). In the diets of *M. rosenbergii* containing different levels of fibre, the O:N ratio varied from 10 (use of carbohydrates) to 49 (use of lipids) (González-Peña and Moreira, 2003). Chen and Nan (1994) observed that different species of marine shrimps fed the same commercial food used different energy substrates: *Penaeus japonicus* (Bate, 1888) and *M. ensis* (de Haan, 1844) used proteins, whereas *P. monodon* (Fabricius, 1798), *P. penicillatus* (Alcock, 1905), and *P. chinensis* (Osbeck, 1765) used lipids. Rosas et al. (2002) showed that the marine shrimp *Litopenaeus vannamei* (Boone, 1931) used proteins (O:N approximately 10) as a source of energy, having and the capacity to synthesize dietary carbohydrates through the gluconeogenic pathway. Although a large number of crustaceans use proteins as an energy substrate, Claybrook (1983) noted that proteins can be used when they occur in excess in the diet, when the profile of amino acids is unbalanced, or when the energy of lipids and carbohydrates is insufficient to supplement metabolic processes. Commercial foods for shrimp are produced based on marine shrimps, but the protein needs of freshwater species may be different.

The atomic O:N ratio suggests the use of proteins as an energy substrate in GC2 and a mixture of proteins and carbohydrates in CC and GC1. Augusto and Masui (2014) verified the use of proteins in TC fed the same food used in our experiments. Although the food exhibits a suitable calorie content (330 kcal (100 g)\(^{-1}\)), which ranges from 310 to 410 kcal (100 g)\(^{-1}\) in crustaceans (Cuzon and Guillaume, 1997), it may be inappropriate in terms of raw materials for growth. The energetic content and the energy:protein ratio are important factors to be considered in the diet because if the diet is very rich in protein, it may lead to an increase in the ingestion rate, and an increase in energy content may reduce food consumption before the protein needs are met (Pezzato et al., 2003). Bautista (1986) and Shiau and Peng (1992) suggested that an energy:protein ratio of 125 mg protein kcal\(^{-1}\) is ideal for growth of the marine
shrimp *P. monodon*. Protein is a limiting growth factor and is needed in higher proportions compared to carbohydrates and lipids. Protein levels from 35 to 45% in the food have been suggested as ideal for the growth of marine shrimps (Chuntapa et al., 1999). Santos et al. (2014) verified higher proteolytic activities in the hepatopancreas of farmed *M. amazonicum* compared to wild shrimps and suggested that changes in farmed prawns may be an adaptation to aquaculture conditions.

Metabolism

The energy expended in metabolic processes, the total sum of all chemical reactions taking place in an organism, as measured by oxygen consumption, is used for the maintenance of homeostasis, including locomotion, growth, and reproduction (Diaz-Iglesias et al., 2012; McGaw et al., 2013; Mazzarelli et al., 2015). The individual oxygen consumption rate in *M. amazonicum* is directly related to the size of the animals, and it is higher in the GC1 and GC2 morphotypes (Table 1). The oxygen consumption verified in TC (0.01 ± 0.003 g O₂ ind⁻¹ day⁻¹) by Augusto and Masui (2014) is even lower than that obtained here for CC (0.03 ± 0.001 g O₂ ind⁻¹ day⁻¹). The oxygen consumption rates in dry specific-mass usually decreases with an increase in body mass. The GC2 morphotype of *M. amazonicum* had a tendency to have a lower specific dry mass oxygen consumption, but there is no statistically significant difference between the morphotypes (Fig. 1). Moraes-Riodades and Valenti (2004) suggested that the GC1 and GC2 morphotypes are more sedentary because they have a very large cheliped that reduces swimming ability. In contrast, the morphotypes TC and CC have smaller chelipeds, which allows them to be more active. The possibility cannot be ruled out that in nature as well as in hatcheries, TC and CC males spend additional energy running away from larger morphotypes such that energy is channelled into locomotion. Under laboratory conditions, however, there were no large differences between the morphotypes.

The oxygen consumption rates of *M. amazonicum* are similar to those of other freshwater decapods (Table 2), especially the carideans *M. rosenbergii* and *Palaemon peringueyi* (Stebbing, 1915) and the marine *Litopenaeus vannamei*. The differences observed in the literature may be the consequence of a species-specific response, or the ontogenetic stage evaluated, temperature, or diet. The size of respirometric chambers can also influence these values because animals that are kept in much smaller spaces will only have their basal metabolism evaluated, whereas those kept in larger spaces will have their intermediate metabolism measured.

**Table 2.** Oxygen consumption (μg (mg MS)⁻¹ h⁻¹) in selected natantian decapods. The studies did not evaluate oxygen consumption between males and females separately.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Oxygen Reference</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Macrobrachium amazonicum</em></td>
<td>Adult 1.5 (GC2) to 2.1 (GC1) (30°C)</td>
<td>This study</td>
</tr>
<tr>
<td><em>M. amazonicum</em></td>
<td>Adult 2.04 ± 0.18 (30°C) (TC)</td>
<td>Augusto and Masui (2014)</td>
</tr>
<tr>
<td><em>M. amazonicum</em></td>
<td>Adult 1.5 (30°C)</td>
<td>Zanders and Rodriguez (1992)</td>
</tr>
<tr>
<td><em>M. rosenbergii</em></td>
<td>Adult 1.3-1.8</td>
<td>Gonzales-Peña and Moreira (2003)</td>
</tr>
<tr>
<td><em>M. acanthurus</em> (Wiegmann, 1836)</td>
<td>Post-larvae 0.6 (20°C)</td>
<td>Moreira et al. (1983)</td>
</tr>
<tr>
<td><em>M. heterochirus</em> (Wiegmann, 1836)</td>
<td>Adult 0.4 (20°C)</td>
<td>Moreira et al. (1983)</td>
</tr>
<tr>
<td><em>M. nipponense</em> (de Haan, 1849)</td>
<td>Adult 0.4-0.5 (25°C)</td>
<td>Wang et al. (2003)</td>
</tr>
<tr>
<td><em>Litopenaeus schmitti</em> (Burkenroad, 1936)</td>
<td>Adult 0.4</td>
<td>Barbieri (2007)</td>
</tr>
<tr>
<td><em>Palaemon peringueyi</em> (Osbeck, 1765)</td>
<td>Adult 1.0 (17 S) and 2.4 (3 S)</td>
<td>Li et al. (2007)</td>
</tr>
<tr>
<td><em>Farfantepenaeus californiensis</em> (Holmes, 1900)</td>
<td>Juvenile 0.7 (30°C)</td>
<td>Ocampo et al. (2003)</td>
</tr>
<tr>
<td><em>Penaeus japonicus</em> (Bate, 1888)</td>
<td>Adult 0.3 (25 S, 25°C)</td>
<td>Kulkarni and Josh (1980)</td>
</tr>
<tr>
<td><em>P. chinensis</em> (Osbeck, 1765)</td>
<td>Adult 1.0</td>
<td>Chen and Nan (1994)</td>
</tr>
<tr>
<td><em>L. vannamei</em></td>
<td>Adult 1.0 (GC2) to 2.1 (GC1) (30°C)</td>
<td>This study</td>
</tr>
</tbody>
</table>

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