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# Balanço Energético Dinâmico de Morfotipos dos Camarões das Espécies *Macrobrachium rosenbergii* e *Macrobrachium amazonicum*

**Samantha Abreu Alves dos Santos**

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**Candidata: Samantha Abreu Alves dos Santos**

**Orientador: Dr. Fabio Stucchi Vannucchi**

**Coorientador: Dr. Gustavo Maruyama Mori**

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**ABSTRACT:** The prawn species *Macrobrachium rosenbergii* De Man 1879 and *Macrobrachium amazonicum* Heller 1862, (Decapoda: Caridea) have different morphotypes for males and females. The polymorphism observed in these prawns is the manifestation of a conditional strategy that, beyond its biological interest, has a strong productive relevance for aquaculture purposes. Four hypotheses have been proposed to explain the proximal mechanisms that cause polymorphic expressions: competition for food, social hierarchy and aggression, altered efficiency of food absorption, and hyperactivity of subordinate individuals. However, understanding these mechanisms involves knowledge of the energy dynamics and the metabolism of these prawns at individual level, something difficult to assess experimentally in the given context. In this work we demonstrate that the DEB theory can reproduce the growth of polymorphic species. This dissertation is divided into four chapters. The first chapter presents the theoretical basis of the Dynamic Energy Budget (DEB) theory. This theory models the dynamic of organisms, from cells to ecosystems, with an approach based on the balance of mass and energy. In the second chapter, we evaluate the hypotheses regarding the morphotypes of *M. rosenbergii* from the perspective of DEB theory. In the third chapter we used DEB theory to reproduce the different physiological characteristics presented by *M. amazonicum* morphotypes. Using experimental data obtained from the literature we parameterized the models of the diverse morphotypes and, based on the parameter estimates, we evaluated the plausibility of the hypotheses raised. Lastly, in the last chapter, we present a general conclusion, discussing how the DEB model can support polymorphism studies in different areas.

**Keywords:** Dynamic Energy Budget (DEB) theory, Alternative reproductive tactics, Polymorphism, Physiological parameterization, *Macrobrachium spp.*.

**RESUMO:** As espécies de camarão *Macrobrachium rosenbergii* De Man 1879 e *Macrobrachium amazonicum* Heller 1862, (Decapoda: Caridea), apresentam diversos morfotipos de machos e fêmeas. O polimorfismo presente nestes camarões é a manifestação de uma estratégia condicional que, para além do interesse biológico, tem relevância produtiva para fins de criação em aquicultura. Quatro hipóteses vêm sendo estudadas para explicar os mecanismos proximais que levam às expressões polimórficas: competição por alimento, hierarquia social e agressividade, eficiência alterada na absorção de alimentos, e hiperatividade de indivíduos subordinados. No entanto, a compreensão acerca desses mecanismos envolve o conhecimento da dinâmica energética do metabolismo em nível individual dos camarões, algo de difícil acesso experimental. Neste trabalho iremos demonstrar que a teoria do Balanço Energético Dinâmico (DEB, do inglês "*Dynamic Energy Budget*") pode reproduzir o crescimento de espécies polimórficas Esta dissertação foi dividida em quatro capítulos. O primeiro capítulo apresenta uma breve descrição da teoria DEB. Tal teoria modela a dinâmica de organismos, desde células até ecossistemas, com uma abordagem baseada no balanço de massa e energia. No segundo capítulo, avaliamos as hipóteses acerca dos morfotipos de *M. rosenbergii* sob a perspectiva da teoria DEB. No terceiro capítulo, utilizamos a teoria DEB para reproduzir as diferentes características fisiológicas apresentadas pelos morfotipos do *M. amazonicum*. Por meio de dados experimentais obtidos na literatura, parametrizamos os modelos dos diversos morfotipos e, com base nas estimativas dos parâmetros, avaliamos a plausibilidade das hipóteses levantadas. No último capítulo, apresentamos uma conclusão geral, demonstrando como o modelo DEB pode auxiliar nos estudos sobre polimorfismo em diferentes áreas.

**Palavras-chave:** Teoria do Balanço Energético Dinâmico (DEB), Táticas reprodutivas alternativas, Polimorfismo, Parametrização fisiológica, *Macrobrachium spp.*.

SUMÁRIO

# INTRODUÇÃO

A maioria das espécies tendem a desenvolver uma unica morfologia em cada sexo, porém em alguns casos a evolução resulta em uma diversidade fenotipica com a existencia de multiplas morfologias em ambos os sexos (Karplus & Barki, 2019). O termo polimorfismo é utilizado para nomear essa diversidade morfológica quando essas formas distintas ocorrem no mesmo habitat, sendo que a mais rara delas não pode ser mantida por mutação recorrente (Ford, 1945; Wilson, 1953). Fenótipos alternativos, ou morfotipos, de machos vêm sendo reportados em várias espécies, e a existência de morfotipos de machos pode resultar em táticas reprodutivas alternativas (Jorge *et al.*, 2014).

As "táticas reprodutivas alternativas" (ART, acrônimo para o termo em inglês *Alternative Reproductive Tatics*) são definidas como a presença de dois ou mais caracteres reprodutivos distintos em indivíduos de mesmo sexo em uma população (Taborsky *et al.*, 2008; Davies *et al.*, 2012). As causas teórico-evolutivos do surgimento e manutenção de caracteres reprodutivos descontínuos permanecem em debate (Brockmann, 2001; Engqvist & Taborsky, 2016; Wade & Shuster, 2005) assim como os mecanismos genéticos e fisiológicos que levam à polimorfia reprodutiva (Oliveira *et al.*, 2005; Schradin *et al.*, 2009). Diversas pesquisas têm procurado caracterizar e sistematizar as táticas reprodutivas alternativas em diversos grupos de animais (Taborsky *et al.*, 2008; Nason & Kelly, 2020; Lichter *et al.*, 2020). O polimorfismo é definido como um conjunto de ART pertencentes a uma estratégia condicional que podem ser consideradas um quase-monomorfismo genético (Gross, 1996) incluindo um "limiar de plasticidade de caracteres" (*phenotypically plastic threshold traits*) como justificativa para essas mudanças fenotípicas. A presença ou ausência de determinado traço está baseada em um mecanismo sutil: uma variável fenotípica hereditária subjacente determina o limiar ambiental a partir do qual o caractere será expresso ou não (Tomkins & Hazel, 2007; Wright, 1920).

As espécies de camarão *Macrobrachium rosenbergii* De Man 1879 e *Macrobrachium amazonicum* Heller 1862, (Decapoda: Caridea), apresentam táticas reprodutivas peculiares que incluem diversos morfotipos de machos (Maciel & Valenti, 2009; New, 2002; Kuris *et al.* 1987; Ra´Anan & Sagi, 1985). Para além do interesse biológico, o estudo da polimorfia destas espécies tem relevância produtiva pois - num contexto de crescente valorização do camarão como produto pesqueiro devido ao seu grande valor econômico, alto valor nutritivo e o aumento da aceitação pelo mercado consumidor - a determinação dos morfotipos tem impacto direto em seu cultivo (New *et al.*, 2009; Banu *et al.*, 2016).

A proporção morfológica é, na maioria das vezes, constante em diversas condições ambientais, porém vários experimentos têm mostrado que a densidade populacional pode afetar essa proporção (D´Abramo *et al.* 1989; Ra´Anan & Sagi, 1985). Simulações de modelos baseados em indivíduos (*Individual Based Model* – IBM) indicam que o aumento da densidade populacional levaria a uma estratégia evolutiva estável que favorece proporcionalmente os machos dominantes (Santos & Vannucchi, 2017; Santos & Vannucchi, 2019). Tais simulações consideraram aspectos comportamentais destes camarões em situações ideais, mas não levavam em conta o custo energético de cada morfotipo e nem os processos de transformação entre os diversos morfotipos. No entanto, compreender como o fluxo de energia resulta em diferentes táticas comportamentais é extremamente difícil em situações naturais ou experimentais. Uma possível alternativa para se comparar diferenças metabólicas em nível individual é por meio da teoria do balanço energético dinâmico (DEB, acrônimo do inglês *Dynamic Energy Budget*).

A teoria DEB tem o propósito de modelar a dinâmica dos sistemas biológicos por meio da descrição quantitativa de fluxos de massas e energia. De acordo com essa teoria, o indivíduo é considerado a unidade de interesse para compreensão de sistemas dinâmicos com níveis superiores de organização (Martin *et al.*, 2012). Em sua versão padrão, a teoria considera um organismo de crescimento isomórfico, descrito quantitativamente por reserva, estrutura, maturidade e reserva reprodutiva. Estas variáveis de estado têm sua dinâmica determinada por um sistema de equações diferenciais ordinárias acopladas, sendo este sistema baseado em processos fisiológicos e em relações alométricas. Diversos aspectos internos e externos ao sistema são introduzidos na teoria por meio de parâmetros e variáveis forçantes. Os parâmetros usados nas equações diferenciais são valores determinados geneticamente, mas envolvem adaptações em escala individual (Kooijman, 2010).

A teoria DEB permite modelar, com sua estrutura quantitativa, desde a aquisição até o uso dos recursos pelos organismos em suas diversas fases ontogenéticas, gerando respostas que se modificam com o tempo e que são essenciais para compreender o ciclo de vida, como o crescimento, maturidade, reprodução e dinâmicas ambientais (Martin *et al.*, 2012). As características distintas de cada organismo (ou espécie) são mapeadas em diferenças nos valores dos parâmetros do sistema de equações diferenciais (Sousa *et al.*, 2008). Essa flexibilidade permite simulações mais complexas, preservando uma estrutura simples e organizada, principalmente em cenários com várias espécies, alto número de coortes, predação, competição e diversidade de alimentos (Saraiva, 2019).

Dentro da teoria DEB existem várias extensões que permitem a flexibilidade dos modelos, com adaptações ou acréscimo de equações diferenciais. Isso permite, por exemplo, incluir diversos tipos de alimentos, considerar outras formas de reserva, e compreender as alterações na forma durante o crescimento, dentre outras extensões (Kooijman, 2010). Huvet *et. al.* (2008), por exemplo, utilizaram esse modelo para demonstrar como o polimorfismo do gene da amilase está ligado ao crescimento da ostra do pacífico, *Crassostrea gigas*. O polimorfismo do gene se relaciona com a ingestão de alimentos, que acaba se expressando em diferença no crescimento dos indivíduos (Huvet *et al.*, 2008). No trabalho de Groeneveld & Westerhoff (2000), a teoria DEB foi utilizada para compreender a mudança metabólica de cepas polimórficas da levedura industrial *Kluyveromyces marxianus* em suas duas formas, esferóide e alongada. As cepas alongadas apresentam um aumento em sua superfície, resultando em uma maior área de superfície e levando a um aumento da capacidade de absorção para nutrientes, permitindo um maior crescimento, ao contrário das cepas esferóides (Groeneveld & Westerhoff, 2000.).

Neste trabalho, utilizaremos a teoria DEB para reproduzir as diferentes formas de crescimento entre as fêmeas e os diversos morfotipos dos machos. Tanto para *M. rosenbergii* como para *M. amazonicum*, dois diferentes modelos foram desenvolvidos, com base nas hipóteses de mecanismos evolutivos para observar as diferenças nas previsões do desenvolvimento dessas espécies polimórficas. Com esses modelos tentaremos recriar as diferentes características fisiológicas entre fêmeas e os morfotipos dos machos para a espécie *M. amazonicum*.

O primeiro capítulo desta dissertação descreve, resumida e matematicamente, conceitos básicos da teoria DEB, focando no crescimento e nos diferentes mecanismos que diferenciam os indivíduos. Além disso, explica os pacotes computacionais e a parametrização dos modelos produzidos para realização deste trabalho.

O segundo capítulo é um manuscrito de artigo científico, intitulado "*Two dynamic energy budget models and the evolution mechanisms for polymorphic prawns Macrobrachium rosenbergii*". Esse artigo apresenta uma perspectiva evolutiva e visa a interpretar quais mecanismos evolutivos de diferenciação podem explicar o polimorfismo no *M. rosenbergii*.

O capítulo 3, é um manuscrito de artigo científico intitulado "*Can a DEB model based on growth data predict physiological characteristics of polymorphic species?*". Esse artigo demonstra como o modelo DEB pode reproduzir adequadamente características fisiológicas para os diferentes morfotipos da espécie *M. amazonicum*.

E por último, temos as conclusões gerais baseadas nos resultados obtidos com a aplicação da teoria DEB para descrever e estudar as espécies *M. amazonicum* e *M. rosenbergii*.

# CAPÍTULO 1 - O Balanço Energético Dinâmico

A teoria de Balanço Energético Dinâmico (DEB, sigla em inglês para "*Dynamic Energy Budget*"), proposto por Kooijman (1986; 2010), descreve matematicamente processos bioenergéticos em nível individual, como desenvolvimento, reprodução e metabolismo de organismos vivos. O "*standard DEB model* (STD)" é o modelo padrão, que considera um organismo genérico isomórfico, ilustrado na Figura 1.1, o qual possui uma reserva que mantém o metabolismo e outra que compõem o organismo e necessita de manutenção (Kooijman , 2010).

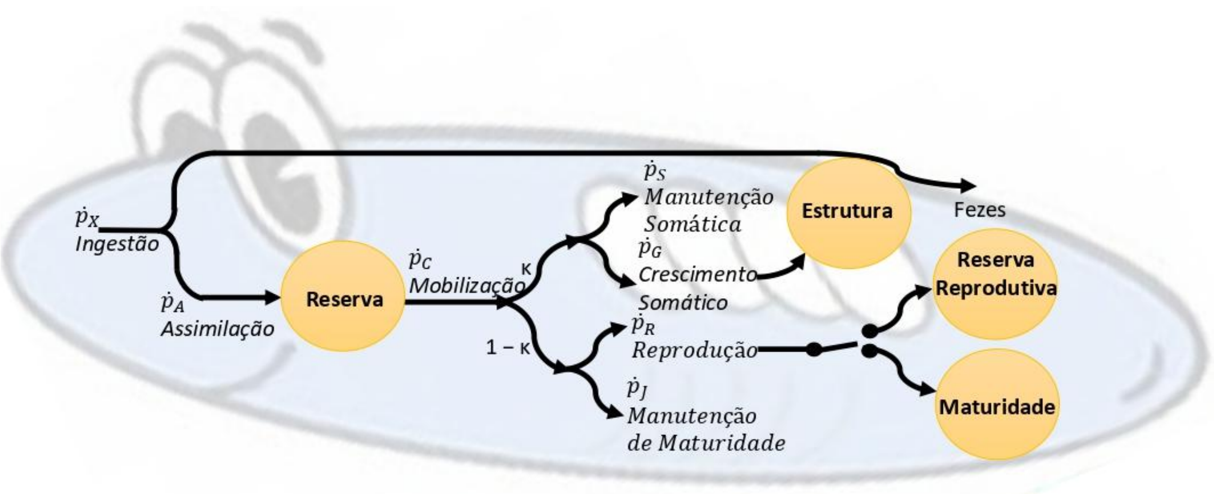

*Figura 1.1: Ilustração dos fluxos de energia em um organismo padrão no modelo DEB proposto por Kooijman (1986, 2010)*

O modelo padrão da teoria DEB utiliza equações diferenciais para descrever um organismo, a teoria pode ser desenvolvida com base em quatro variáveis de estado (Kooijman, 1986; Kooijman, 2009):

- Reserva $E$, a quantidade de energia armazenada por todo organismo;
- Estrutura $V$, o volume estrutural, $V = L^3$, onde $L$ representa o comprimento estrutural;
- Reserva alocada na maturação $E_H$, a energia (ou informação) referente à maturidade do indivíduo acumulada ao longo da vida. Cada etapa da vida está associada a um limiar de $E_H$, e com base nessas quantidades pode-se definir o estágio de desenvolvimento do indivíduo;
- Reserva reprodutiva $E_R$, a energia destinada para reprodução após a maturidade.

A teoria DEB supõe alguns conceitos homeostáticos, como homeostase forte, homeostase fraca, homeostase estrutural, homeostase de aquisição e homeostase termal (Kooijman, 2009; Kooijman, 2010; Souza *et al.* 2010).

- Homeostase forte são os componentes do metabolismo com compostos generalizados, que não alteram a composição, como alimento, tecido de reserva, estrutura reprodutiva e somática. Por exemplo, o indivíduo se alimenta de substrato e no modelo padrão DEB assume-se que a composição química desse alimento é fixa (Kooijman, 2009; Kooijman, 2010; Souza *et al.* 2010).
- Homeostase fraca é a composição do indivíduo que não se altera ao longo da vida em ambientes com fornecimento de alimento constante. A razão entre reserva e estrutura somática representa a composição, que altera em diferentes ambientes e disponibilidade de alimento. Quando acompanhamos o crescimento de um indivíduo, com uma alimentação constante, o seu peso corporal é proporcional a quantidade de estrutura (Kooijman, 2009; Kooijman, 2010; Souza *et al.* 2010).
- Homeostase estrutural, o indivíduo não altera sua forma ao longo da vida (isomorfo) (Kooijman, 2009; Kooijman, 2010; Souza *et al.* 2010).
- Homeostase de aquisição, o indivíduo se alimenta da quantidade necessária para se saciar e não depende da disponibilidade de alimento no ambiente (Kooijman, 2009; Kooijman, 2010; Souza *et al.* 2010).
- Homeostase termal, o indivíduo gasta energia para manter a temperatura corporal constante, esse conceito é fundamental para organismos endotérmicos (Kooijman, 2009; Kooijman, 2010; Souza *et al.* 2010).

O fluxo de massa e energia são definidos por equações diferenciais, e se inicia com a ingestão do alimento (Kooijman, 2010; Souza *et al.* 2010).

## 1.Ingestão e assimilação

No modelo padrão da teoria DEB a ingestão de alimento é proporcional à área estrutural externa do organismo. Essa relação pode ser expressa por $\dot{p}_X = \{\dot{p}_X\}L^2$, em que $\dot{p}_X$ é o fluxo de ingestão, $L^2$ é a área estrutural externa do organismo e $\{\dot{p}_X\}$ é a capacidade de ingerir alimento por unidade de área ao longo do tempo (Kooijman, 2009, pág.: 24-34; Kooijman, 2010, pág.: 15-17). Porém, essa relação não demonstra a relação entre o consumo e a disponibilidade de alimento. Inserindo uma nova variável forçante, a resposta funcional $f$, é possível descrever a relação entre a ingestão do organismo com o alimento existente no meio (Kooijman, 2009, pág.: 24-34; Kooijman, 2010, pág.: 15-17). A resposta funcional $f$ é adimensional, variando entre 0 e 1, sendo 0 a ausência total de alimento e 1 a alimentação máxima. O método mais comum para modelar a resposta funcional na teoria DEB é a função hiperbólica de Holling do tipo II:

$$f = \frac{X}{X_k + X},$$

(1.1)

sendo $X_k$ é uma constante de meia-saturação indicando a concentração de alimento em que a ingestão é metade da ingestão máxima, e $X$ é a concentração de alimento no ambiente (Kooijman, 2009, pág.: 24-34; Kooijman, 2010, pág.: 15-17). O comportamento dessa curva é demonstrado na figura 1.2.

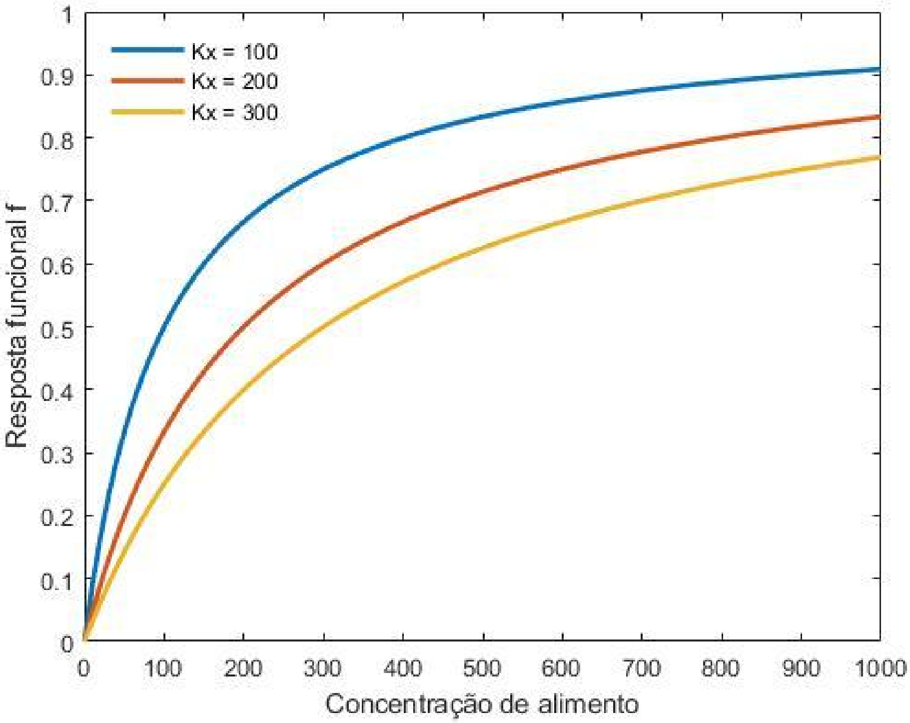

*Figura 1.2: Resposta funcional f para uma concentração de alimento hipotético no modelo DEB.*

Dessa forma a ingestão de alimento pode ser escalonada com a resposta funcional, obtendo assim a potência de ingestão de um organismo, que é representada por (Kooijman, 2009, pág.: 24-34; Kooijman, 2010, pág.: 15-17):

$$\dot{p}_X = \{\dot{p}_{Xm}\} L^2 f.$$

(1.2)

No contexto da teoria DEB, a definição de assimilação é a transformação do alimento em reserva, porém o alimento não é completamente assimilado pelo organismo, sendo parte convertida em fezes (Kooijman, 2009, pág.: 35; Kooijman, 2010, pág.: 18).

A proporção de alimento assimilado em relação ao total consumido é nomeado de $\kappa_X$, logo, $\dot{p}_X = \kappa_X \dot{p}_A$, onde $\dot{p}_A$ é a taxa de assimilação do organismo. Essa equação, no modelo padrão, também pode levar em conta a superfície de absorção por unidade de área, semelhante à equação de ingestão $\dot{p}_X$. Nesse caso, a energia máxima que o organismo é capaz de assimilar por unidade de superfície e de tempo é chamada de $\{\dot{p}_{Am}\}$ (Kooijman, 2009, pág.: 35; Kooijman, 2010, pág.: 18):

$$\dot{p}_A = \{\dot{p}_{Am}\} L^2 f. \tag{1.3}$$

## 2.Reserva

A reserva $E$ armazena energia que é utilizada para todas as funções do organismo, além de amenizar os impactos da instabilidade no fornecimento de alimento do meio. A equação que representa a dinâmica da reserva é (Kooijman, 2009, pág.: 35-40; Kooijman, 2010, pág.: 18-19):

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C. \tag{1.4}$$

Essa equação demonstra o balanço energético entre a assimilação $\dot{p}_A$ e a energia mobilizada $\dot{p}_C$. Assim como na ingestão e assimilação, uma nova variável pode ser inserida, nesse caso, a quantidade de energia por unidade de volume, $[E]$ (Kooijman, 2009, pág.: 35-40; Kooijman, 2010, pág.: 18-19):

$$[E] = \frac{E}{V}. \tag{1.5}$$

Se derivarmos $[E]$, com a regra do quociente, substituindo $\frac{dE}{dt}$ por $\dot{p}_A - \dot{p}_C$ e acrescentando uma taxa de crescimento relativa $\dot{r} = \frac{1}{V}\frac{dV}{dt}$, que representa a variação do volume do organismo por unidade de volume, chegamos em (Kooijman, 2009, pág.: 35-40; Kooijman, 2010, pág.: 18-19):

$$\frac{d[E]}{dt} = [\dot{p}_A] - [\dot{p}_C] - [E]\,\dot{r} \tag{1.6}$$

Seguindo as premissas da homeostase fraca e forte, de acordo com as quais a mobilização da reserva é independente do alimento disponível no meio e outra que indica que o organismo distribui de forma proporcional a sua reserva para todos os tecidos, é possível simplificar a equação da taxa de mobilização do organismo (Kooijman, 2009, pág.: 35-40; Kooijman, 2010, pág.: 18-19):

$$\dot{p}_C = E\left(\frac{\dot{v}}{L} - \dot{r}\right). \tag{1.7}$$

O parâmetro $\dot{v}$ representa a condutância de energia, ou seja, a movimentação de energia no organismo. Sendo assim, substituindo $\dot{p}_A$, $\dot{p}_C$, $\dot{r}$ e considerando $L^3$ como o volume estrutural, obtém-se a equação para a dinâmica da reserva do organismo, (Kooijman, 2009, pág.: 35-40; Kooijman, 2010, pág.: 18-19)

$$\frac{d[E]}{dt} = \frac{\{\dot{p}_{Am}\}}{L} f - [E]\,\frac{\dot{v}}{L}. \tag{1.8}$$

## 3.Kappa e manutenção somática

Na teoria DEB a reserva é destinada para os processos metabólicos do organismo, como mostrado na Figura 1.1. A manutenção somática ($\dot{p}_S$), crescimento ($\dot{p}_G$), manutenção reprodutiva ($\dot{p}_J$) e a reprodução ($\dot{p}_R$), são os processos que mobilizam a reserva, por isso a mobilização de energia pode ser demonstrada por: $\dot{p}_C = \dot{p}_S + \dot{p}_G + \dot{p}_J + \dot{p}_R$ (Kooijman, 2009, pág.: 40-44; Kooijman, 2010, pág.: 19).

Uma suposição comum a diversos modelos da teoria DEB (o modelo padrão inclusive) assume que uma proporção fixa dessa energia mobilizada é destinada para manutenção e crescimento, essa porção é chamada de fração *kappa* e é representada por κ. Essa proporção permanece fixa, no modelo padrão, durante todo o ciclo de vida e os custos com a manutenção de estrutura são supridos prioritariamente. O excedente de energia, $1 - \kappa$, é utilizado nos processos metabólicos restantes: manutenção de maturidade, maturação e reprodução (Kooijman, 2009, pág.: 40-44; Kooijman, 2010, pág.: 19).

A manutenção somática é o gasto que o organismo tem para manter a homeostase fisiológica, incluindo processos como termorregulação, regulação osmótica, reposição de proteínas e outros (Kooijman, 2009, pág.: 40-44; Kooijman, 2010, pág.: 19). Esses custos podem ser expressos pela taxa $\dot{p}_S$ e é definida por:

$$\dot{p}_S = \left[\dot{p}_M\right]L^3 + \left\{\dot{p}_T\right\}L^2, \tag{1.9}$$

sendo $\left[\dot{p}_M\right]$ o custo geral da manutenção por unidade de volume e $\left\{\dot{p}_T\right\}$ o gasto com manutenção relacionado à área do organismo em contato com o meio (Kooijman, 2009, pág.: 40-44; Kooijman, 2010, pág.: 19). Esse último parâmetro pode estar, por exemplo, ligado à perda de calor para o meio em organismos endotérmicos, mas também pode ser usado para descrever outras formas de perda de energia para o ambiente, como o custo energético da osmorregulação (Kooijman, 2009, pág.: 40-44; Kooijman, 2010, pág.: 19).

## 4.Crescimento

O excedente energético entre a fração *kappa* e a manutenção somática é destinada para o crescimento, e assim temos que $\dot{p}_G = \kappa\dot{p}_C - \dot{p}_S$. A taxa de crescimento $\dot{p}_G$, por outro lado, também está relacionada com o custo de energia por unidade de volume da estrutura $[E_G]$ e de quanto o volume varia $\frac{dV}{dt}$, então $\dot{p}_G = [E_G]\frac{dV}{dt}$. A partir das duas equações temos que

$\left[E_G\right]\frac{dV}{dt} = \kappa\dot{p}_C - \dot{p}_S$. Substituindo $\dot{p}_C$ e $\dot{p}_S$, considerando $L = V^{1/3}$ e isolando $\frac{dV}{dt}$, obtemos a equação diferencial do crescimento em termos de volume para organismo isomórficos (Kooijman, 2009, pág.: 48-49; Kooijman, 2010, pág.: 21-22):

$$\frac{dV}{dt} = \frac{\kappa E\frac{\dot{v}}{V^{1/3}} - \left[\dot{p}_M\right]V - \left\{\dot{p}_T\right\}V^{2/3}}{\frac{\kappa E}{V} + [E_G]} . \tag{1.10}$$

Outra forma de se obter a variação do volume é relacionar o tamanho com unidade de comprimento estrutural do organismo, substituindo $E$ por $[E]V$ e $V$ por $L^3$. Desta maneira, temos a representação do crescimento em termos do comprimento (Kooijman, 2009, pág.: 48-49; Kooijman, 2010, pág.: 21-22):

$$\frac{dL}{dt} = \frac{\left[\dot{p}_M\right]}{3\left([E]\kappa + [E_G]\right)}\left(\frac{\kappa[E]\dot{v} - \left\{\dot{p}_T\right\}}{\left[\dot{p}_M\right]} - L\right) \tag{1.11}$$

que, em conjunto com a Eq. 1.8, representa o sistema de equações diferenciais que determina o crescimento de um organismo (após seu nascimento) de acordo com o modelo padrão (Kooijman, 2009, pág.: 48-49; Kooijman, 2010, pág.: 21-22).

## 4.1. Crescimento no *standard DEB model (STD)*

Seguindo a premissa da homeostase fraca, em concentrações de alimento constante não há variação na razão entre estrutura e reserva e a densidade de reserva é constante, $[E] = [E]^*$. Portanto, quando a concentração de alimento é constante, $\frac{d[E]}{dt}$ tende a zero. Assim podemos simplificar a equação 1.11 que representa o crescimento em termos do comprimento, chegando em (Kooijman, 2009, pág.: 48-51; Kooijman, 2010, pág.: 21-22):

$$\frac{dL}{dt} = \dot{r}_B\left(L_\infty - L\right) . \tag{1.12}$$

O tamanho máximo assimptótico do organismo é representado por $L_{\infty} = \frac{\kappa[E]^{*}\dot{v} - \{\dot{p}_T\}}{[\dot{p}_M]}$ e o coeficiente de crescimento de von Bertalanffy é $\dot{r}_B = \frac{[\dot{p}_M]}{3([E]^{*}\kappa + [E_G])}$. Para conseguirmos o crescimento em função do tempo integra-se a equação, obtendo (Kooijman, 2009, pág.: 48-51; Kooijman, 2010, pág.: 21-22):

$$L(t) = L_{\infty} - (L_{\infty} - L_b)e^{-\dot{r}_B t},$$

(1.13)

onde $L_b$ é o comprimento do organismo ao nascer. Essa equação é conhecida como "curva de crescimento de von Bertalanffy" (Kooijman, 2009, pág.: 48-51; Kooijman, 2010, pág.: 21-22), exemplificada para diversos valores de $L_{\infty}$ e $\dot{r}_B$ na Figura 1.3.

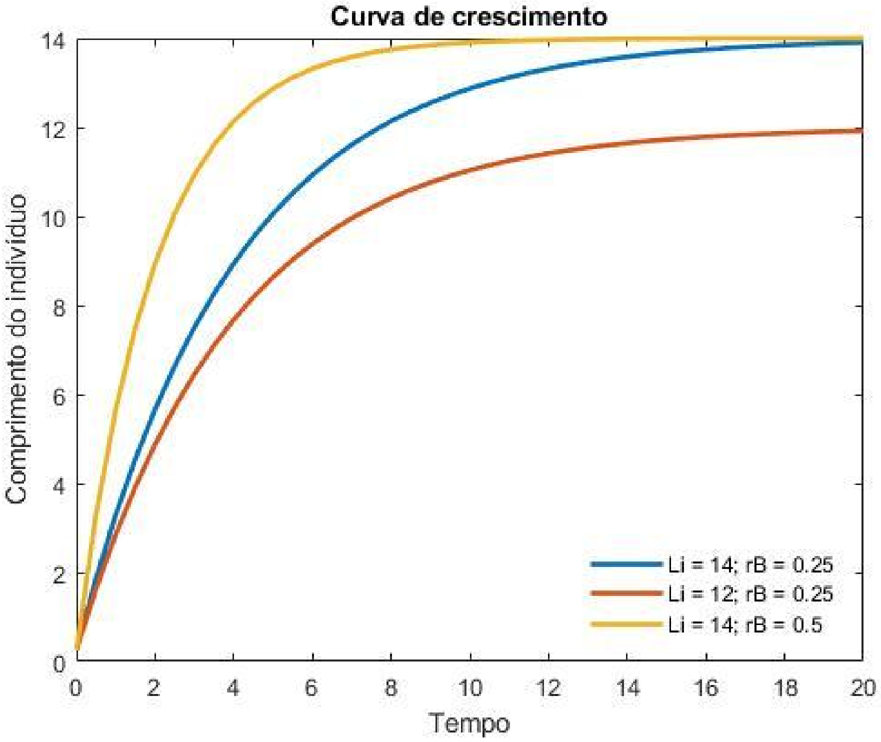

*Figura 1.3: Curva de crescimento análoga à de von Bertalanffy para um organismo hipotético no modelo DEB*

### 4.2. Crescimento com fase de aceleração (ABJ)

O modelo padrão, *standard DEB model (STD)*, considera o metabolismo de um organismo isomorfo, que não muda ao longo da vida. Entretanto, como nem todo organismo segue esse tipo de desenvolvimento, e para lidar com essas características, a teoria DEB apresenta diversas extensões. Uma delas é o modelo ABJ. No geral, esse modelo é semelhante ao modelo STD, mas apresenta uma aceleração entre o nascimento e a metamorfose do tipo *V1-morph*, na qual um organismo que muda de forma durante o crescimento de tal forma que a sua área de superfície é proporcional ao seu volume (Kooijman, 2009, pág.: 122-127; Kooijman, 2010, pág.: 30-31). Nesse período de aceleração no crescimento, a unidade de volume substitui a unidade de área na Eq. (1.3). Antes e depois desse período de aceleração, o organismo é isomórfico. A metamorfose antes da puberdade ocorre com maturidade $E_H^j$, que pode ou não corresponder a mudanças na morfologia (Kooijman, 2009, pág.: 122-127; Kooijman, 2010, pág.: 30-31).

O crescimento larval apresenta essa aceleração resultando em um desenvolvimento distinto, o qual podemos representar por (Kooijman, 2009, pág.: 122-127; Kooijman, 2010, pág.: 30-31):

$$L(t) = L_b e^{\dot{r}_j \frac{(t-t_b)}{3}}. \tag{1.14}$$

Onde $\dot{r}_j = \frac{\left(\frac{f\kappa\{\dot{p}_{Am}\}-\{\dot{p}_T\}}{L_b}\right)-[\dot{p}_M]}{f\kappa[E_m]+[E_G]}$. A metamorfose marca o fim da fase larval, então para $t = t_j$ (Kooijman, 2009, pág.: 122-127; Kooijman, 2010, pág.: 30-31), temos:

$$L_j = L(t_j) = L_b e^{\dot{r}_j \frac{(t_j-t_b)}{3}}. \tag{1.15}$$

Considerando a continuidade dos fluxos obtemos, após a metamorfose (Kooijman, 2009, pág.: 122-127; Kooijman, 2010, pág.: 30-31),

$$L(t) = L_\infty - \left(L_\infty - L_j\right)e^{-\dot{r}_B(t-t_j)}, \tag{1.16}$$

sendo, no modelo ABJ, $L_\infty = \frac{s_M\kappa\{\dot{p}_{Am}\}f-\{\dot{p}_T\}}{[\dot{p}_M]}$ e $s_M = \frac{L_j}{L_b}$ (Kooijman, 2009, pág.: 122-127; Kooijman, 2010, pág.: 30-31).

## 5. Manutenção de maturidade

A fração $1 - \kappa$ da reserva mobilizada, é destinada para a maturação e a de manutenção de maturidade, no caso de embriões e juvenis, e para a reprodução, nos adultos.

A maturação é a utilização da reserva para aumentar o nível de maturidade $E_H$, este nível controla as alterações do metabolismo em diferentes fases da vida (Kooijman, 2009, pág.: 44-45; Kooijman, 2010, pág.: 20; Souza *et al.*, 2010). A manutenção de maturidade é a reserva usada para manter a complexidade da estrutura, e deve incluir a manutenção da regulação e o sistema de defesa, e é proporcional à maturidade(Kooijman, 2009, pág.: 47-48; Kooijman, 2010, pág.: 20; Souza *et al.*, 2010).

$$\dot{p}_J = \dot{k}_J E_H, \tag{1.17}$$

onde $\dot{k}_J$ é o coeficiente de manutenção da taxa de maturidade, que pode ser comparado ao coeficiente de manutenção somática $\dot{k}_M$. Nos casos em que a razão de manutenção, $k = \frac{\dot{k}_J}{\dot{k}_M}$, for igual a 1, esse fluxo é proporcional ao volume estrutural fixo e considerando $l_T = 0$, podemos simplificar a equação 1.17 (Kooijman, 2009, pág.: 47-48; Kooijman, 2010, pág.: 20; Souza *et al.*, 2010):

$$\dot{p}_J = (1 - \kappa) l^3. \tag{1.18}$$

Nos adultos, $\dot{p}_J$ é constante já que a maturidade é constante, $E_H = E_H^p$ (Kooijman, 2009, pág.: 47-48; Kooijman, 2010, pág.: 20; Souza *et al.*, 2010).

### 6.Reprodução

A reserva mobilizada começa a ser destinada para reprodução na puberdade, com o fim da maturação. A energia alocada para reprodução é:

$$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J, \tag{1.19}$$

onde $\dot{p}_J = \dot{k}_J E_H^p$, o $E_H$ é substituído pela constante $E_H^p$, pois o fluxo de maturidade é redirecionado para reprodução (Kooijman, 2009, pág.: 66-68; Kooijman, 2010, pág.: 22; Souza *et al.*, 2010).

A conversão da reserva da mãe para reserva da prole tem eficiência constante, porém essa alocação de energia é pequena, e é acumulada em uma reserva reprodutiva ao decorrer da vida. A reserva reprodutiva é convertida em reserva da prole, a quantidade de ovos produzidos são específicos das espécies e têm influência da temperatura e da quantidade de reserva reprodutiva (Kooijman, 2009, pág.: 66-68; Kooijman, 2010, pág.: 22; Souza *et al.*, 2010).

Uma fração da reserva reprodutiva $\kappa_R$ fixa é destinada aos ovos e o restante $\left(1 - \kappa_R\right)$ é dissipado. O custo por ovo é igual ao seu montante inicial de reserva $E_0$ e, considerando que a reprodução é um processo contínuo, a taxa de reprodução é (Kooijman, 2009, pág.: 66-68; Kooijman, 2010, pág.: 22; Souza *et al.*, 2010):

$$\dot{R} = \frac{\kappa_R \dot{p}_R}{E_0}. \tag{1.20}$$

Com base nesses conceitos, demonstraremos nos capítulos 2 e 3 diferentes aplicações de modelos DEB para descrever o crescimento das espécies polimórficas *Macrobrachium rosenbergii* e *M. amazonicum*.

## 7.Teoria DEB e palemonídeos

No portal "Add My Pet", que reúne os modelos feitos com base na teoria DEB para diversas espécies, existem quatro modelos para espécies da família *Palaemonidae*. As espécies *Palaemonetes pugio, Palaemonetes varians, Palaemon elegans* e *Macrobrachium vollenhoveni* possuem modelo DEB do tipo ABJ. Em todos esses modelos é interessante notar que foi considerado $\left\{\dot{p}_T\right\} = 0$, mostrando que a manutenção somática associada à superfície de área é praticamente nula, indicando o baixo investimento de energia nessa manutenção, um exemplo de manutenção somática associada a área externa do indivíduo é o controle da osmose.

O modelo da espécie *Palaemonetes pugio* apresenta o crescimento desde o nascimento até a fase adulta. Para a espécie *Palaemonetes varians* o modelo apresenta o crescimento da fase adulta da espécie e a influência da temperatura na duração da fase larval. No caso do *Palaemon elegans* temos o crescimento da fase adulta ao decorrer do tempo e a relação de fecundidade e comprimento. Para *Macrobrachium vollenhoveni* o modelo possui o crescimento ao decorrer do tempo ao longo da vida.

Os modelos dessas espécies não diferenciam machos e fêmeas, mesmo existindo características, sejam elas apenas fenotípicas ou fisiológicas, que diferenciam os sexos. Várias espécies apresentam características que diferenciam os indivíduos entre os gêneros e até mesmo diferenças entre indivíduos do mesmo gênero, e essas diferenças podem ser observadas no fluxo energético. Porém, a maioria dos modelos DEB não descrevem essas diferenças entre gêneros ou morfotipos.

As espécies polimórficas *Macrobrachium rosenbergii* e *M. amazonicum* apresentam morfotipos com características distintas. As principais características que diferem os morfotipos são o tamanho corporal e a coloração, e essas diferenças morfológicas se relacionam com as diferenças comportamentais que cada morfotipo apresenta. Essas diferenças entre os grupos morfológicos das espécies *M. rosenbergii* e *M. amazonicum*, as tornam ótimos objetos de estudo para observar como o fluxo de energia resulta em diferentes táticas comportamentais e características fisiológicas.

# CAPÍTULO 2 - “Two dynamic energy budget models and the evolutionary mechanisms for polymorphic prawns *Macrobrachium rosenbergii*”

Samantha Abreu Alves dos Santos[1, *], Tan Tjui Yeuw[1], Fabio Stucchi Vannucchi[1]

[1]Biosciences Institute, São Paulo State University - UNESP, São Vicente, São Paulo, Brazil

*E-mail: samantha.abreu@unesp.br

Highlights

- Dynamic Energy Budget (DEB) theory models the dynamics of organisms and can describe polymorphic species.
- We simulate two models for the prawn *Macrobrachium rosenbergii*: morphotype-specific assimilation with different assimilation rates and morphotype-specific somatic maintenance model with different somatic maintenance rates.
- By modifying a parameter we can simulate different growth curves in the same species
- Each model simulated hypotheses that cause polymorphic expressions.
- DEB theory can simulate different characteristics of polymorphic species.

## Abstract

In many animal species, from invertebrates to vertebrates, individuals of the same sex, usually males, exhibit more than one reproductive tactic. The species of prawns *Macrobrachium rosenbergii* De Man 1879, (Decapoda: Caridea), expressess different male morphotypes. This polymorphism is the manifestation of a conditional strategy which includes diverse alternative reproductive tactics that, besides biological interest, has a productive relevance. Four hypotheses have been studied to explain the mechanisms that cause polymorphic expressions: competition for food, social hierarchy and aggression, altered efficiency of food absorption, and hyperactivity of subordinate individuals. However, understanding these mechanisms involves knowledge of the energy dynamics and metabolic demands of these prawns at an individual level, a task that is difficult to access experimentally. Theoretical models can be an alternative to understand this mechanism. The Dynamic Energy Budget (DEB) theory models the dynamics of organisms, from cells to ecosystems, with an approach based on the balance between forms and energy. We parameterized two models differentiating morphotypes:

morphotype-specific assimilation (different assimilation rates) and morphotype-specific somatic maintenance (different somatic maintenance rates). Both models fit the data, but, overall, the relative errors of morphotype-specific assimilation model were smaller. This model relates to the hypotheses of altered efficiency of food absorption and social hierarchy and aggression. The population dynamics showed a hierarchy among males, which suggests that the social hierarchy and aggression hypothesis may be the cause of the differentiation in individuals.

**Keywords:** Dynamic Energy Budget theory, Polymorphism, *Macrobrachium rosenbergii*.

## 1.Introduction

Usually each sex of an animal develops a single morphology, but evolution can result in extreme phenotypic diversity among males and/or females. Normally this morphological diversity develops in males, exhibiting more than one reproductive tactic. Such matting mechanisms based on sexual selection are common among decapod crustaceans, including the genus *Macrobrachium* (Jorge *et al*. 2014; Karplus & Barki, 2019).

An example of species of the genus *Macrobrachium* that has polymorphism in males is the Malaysian giant prawn, *Macrobrachium rosenbergii* De Man 1879 (Decapoda: Caridea). Native to the Indo-Pacific (Freire & Silva, 2008), is extensively cultivated around the world and is one of the most important freshwater species in aquaculture. The species is highly resistant to diseases, has high growth rates and fecundity, and reproduces easily in captivity (Lima *et al.* 2015; Valenti *et al.* 2018).

*M. rosenbergii* presents polymorphism in adult males. At least three groups are described: Blue Claw (BC), Orange Claw (OC) and Small Male (SM). Each group has distinct morphology and behavior. BC males are large, dominant and territorial. The OC have an intermediate size and are submissive to BC males. And the SM males are smaller, submissive and highly mobile (Cohen *et al.*, 1981, Kuris *et al.*, 1987, Sagi & Ra´anan, 1985). Small males grow into other morphotypes in succession – SM-OC-BC – depending on the environment and ecological conditions, but not all males will reach the largest morphotypes. All morphotypes are stable and produce efficient gametes. The phenotype ratio tends to be fixed, SM:OC:BC = 5:4:1, but studies have demonstrated this ratio may change at high densities (D´Abramo *et al.* 1989; Karplus *et al.* 1986; Moraes-Riodades & Valenti, 2004).

Four hypotheses have been proposed to explain the mechanism that results in polymorphic expressions (Ibrahim, 2011). Food competition, social hierarchy and aggression, altered efficiency in food absorption and hyperactivity of subordinates.

Food competition, dominant individuals may deprive subordinates of food. Thus the dominant consumes more, increasing their growth and reducing the development of the subordinates. This mechanism is expected to be observed when food can be stored and is limited in time and space (Cioni & Gherardi, 2004; Segal, 1975).

Social hierarchy and aggression, Agonistic interactions between individuals can establish dominance in social hierarchy. According to this hypothesis, even in a scenario with abundant food, subordinates will eat less (Cobb & Tamm, 1975; Cobb *et al.*, 1982).

Altered efficiency in food absorption, subordinates may have a reduced feed input efficiency, digestibility or a metabolism with low food conversion (Karplus *et al.* 1992).

Hyperactivity of subordinates, as the smallest individuals are usually more active, they present evasive maneuvers to evade dominant ones, resulting in increased energy expenditure and reduced growth (Cobb & Tamm 1975; Cobb *et al.* 1982).

All hypotheses described above involve behavior and feeding. These characteristics are linked to the flow of energy and mass at the metabolic level (Careau *et al.*, 2004). However, understanding how these flows result in different morphology and behavioral tactics is extremely difficult in environmental and experimental situations, and theoretical models can help understand how these different conditions influence the species.

The theory of dynamic energy budget (DEB) describes metabolism at the individual level, such that distinct feeding and activity conditions can be modeled using coefficients from the theory. By simulating different individuals under different conditions we can observe how these conditions influence the different characteristics of the morphotypes (Kooijman, 2010; Martin *et al.*, 2012). Each hypothesis relates to an element of the DEB theory, The competition for food hypothesis relates to the amount of food in the environment, the social hierarchy and aggression hypothesis with ingestion rate, the altered efficiency in food absorption with ingestion efficiency and the hyperactivity of subordinates hypothesis with somatic maintenance.

In this study we created two DEB models to approach the different hypotheses and understand which mechanism that leads to differentiation of morphotypes. In both models the individuals are equal until puberty, then in one of the models the assimilation rates are differentiated between morphotypes showing higher rates of assimilation for the larger morphotypes. In the other model the somatic maintenance rates are differentiated between morphotypes resulting in high somatic maintenance for the smaller morphotypes.

# 2.Methodology

## 2.1.Model description

DEB theory quantifies the flows of matter and energy in the organism. Reserve $E$, structure $V$, maturation $E_H$ and reproductive buffer $E_R$ are the main variables of the model. Figure 2.1 illustrates a simplified scheme of the DEB theory, starting with the energy flow in the ingestion, the organism's capacity to ingest food is proportional to the structural area. Food available in the environment is represented by the functional response $f$.

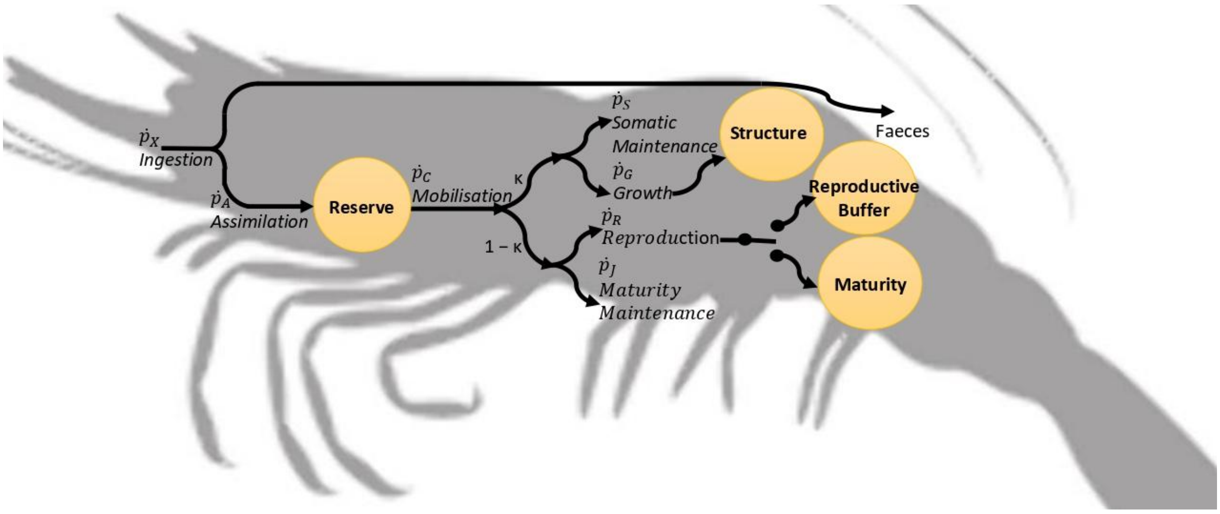

Figure 2.1: Representation simplified of the dynamic energy budget scheme.

Assimilation is the transformation of food into reserves, but part of the food is not assimilated and it is converted into faeces. $\dot{p}_A$ is the assimilation power of the ingested food. The proportion of food assimilated to total food consumed is $\kappa_X$ (ingestion efficiency), and $\dot{p}_X$ is power ingestion per unit of time, therefore, $\dot{p}_A = \kappa_X \dot{p}_X$. The assimilation power also relates to the functional response so that:

$$\dot{p}_A = \{\dot{p}_{Am}\} L^2 f, \tag{2.1}$$

The maximum absorption capacity, per unit area, is $\{\dot{p}_{Am}\}$ and $L$ the structural length, $V = L^3$.

The reserve dynamics is used in all functions of the organism and mitigates instability in the food supply and it is the difference between assimilation and mobilization. The mobilization of the reserve is independent of the food available and the reserve density is assumed to be distributed proportionally in reserve tissue. The mobilized reserve power, $\dot{p}_C$, is used for somatic maintenance $\dot{p}_S$, growth $\dot{p}_G$, maturity maintenance $\dot{p}_J$ and reproduction $\dot{p}_R$. A fixed fraction of the mobilized energy, κ, is channeled to somatic maintenance and growth and the surplus, $1 - \kappa$, is used in the remaining metabolic processes.

Somatic maintenance is the cost that the organism has to maintain physiological homeostasis. Somatic maintenance is related to the general maintenance cost per unit of volume, $[\dot{p}_M]$, for example the molt, and the maintenance expenditure per external area of the organism, $\{\dot{p}_T\}$, for example, temperature regulation. The somatic maintenance power may be modeled as

$$\dot{p}_S = [\dot{p}_M] L^3 + \{\dot{p}_T\} L^2. \tag{2.2}$$

In this work we consider $\{\dot{p}_T\} = 0$ for *M. rosenbergii*, because the superficial maintenance expenditure is practically null, like for other crustacean species such as *Fenneropenaeus chinensis*, *Macrobrachium vollenhoveni* and *Palaemon elegans* (AmP Parameter Estimation, 2020). The energy of the κ portion that was not mobilized in the somatic maintenance is destined for growth $\dot{p}_G$. The energy used for maintenance and growth is represented by $\kappa\dot{p}_c$, from this total we subtract somatic maintenance $\dot{p}_S$, then $\dot{p}_G = \kappa\dot{p}_c - \dot{p}_S$.

Growth in species of type *V1-morph*, that exhibit an acceleration between birth and metamorphosis, has an accelerated larval growth, represented by:

$$L(t) = L_b e^{\dot{r}_j \frac{(t-t_b)}{3}}. \tag{2.3}$$

Metamorphosis is the end of the larval stage, so for $t = t_j$, we have:

$$L_j = L(t_j) = L_b e^{\dot{r}_j \frac{(t_j-t_b)}{3}}. \tag{2.4}$$

Considering the continuity of the flows, we obtain, after metamorphosis:

$$L(t) = L_\infty - \left(L_\infty - L_j\right) e^{-\dot{r}_B (t-t_j)}, \tag{2.5}$$

where $L_\infty = \frac{s_M \kappa \{\dot{p}_{Am}\}}{[\dot{p}_M]}$ and $s_M = \frac{L_j}{L_b}$.

## 2.2.Morphotype differentiation

The hypotheses for differentiating male implemented by dynamic modifications to the parameters and forcing variables of the theory. The rates of ingestion efficiency and availability of food in the environment are extremely related to assimilation rate, so models that differentiate these rates would present equal results, so we developed two models focusing on the differences in assimilation and somatic maintenance rates. The differentiation between female and male morphotypes happens during puberty, implying that all juveniles share the same set of parameters.

The hypotheses described above can be mapped into changes in the parameters $\{\dot{p}_{Am}\}$, $f$ , $\{\dot{p}_{Xm}\}$ and $[\dot{p}_M]$. However, parameters $\{\dot{p}_{Am}\}$, $\{\dot{p}_{Xm}\}$ and $f$ are related and contribute jointly to the assimilation of the organism and cannot be differentiated by means of growth curves. Therefore, we only analyzed the parameters $\{\dot{p}_{Am}\}$ and $[\dot{p}_M]$.

## 2.3.Typified models morphotype-specific assimilation and morphotype-specific somatic maintenance

Eq. (2.5) is considered for males until puberty, when $t = t_p$ and $L(t_p) = L_p$. After that we have, for each morphotype $i$,

$$L^i(t) = L^i_\infty - \left(L^i_\infty - L_p\right)e^{-\dot{r}^i_B(t-t_p)} ,$$

(2.6)

### 2.3.1.Morphotype-specific assimilation

The change in absorption efficiency occurs differentiating $\left\{\dot{p}_{Am}\right\}$, after puberty of the males. In Eq. (2.6), $\dot{r}^i_B = \frac{\left[\dot{p}_M\right]\dot{v}}{3\left(\left\{\dot{p}^{i}_{Am}\right\}f\kappa+[E_G]\dot{v}\right)}$ and $L^i_\infty = \frac{s_M\kappa\left\{\dot{p}^{i}_{Am}\right\}}{\left[\dot{p}_M\right]}$, with $\left\{\dot{p}^{i}_{Am}\right\}$ representing the specific surface assimilation rate for each morphotype.

### 2.3.2.Morphotype-specific somatic maintenance

The change in the subordinates' activity is modeled through variation in $\left[\dot{p}_M\right]$. In this case, Eq. (2.5) remains valid until puberty of the males, when $t = t_p$ e $L(t_p) = L_p$. After that ,we have for each morphotype $i$, the Eq. (6), but $\dot{r}^i_B = \frac{\left[\dot{p}^{i}_M\right]\dot{v}}{3\left(\left\{\dot{p}_{Am}\right\}f\kappa+[E_G]\dot{v}\right)}$ and $L^i_\infty = \frac{s_M\kappa\left\{\dot{p}_{Am}\right\}}{\left[\dot{p}^{i}_M\right]}$, with $\left[\dot{p}^{i}_M\right]$ representing the somatic maintenance rate for each morphotype.

## 2.4.Data compiled for the parameter estimation

We used experimental data and observations from nature to describe the development of the species. All data of measured body size can be found in the data repository linked in this article in section 2.5. The data is categorized into zero-variate data that represents fixed data, such as age at birth and life span, and uni-variate data that is data dependent on other data, such as weight over time and the relationship between weight and length (AmP Parameter Estimation, 2020).

### 2.4.1.Development time and Longevity

To estimate the parameters we used mean values of the age at birth $a_b$ (duration until hatching), the time at end of acceleration $t_j$ (larval development time), the time at puberty $t_p$ (juvenil development time) and life span $a_m$ (time from birth to death). These data were obtained from surveys with similar conditions (Pinheiro & Hebling, 1998; Valenti, 2000), such as 28°C and *ad libitum* food intake. All these data are considered the same for all the individuals in the population, regardless of sex and morphotype.

### 2.4.2.Reproduction

The reproduction is continuous during the year and a female only reproduces during the molt. In a single copulation, a female can produce on average one hundred thousand eggs (Da Silva *et al.*, 2004). The average egg production was divided by 30 days, to obtain the maximum daily reproduction per female $R_i$.

### 2.4.3.Length over time

The growth rates of females and of each male morphotype differ after puberty, that's why we include the ultimate total wet weights, $Ww_i$, for the females the ultimate total wet weights is 21.35g, and males weigh 45g, 31.2g, 6.5g for BC, OC and SM respectively, and the relationship of size and time for the males, $tW$ (Ra'Anan *et al.*, 1991).

## 2.5.Parameter estimation

We used the software package DEBtool written in MATLAB (The Mathwork, 2020.), that has the data, equations and offers a routine for fast and automated estimation. We followed the DEBtool guidelines available in http://www.bio.vu.nl/thb/deb/deblab/. DEBtool uses three different files called, “mydata”, “pars_init” and “predict”. The mydata file has all experimental and observed data from nature used in the estimates. The pars_init file defines the initial parameters for the estimates. The predict file contains the functions used to predict life history based on the data defined in mydata.

Two DEBtool files were created separately for the models morphotype-specific assimilation and morphotype-specific somatic maintenance. The set of initial parameters was obtained from species that have a similar life cycle to the species studied, *Macrobrachium vollenhoveni*, to parameterize the morphotype-specific assimilation model. The final parameters obtained in the morphotype-specific assimilation model were used as initial parameters in the morphotype-specific somatic maintenance model. The maximum assimilation rate of the females in the morphotype-specific assimilation model was used as the maximum assimilation rate for all groups in the morphotype-specific somatic maintenance model.

Specific formulas for differentiating morphotypes are in the predict file. The predictions are evaluated simultaneously by a loss function. The parameters were adjusted to minimize the loss function and optimize the model, based on Nelder-Mead method (Marques *et al*. 2019). When the loss function converged with the minimum stable, the routine ended. All DEBtool files used in this study can be found in the data repository linked in this article: https://github.com/SAMANTHA-ABREU/Morfotipo_Macrobrachium.

### 2.6.Goodness of fit criteria

The mean relative error (MRE) and the symmetric mean squared error (SMSE) were considered in both models to measure divergences between empirical data and modeled values. The MRE measures the difference between data and predictions, with values from 0 to infinity. The SMSE also measures the difference between data and predictions, but its value ranges from 0 to 1. In both cases, values close to 0 indicate that the predictions match the data.

## 3. Results and Discussion

Both models were able to predict, in general, values similar to the data, showing that both models can describe the development of female and males morphotypes. The morphotype-specific assimilation model obtained the smaller MRE, and their growth curves showed behaviors nearly to the experimental data. The morphotype-specific somatic maintenance model presented smaller SMSE and the curves although similar to the data values the curve behavior did not correspond to reality.

### 3.1. Growth

Our findings showed that the models we developed were able to recover empirical measurements (Lalrinsanga *et al*., 2012), regarding the relationship between wet weight and length for both females (Figures 2.2) and males (Figure 2.3). The MRE for morphotype-specific assimilation model and morphotype-specific somatic maintenance model were 0.1027 and 0.1029, for females, respectively. The graphs in Figure 2.2, when visually compared, are identical, but the relative error of this graphic of model morphotype-specific assimilation is smaller.

Regarding the results obtained for *M. rosenbergii* males, we observed that, as expected, both initiate at the same period after puberty, differentiating the males, and reach the maximum wet weight of each morphotype (Figure 2.3). The morphotype-specific somatic maintenance model obtained relative error (RE) of 0.2099, 0.3762 and 0.3411 for males BC, OC and SM, respectively and in the model morphotype-specific assimilation the relative errors (RE) were 0.1772, 0.3231 and 0.1426 for males BC, OC and SM, respectively.

Table 2.1 presents all zero-variant history data of both models. The results were similar for the ultimate wet weight for females and males morphotypes. All these results indicate that both models can predict the species' growth based on the low relative errors obtained. These parameters influence growth and development, being essential to understand the morphological differentiation in males of this *M. rosenbergii*.

Table 2.1: Zero-variate history data of *M. rosenbergii* and model predictions in the typified models morphotype-specific assimilation and morphotype-specific somatic maintenance.

| Symbol | Units | Description | Data | Prediction in $[\dot{p}_M]$ | Relative Error (RE) | Prediction in$\{\dot{p}_{Am}\}$ | Relative Error (RE) | Reference |
|---|---|---|---|---|---|---|---|---|
| $a_b$ | d | Age at birth (embryonic development) | 19 | 10.73 | 0.4354 | 3.424 | 0.8198 | (Pinheiro & Hebling, 1998) |
| $t_j$ | d | Time since hatching at metamorphosis | 18 | 22.66 | 0.2589 | 20.76 | 0.1531 | (Pinheiro & Hebling, 1998) |
| $t_p$ | d | Time since metamorphosis at puberty | 110 | 47.5 | 0.5682 | 41.11 | 0.6263 | Guess* |
| $a_m$ | d | Maximum age | 1095 | 1095 | 0.0002679 | 1095 | 1.285e$^{-08}$ | (Valenti, 2000) |
| $L_p$ | cm | Length at puberty | 2.5 | 2.307 | 0.07704 | 2.12 | 0.1521 | Guess* |
| $R_i$ | #/d | Ultimate reproduction rate | 3333 | 3193 | 0.04218 | 3228 | 0.03145 | (Da Silva *et al*., 2004) |
| $Ww_i\_f$ | g | Ultimate total wet weight of female | 21.35 | 21.87 | 0.02447 | 21.41 | 0.002985 | (Ra´anan *et al*., 1991) |
| $Ww_i\_BC$ | g | Ultimate total wet weight of BC | 45 | 57.7 | 0.2822 | 58.36 | 0.2969 | (Ra´anan *et al*., 1991) |
| $Ww_i\_OC$ | g | Ultimate total wet weight of OC | 31.2 | 29.25 | 0.06247 | 30.45 | 0.0239 | (Ra´anan *et al*., 1991) |
| $Ww_i\_SM$ | g | Ultimate total wet weight of SM | 6.5 | 4.829 | 0.2571 | 5.868 | 0.09722 | (Ra´anan *et al*., 1991) |

*Data obtained from preliminary results of experiments conducted at the Unesp Aquaculture Center - Caunesp

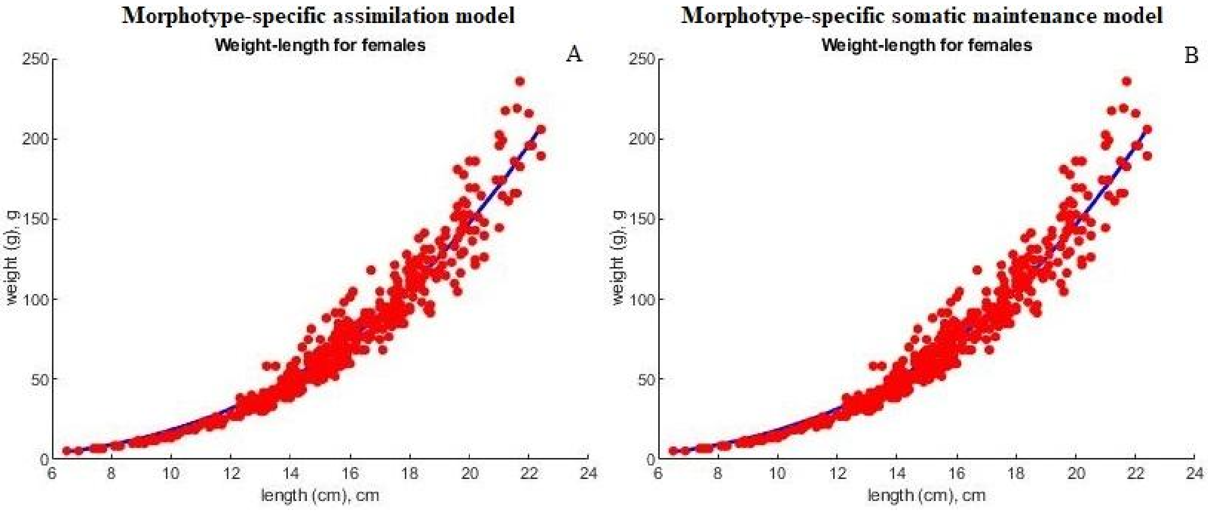

Figure 2.2: Allometric relationships of *M. rosenbergii* based on empirical data and DEB modeling. Graph of total length (cm) x total weight (g), referring to females. Red dots correspond to the data from Lalrinsanga *et al.*, 2012 and the blue line corresponds to the prediction of the model. A: Morphotype-specific assimilation model, relative error (RE): 0.1027. B: Morphotype-specific somatic maintenance model, relative error (RE): 0.1029.

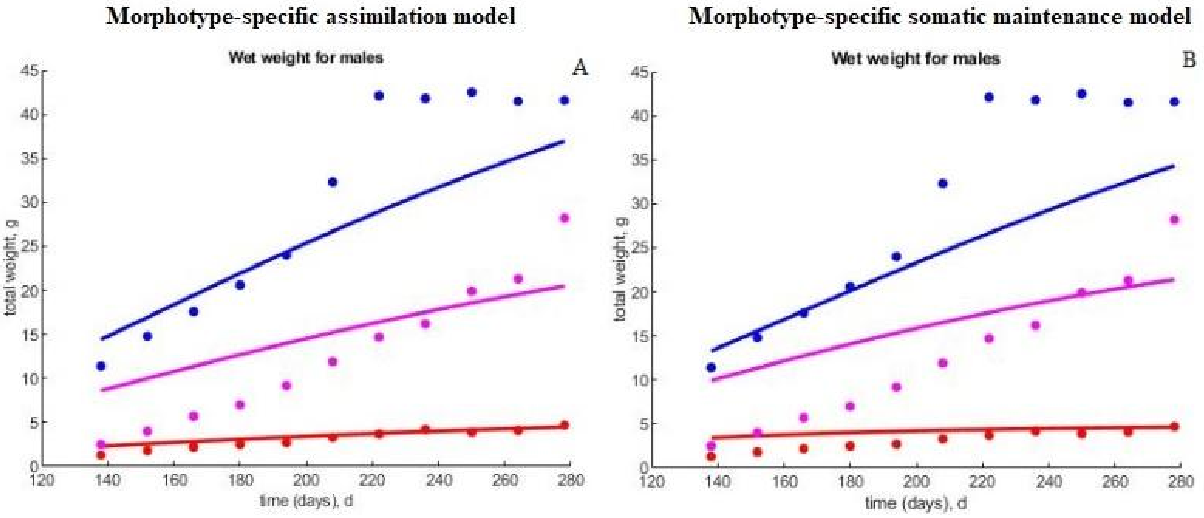

Figure 2.3: Growth curves of *M. rosenbergii* based on empirical data and DEB modeling. Graph of total wet weight (g) x time (days) for males morphotypes. The points correspond to the data from Ra'anan *et al.*, 1991 and the lines correspond to the model prediction. A: Morphotype-specific assimilation model, red line: SM males, relative error (RE): 0.1426, pink line: OC males, relative error (RE): 0.3231, blue line: BC males, relative error (RE): 0.1772. B: Morphotype-specific somatic maintenance model, red line: SM males, relative error (RE): 0.3411, pink line: OC males, relative error (RE): 0.3762, blue line: BC males, relative error (RE): 0.2099.

### 3.2.Parameters estimates

All parameters used in the typified models and optimal fit values for each model are presented in Table 2.2. The number of estimated parameters was the same in both models, but in morphotype-specific assimilation model uses the $\left\{\dot{p}_{Am}\right\}$ as a parameter for differentiation. The morphotype-specific somatic maintenance model utilizes different $\left[\dot{p}_M\right]$ for females and males morphotypes. These parameters indirectly control estimates of the other model parameters, connected to the state variables by mathematical functions based on the rules of DEB theory.

Table 2.2: DEB parameters of the typified models morphotype-specific assimilation and morphotype-specific somatic maintenance.

| Symbol | Unit | Interpretation | $\{\dot{p}_{Am}\}$ | $[\dot{p}_M]$ |
|---|---|---|---|---|
| Fixed model parameters | | | | |
| $\kappa_R$ | – | Reproduction efficiency | 0.95 | 0.95 |
| $\{\dot{p}_T\}$ | J $d^{-1}$ $cm^{-2}$ | Surface-area-specific somatic maintenance rate | 0 | 0 |
| $\dot{k}_J$ | $d^{-1}$ | Maturity maintenance rate coefficient | 0.002018 | 0.002018 |
| $T_A$ | K | Arrhenius temperature | 8000 | 8000 |
| $T_{REF}$ | K | Reference temperature | 293.1 | 293.1 |
| Estimated model parameters | | | | |
| $\dot{v}$ | cm/d | Energy conductance | 0.01505 | 0.001519 |
| $\kappa$ | – | Allocation fraction to soma | 0.3674 | 0.494 |
| $[\dot{p}_M]$ | J $d^{-1}$ $cm^{-3}$ | Volume-specific somatic maintenance rate | 70.28 | 1807 |
| $\{\dot{p}_{Am}\}$ | J $d^{-1}$ $cm^{-2}$ | Surface-area-specific maximum assimilation rate | 60.6390 | 385.1763 |
| $[E_G]$ | J/$cm^{-3}$ | Volume-specific costs for structure | 4443 | 4442 |
| ${E_H}^b$ | J | Maturity level at birth | 0.1321 | 0.0195 |
| ${E_H}^j$ | J | Maturity level at metamorphosis | 46.44 | 7.177 |
| ${E_H}^P$ | J | Maturity level at puberty | 725.6 | 96.36 |
| $\ddot{h}_a$ | $d^{-2}$ | Weibull aging acceleration | $7.765e^{-09}$ | $2.559e^{-08}$ |
| $\delta_M$ | – | Shape coefficient | 0.2062 | 0.06509 |
| $\{\dot{p}_{Am}\}_{BC}$ | J $d^{-1}$ $cm^{-2}$ | Surface-area-specific maximum assimilation rate for male BC | 80.4758 | – |
| $\{\dot{p}_{Am}\}_{OC}$ | J $d^{-1}$ $cm^{-2}$ | Surface-area-specific maximum assimilation rate for male OC | 67.0281 | – |
| $\{\dot{p}_{Am}\}_{SM}$ | J $d^{-1}$ $cm^{-2}$ | Surface-area-specific maximum assimilation rate for male SM | 41.7395 | – |
| $[\dot{p}_M]_{BC}$ | J $d^{-1}$ $cm^{-3}$ | Volume-specific somatic maintenance rate for males BC | – | 1309 |
| $[\dot{p}_M]_{OC}$ | J $d^{-1}$ $cm^{-3}$ | Volume-specific somatic maintenance rate for males OC | – | 1641 |
| $[\dot{p}_M]_{SM}$ | J $d^{-1}$ $cm^{-3}$ | Volume-specific somatic maintenance rate for males SM | – | 2988 |

The final parameter sets obtained by the models had very different values. The difference may indicate that the value sets are not the most appropriate, which could be solved by including more data in the models and estimating the parameters again. The estimates made in the morphotype-specific assimilation model fit the data better, indicating that the set of parameters in this model may be the closest to the optimal set.

## 3.3.Morphotype-specific assimilation VS morphotype-specific somatic maintenance models

Both models presented good fits to the data according to the MRE and SMSE. The morphotype-specific assimilation model presented lower MRE with a value of 0.211 and largest SMSE, 0.289, but morphotype-specific somatic maintenance model showed a lower SMSE, 0.224 and the MRE is higher, 0.217. MRE uses relative errors of the zero-variates and univariates, and the best scenario is with MRE near zero.

### 3.3.1.Zero-variate data predictions

Most zero-variate data produced by both models had the deviations below 15.5% (Table 2.1). The age and life stage data presented the largest errors compared to the predicted individual length and weight data, $a_b$ and $t_p$ obtained the largest relative errors, in the case of $t_p$ this may be due to the difficulty of determining when puberty occurs in these animals through morphological characteristics. In general, the morphotype-specific somatic maintenance model exhibited the largest errors, so that between the two models, the morphotype-specific assimilation model is the most suitable for the species. The high deviations is likely due the limited data describing the life cycle.

### 3.3.2.Predictions of weight and length at time

The predictions of growth over time (Figures 2.2 and 2.3) presented RE below 33% and 38% regarding morphotype-specific assimilation and morphotype-specific somatic maintenance models, respectively. The length of females over time resulted in similar growth curves, with approximate deviations between the models (data not shown). Between the models, morphotype-specific assimilation had a slightly better fit.

The morphotype-specific assimilation model has the smaller error (Figure 2.3). Both graphs presented similar curves. The OC curve showed the largest errors, showing that these curves did not completely fit the data. The SM curve fits the data better. In the case of the BC, both curves fit the data, but the morphotype-specific assimilation model showed a growth rate closer to the data. These findings (Figure 2.2. and 2.3) indicated the morphotype-specific assimilation model best fits the data.

### 3.4.Evolutionary aspects

Comparing the models, the differentiation of assimilation between females and males morphotypes fits the distinct development between them. This result reinforces the hypotheses that altered efficiency in food absorption and social hierarchy and aggression explain the evolution of polymorphism for *M. rosenbergii*.

The hypothesis of altered efficiency in food absorption is directly linked to the assimilation power. Karplus *et al*. (1992) suggested that, for *M. rosenbergii*, SM males grew less in the presence of BC males and when cultivated alone, SM males had larger body sizes. Toguyeni *et al.* (1997), researched the social interactions between males and females in the fish species *Oreochromis niloticus*, and concluded that the stress of these interactions increases the metabolic requirements affecting food conversion and decreasing growth. In both researches the authors concluded that the altered efficiency of food absorption resulted in morphological differentiation of individuals. However, both researches did not explain the physiological mechanisms that would cause this change in absorption efficiency. Augusto & Valenti (2016) demonstrated the differences in physiological characteristics between females and males morphotypes of *M. amazonicum* species, and concluded that food absorption was the same for all individuals.

The hypothesis of social hierarchy and aggression is related to food ingestion. The rates of assimilation and ingestion are very connected and would present models with equal results, so the morphotype-specific assimilation model can represent this hypothesis.

Crustacean species that exhibit heterogeneous growth tend to establish social hierarchy in the population (Augusto & Valenti, 2016). Cobb *et al*. (1975) and Cobb *et al.* (1982) showed that the dominance relationship observed in the american lobster, *Homarus americanos*, could be explained by the observation that dominant individuals grew faster and molt earlier, determining the hierarchy of individuals in the population. Barki *et al*. (1992) studied the hierarchy process based on the corporeal development of males morphotypes *M. rosenbergii*. Individuals of morphotypes BC demonstrated dominance actions over OC males frequently, guaranteeing BC males priority to resources, such as food and shelter. Silva & arruda (2015) also researched dominance relations in *M. rosenbergii*, but in the juvenile phase. Larger individuals have aggressive behavior, establishing dominance and developing more rapidly. The repetition of agonistic interactions can result in a hierarchical structure in the population (Holekamp & Straus, 2016). The competition for food hypothesis is common in scenarios where the food supply is limited, which is not in accordance with the experimental protocols of the research in which the data for the models were obtained - food guarantees satiety for all individuals. The morphotype-specific somatic maintenance model we developed aimed to test the hyperactivity of subordinates hypothesis. Although the model fit the data, its errors were generally larger, disfavoring this hypothesis to explain the differentiation of morphotypes in *M. rosenbergii*.

## 4.Conclusion

Comparing the results of morphotype-specific assimilation and morphotype-specific somatic maintenance models, we can conclude that the morphotype-specific assimilation model matched the data better. This indicates that the hypotheses of social hierarchy and aggression and altered efficiency in food absorption may explain the differentiation of morphotype. Population dynamics is based on social hierarchy indicating that between two hypotheses, the best fit is the hypothesis of social hierarchy and aggression.

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# CAPÍTULO 3 - "Can a DEB model based on growth data predict physiological characteristics of polymorphic species?"

Samantha Abreu Alves dos Santos[1],*, Tan Tjui Yeuw[1], Fabio Stucchi Vannucchi[1]

[1]Biosciences Institute, São Paulo State University - UNESP, São Vicente, São Paulo, Brazil

*E-mail: samantha.abreu@unesp.br

## Abstract

Polymorphism, in addition to phenotypic characteristics, results in distinct physiologies among morphotypes. The prawns species *Macrobrachium amazonicum* Heller 1862, (Decapoda: Caridea), presents a diverse morphotype in males. The polymorphism results in differing physiological characteristics that, besides biological interest, has productive relevance. The species presents two populations, continental and coastal, and the high diversity among individuals makes it extremely important to understand the mechanism of heterogeneous growth, and to propose new management techniques. An alternative to understand the different physiological characteristics, is the use of theoretical models and in this work we employed the Dynamic Energy Budget (DEB), a theory that represents and quantifies the flows of matter and energy in an organism. We formulated two DEB models in which the assimilation rate and somatic maintenance, respectively, differentiate morphotypes. The models were parametrized using data from literature and physiological characteristics such as mass gained, daily growth, ingestion, faeces, excretion and respiration rates were simulated and then compared with empirical data. Both models showed similar patterns to the compared experiments, but at different rates. The morphotype-specific somatic maintenance model presented results that were closest to the experiments. Low complexity models, with only growth data, can estimate other physiology characteristics approximately.

**Keywords:** Dynamic Energy Budget theory, Polymorphism, Physiology, *Macrobrachium amazonicum*.

## 1.Introduction

Understanding the evolution of alternative phenotypes requires an integrative approach including developmental, physiological, morphological and behavioral studies (Jorge *et al.* 2014). The polymorphism, in addition to phenotypic characteristics, results in distinct physiologies among morphotypes, and the genus *Macrobrachium* constitutes a model organism due to the high physiological diversity among its morphotypes (Karplus & Barki, 2019).

The shrimp species *Macrobrachium amazonicum*, native to South America, has a distribution that ranges from Caribbean and Atlantic coasts of South America to northern Argentina, Paraguay and eastern slopes of the Andes in Ecuador, Bolivia, Peru and Atlantic coasts of northeastern Brazil (Valenti, 2000; New *et al.*, 2009). The fishing of *M. amazonicum* is mainly artisanal, but it has a great potential for cultivation since it has disease resistance and high survival rate, which makes it ideal for culture (Maciel & Valenti, 2009). Additionally, the use of native species follows the directives of sustainability and environment management, mitigating the risk of accidental escape (de Almeida Marques & Moraes-Valenti, 2012; Maciel & Valenti, 2009).

Based on morphological, reproductive and ontogenetic traits, there are three population classified groups of prawns: a coastal amphidromous population in the northernmost regions; and two continental hololimnetic populations, one in the Amazon region and other in the Parana and Paraguay basins (Perroca *et al.* 2021). Continental populations are smaller in size, low fecundity and the larvae complete metamorphosis in fresh water. The coastal populations are large, with high fecundity and their larvae develop in brackish water. Four adult male morphotypes are most frequently observed in coastal populations, Moraes-Riodades & Valenti (2004) described these groups. Each group is differentiated in color, spine, size and growth and are named as Translucent Claw (TC), the smallest males, Cinnamon Claw (CC), with intermediate sizes, Green Claw 1 (GC1) and Green Claw 2 (GC2), the largest males, but GC2 presents the largest claw. Depending on the environment and ecological conditions, a male TC grows into other morphotypes, in succession – CC-GC1-GC2 –, but not all males will reach the largest morphotypes. All morphotypes produce efficient gametes (Moraes-Riodades & Valenti, 2004).

The demand of the consumer market requires a uniform product throughout the year. Therefore it is of extreme importance to understand the mechanisms of heterogeneous growth to propose new management techniques. Because physiological mechanisms could underlie such morphological differences, functional traits like growth, ingestion, faecal production, respiration and nitrogenous excretion have been previously compared between morphotypes (Augusto & Masui, 2014, Augusto & Valenti, 2016). These researchers analyzed the physiology of ovigerous and non-ovigerous females and the males morphotypes individually; the physiological differences observed between those individuals reflect differences in activity, growth, reproduction, behavior and function in the population. Understanding these differences is essential to develop new cultivation techniques for this species.

This shrimp has great diversity in physiological responses, which vary by sex, morphology and enviroment. The use of DEB theory may allow one to explore and test hypotheses about the physiological mechanisms that are related to the existence of intraspecific species differences. Yang *et al.* (2020) demonstrated that the DEB model can be applied in aquaculture and stock enhancement, their work showed the differences in development between sexes and locations for *Fenneropenaeus chinensis*. Ren *et al.* (2020) used DEB theory for *Larimichthys polyactis* demonstrating the differences in populations from different geographic distributions.

In this study, we developed two DEB models considering that different rates of assimilation and somatic maintenance differentiate morphotypes after puberty throughout life. We tested the applicability of these models in describing physiological characteristics of the morphotypes of *M. amazonicum*.

## 2.Methodology

### 2.1.Basic and general description

The DEB theory represents and quantifies flows of matter and energy in an organism. Obtaining energy starts with food, and the energy it provides is distributed for maintenance, growth, maturation and reproduction processes, respecting the law of conservation of mass and energy. In a simple DEB model, the growth of an organism can be described based on its reserve energy, structural volume (or, alternatively, its structural length or structural area), level of maturity and the reproduction buffer (Kooijman, 2010).

### 2.1.1.Ingestion and Faeces

The ingestion is the energy and mass acquired through feeding. DEB theory assumes that feeding rates are proportional to the organism's capacity to ingest food and to its structural area, being also dependent on the availability of food in the environment and the body temperature. Part of the food that is ingested but not assimilated by the organism is converted into faeces. As the ingestion is related to the size of the organism, DEB theory can provide the rate of ingestion and of faeces production based on the body structure of the individual.

### 2.1.2.Growth

In DEB theory the assimilated food is destined to the reserve and is mobilized for all the organism´s functions. A fixed portion of energy and mass mobilized is allocated to somatic maintenance and growth. Somatic maintenance has priority and the rest is destined to the growth of the structure, this flow of energy can be described in terms of volume; the conversion of reserve into structure is supposed to have constant efficiency. It can be shown, in the context of DEB theory, that if the available food density is constant, this relationship results in an equation analogous to the von Bertalanffy equation which describes a growth curve estimating structural length throughout life (Kooijman, 2010). In species like *M. amazonicum*, the larval development presents a different growth, it is accelerated, where its surface area is proportional to its volume, resulting in an exponential growth (Kooijman, 2010).

### 2.1.3.Reproduction

Until puberty, the energy is used for maturation, then it is redirected to offspring production. The fraction of mobilized reserve that was not destined for somatic maintenance and growth, minus the amount allocated for maturity maintenance, is allocated to reproduction in adults; the conversion of the mother's reserve into the reserve of offspring is constant. This flux is a continuation of maturation flux.

### 2.1.4.Respiration and Excretion

DEB theory assumes that all mass fluxes are weighted sums of three basic fluxes: assimilation, dissipation and growth. The dissipation is the sum of somatic and maturity maintenance, maturation and reproduction overhead. Animal physiology considers the ratio of carbon dioxide production and dioxygen consumption is constant independently of size and nutritional condition. In DEB theory this ratio is constant when the composition of reserve and structure are identical. As well as the ratio between carbon dioxide production and dioxygen consumption, the nitrogen balance defined as the ratio of nitrogen-waste and dioxygen consumption is constant and the composition of reserve and structure must be identical. In the animals, the composition of reserve and structure do not differ, so the dioxygen consumption is proportional to the flux of mobilized reserve and the nitrogen balance is linked to assimilation, maintenance and growth (Kooijman, 2010). In this study, we used the growth data to estimate respiration rate (as $O_2$ consumption) and the excretion rate (as $NH_3$ production), based on the sum of the flows.

### 2.2.Morphotype differentiation

DEB theory uses differential equations with parameters that quantify physiological processes. The maximum assimilation rate and somatic maintenance rate are examples of parameters used in DEB theory. The maximum assimilation rate $\left\{\dot{p}_{Am}\right\}$ represents the maximum amount of food that is absorbed by the individual. The somatic maintenance rate $\left[\dot{p}_M\right]$ is the turnover of structure and activity. All individuals share the same set of parameters until puberty, when the differentiation between females and males morphotypes begins. This differentiation may be the result of different rates of assimilation $\left\{\dot{p}_{Am}\right\}$ or somatic maintenance $\left[\dot{p}_M\right]$.

One of the models consider that the parameter that differentiates the morphotypes is assimilation rate $\left\{\dot{p}_{Am}\right\}$, morphotype-specific assimilation model, and the other the somatic maintenance $\left[\dot{p}_M\right]$, morphotype-specific somatic maintenance model. In the first, we assume that after puberty, males exhibit different rates of food assimilation $\left\{\dot{p}_{Am}\right\}$, resulting in the differentiation of morphotypes. In this case, individuals that assimilate more food grow more and become the largest morphotypes. In the second model, we consider that the causes the differentiation after puberty are different rates of energy expenditure for body maintenance $\left[\dot{p}_M\right]$ in males. In this scenario, the most active individuals grow less and become the smallest morphotypes.

## 2.3.Data compiled for the parameter estimation

Observed nature data and experimental data were used to develop two independent models. The data is categorized into zero-variate and uni-variate data. The zero-variate data (Table 3.1) is a dependent data in the form of a single number (AmP Parameter Estimation, 2020). The uni-variate data (Figure 3.1-3.3) is a vector of dependent variables with an independent data point associated (AmP Parameter Estimation, 2020). All these data were obtained in experiments growing the individuals together under similar environmental conditions. The completeness of the data was used to compare parameters between models using a system from 0 (low) to 10 (high). (AmP Parameter Estimation, 2020).

## 2.4.Parameter estimation

We used the software package DEBtool written in MATLAB (The Mathwork, 2020), that makes data and equations available and offers a routine for fast and automated estimation. The guide to using DEBtool may be found at http://www.bio.vu.nl/thb/deb/deblab/. We created two DEBtool files, and two distinct files to estimate physiological characteristics for the models morphotype-specific assimilation and morphotype-specific somatic maintenance. All files used in this study can be found in the data repository linked in this article: https://github.com/SAMANTHA-ABREU/Morfotipo_Macrobrachium

## 2.5.Goodness of fit criteria

The mean relative error (MRE) measures the difference between data and predictions, with values from 0 to infinity, and the symmetric mean squared error (SMSE) also measures the difference between data and predictions, but its value ranges from 0 to 1. In both cases, values close to 0 indicate that the predictions match the data.

## 2.6.Comparison between the models and experiments

We calculated several physiological characteristics, for both models, based on the previous parametrization, in order to compare with experimental results from Augusto & Masui (2014) and Augusto & Valenti (2016). The physiological characteristics were: ingestion, faeces production, mass gain, daily growth, respiration and excretion. To achieve this goal, we simulated 30-day period growth curves for 50 adult individuals of each group (non-ovigerous females and the three distinct male morphotypes. The initial size of each simulated individual follows a normal distribution with mean value corresponding to the average between the size at puberty and the group-dependent ultimate size. The standard deviation of the normal distribution was considered one sixth of the difference between puberty and ultimate sizes (values below the size at puberty or above ultimate size were disregarded and new draws were then carried out).

We compared the model predictions with the mean values and standard variations published by Augusto & Masui (2014) and Augusto & Valenti (2016), through a boxplot graph made in the R language (R Core Team, 2020). We performed z-tests, at a significance level of 5%, to statistically compare the results of the models with the experimental ones.

## 3.Results and Discussion

The two DEB models demonstrated similar results, the graphs showed equal results and both models obtained the growth curves of the morphotypes. In both cases the models have shown similar patterns to the results of physiological experiments. The morphotype-specific somatic maintenance model had the smallest MRE and SMSE and exhibited the closest results to the experimental data.

### 3.1.Models morphotype-specific assimilation and morphotype-specific somatic maintenance.

Most zero-variate data reproduced by both models had deviations from the experimental values below 10% (Table 3.1). In general, the morphotype-specific somatic maintenance model presented smaller errors, but the morphotype-specific assimilation model exhibited the smaller errors of the most zero-variates data.

Table 3.1: Zero-variate history data of *M. amazonicum* and model predictions in the typified models morphotype-specific assimilation and morphotype-specific somatic maintenance.

| Symbol | Units | Description | Data | Prediction in $[\dot{p}_M]$ | Relative Error (RE) | Prediction in$\{\dot{p}_{Am}\}$ | Relative Error (RE) | Reference |
|---|---|---|---|---|---|---|---|---|
| $a_b$ | d | Age at birth (embryonic development) | 15 | 9.278 | 0.3815 | 9.252 | 0.3832 | (Maciel, 2009) |
| $Wd_b$ | g | Dry weight at birth | $5.86e^{-06}$ | $6.097e^{-06}$ | 0.04041 | $6.045e^{-06}$ | 0.03164 | (Hayd, 2007) |
| $t_j$ | d | Time since birth at metamorphosis | 21 | 26.21 | 0.2482 | 25.99 | 0.2377 | (Anger *et al*., 2009) |
| $Ww_j$ | g | Wet weight at metamorphosis | 0.068 | 0.07043 | 0.0357 | 0.07005 | 0.0301 | (Freire, 2019) |
| $L_i\_f$ | cm | Ultimate total length of female | 12.66 | 10.96 | 0.1342 | 10.94 | 0.1359 | (Silva, 2006) |
| $L_i\_GC2$ | cm | Ultimate total length of GC2 | 14 | 12.84 | 0.08272 | 12.36 | 0.117 | (Silva, 2006) |
| $Ww_i\_GC2$ | g | Ultimate total wet weight of GC2 | 14.4 | 15.88 | 0.1026 | 15.7 | 0.09004 | (Moraes, 2005) |
| $Ww_i\_GC1$ | g | Ultimate total wet weight of GC1 | 11.8 | 12.43 | 0.05322 | 12.32 | 0.04446 | (Moraes, 2005) |
| $Ww_i\_CC$ | g | Ultimate total wet weight of CC | 3.8 | 4.049 | 0.06546 | 4.108 | 0.0811 | (Moraes, 2005) |
| $Ww_i\_TC$ | g | Ultimate total wet weight of TC | 2.3 | 2.342 | 0.01813 | 2.377 | 0.03329 | (Moraes, 2005) |
| $R_i$ | #/d | Ultimate reproduction rate | 112.5 | 119.9 | 0.06603 | 119.4 | 0.06142 | (Silva, 2006) |

The predictions of growth over time (Figure 3.3) showed similar errors between the models, but the morphotype-specific somatic maintenance model is slightly smaller. The growth curves were similar between the models. Figure 3.1 presents the relationship between number of eggs per day and total length, this curve demonstrates that larger females produce higher numbers of eggs. The expressive relative errors (approximately 44%) are probably related with the dispersion of data. Figure 3.2 presents the allometric relationships between weight and length for females, this relationship is allometrically positive and the models were able to predict this relationship. Figure 3.3 compares the predictions between the models to relate wet weight over time for males; these curves exhibited errors below 13.5%, demonstrating that the predictions matched the data.

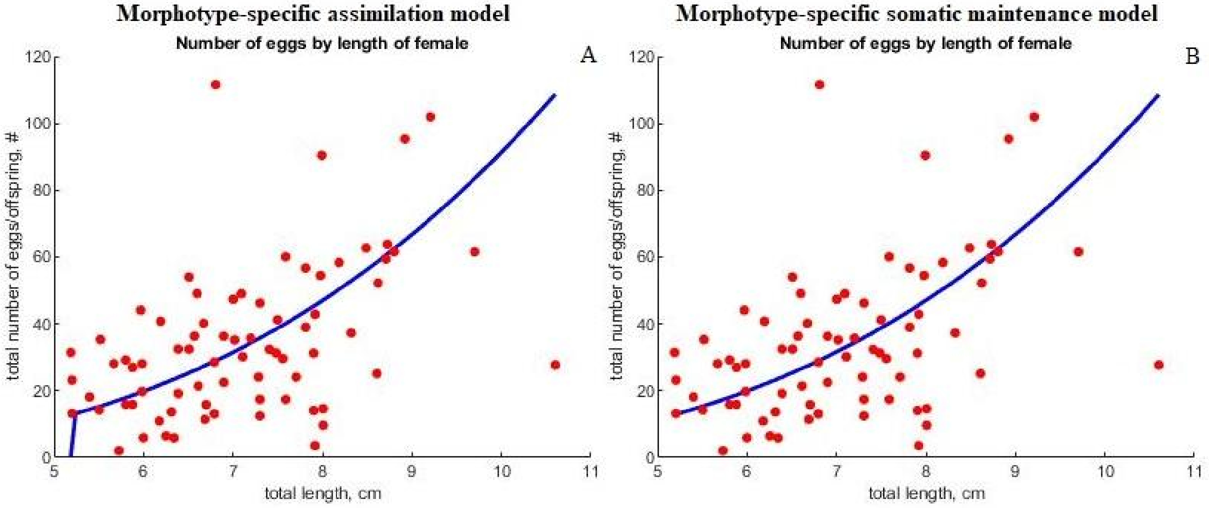

Figure 3.1: Fecundity and total length ratio of *M. amazonicum* based on empirical data and DEB modeling. Graphs total length (cm) x number of eggs per day for females, the points in red correspond to the data from Silva (2006) and the blue line corresponds to the prediction of the model. A: Morphotype-specific assimilation model, relative error (RE): 0.4442. B: Morphotype-specific somatic maintenance model, relative error (RE): 0.4392.

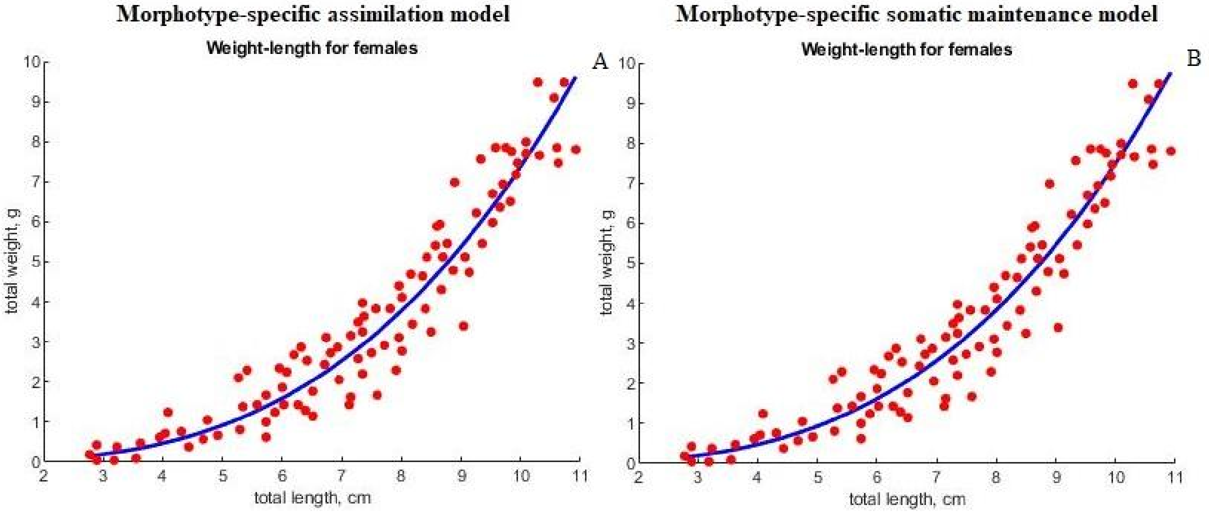

Figure 3.2: Allometric relationships of *M. amazonicum* based on empirical data and DEB modeling. Graphs total weight (g) x total length (cm) for females, the points in red correspond to the data from Silva (2006) and the blue line corresponds to the prediction of the model. A: Morphotype-specific assimilation model, relative error (RE): 0.1655. B: Morphotype-specific somatic maintenance model, relative error (RE): 0.1641.

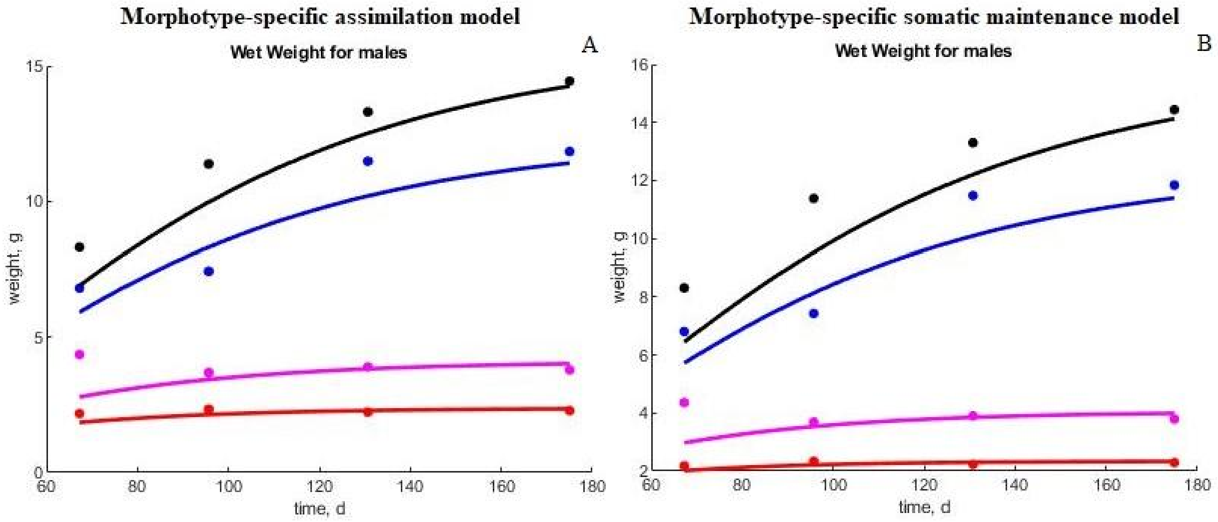

Figure 3.3: Growth curves of *M. amazonicum* based on empirical data and DEB modeling. Total wet weight (g) x time (days) for males morphotypes after puberty. The points correspond to the data from Moraes-Riodades (2005) and the lines correspond to the model prediction. A: Morphotype-specific assimilation model, red line: TC males, relative error (RE): 0.07254, pink line: CC males, relative error (RE): 0.1349, blue line: GC1 males, relative error (RE): 0.09272, black line: GC2 males, relative error (RE): 0.08003. B: Morphotype-specific somatic maintenance model, red line: TC males, relative error (RE): 0.04506, pink line: CC males, relative error (RE): 0.1139, blue line: GC1 males, relative error (RE): 0.09658, black line: GC2 males, relative error (RE): 0.1081.

Both models presented good fits to the data according to the MRE and SMSE. The morphotype-specific somatic maintenance model resulted in MRE and SMSE values of 0.129 and 0.152, respectively, and the morphotype-specific assimilation model had MRE of 0.132 and SMSE of 0.155. The morphotype-specific somatic maintenance model showed lower SMSE and MRE indicating that this model may describe the species better. Nevertheless, the morphotype-specific assimilation model should not be discarded, since the MRE and SMSE were also quite low.

## 3.2.Parameter estimates

All parameters used in the typified models and optimal fit values for each model are presented in Table 3.2. The number of estimated parameters were the same in both models, but morphotype-specific assimilation model uses the $\{\dot{p}_{Am}\}$ as a parameter for differentiation. The morphotype-specific somatic maintenance model utilizes different $[\dot{p}_M]$ for females and males morphotypes. These parameters indirectly control estimates of the other model parameters, connected to the state variables by mathematical functions based on the rules of

DEB theory. In the case of the morphotype-specific assimilation model, the morphotype with the smallest sizes, TC, has the lowest assimilation rate, and the morphotypes with larger sizes, GC1 and GC2, has the highest assimilation rates this may indicate that the larger individuals have greater access to or absorb more food. Research has shown that species with an established social hierarchy, even in a scenario with abundant food, dominant individuals deprive subordinates of food (Cobb & Tamm, 1975; Cobb *et al.*, 1982; Ibrahim, 2011). The morphotype-specific somatic maintenance model resulted in higher somatic maintenance rate in TC morphotypes and the lowest rates in GC2 and GC1 morphotypes, showing that individuals with high maintenance cost of structure and activity have the smallest growth, subordinate individuals tend to be more active to avoid agonistic interactions with the dominant (Cobb & Tamm 1975; Cobb *et al*. 1982).

Table 3.2: DEB parameters of the typified models morphotype-specific assimilation and morphotype-specific somatic maintenance.

| Symbol | Unit | Interpretation | $\{\dot{p}_{Am}\}$ | $[\dot{p}_M]$ |
|---|---|---|---|---|
| Fixed model parameters | | | | |
| $\kappa_R$ | – | Reproduction efficiency | 0.95 | 0.95 |
| $\{\dot{p}_T\}$ | J d$^{-1}$.cm$^{-2}$ | Surface-area-specific somatic maintenance rate | 0 | 0 |
| $\dot{k}_J$ | d$^{-1}$ | Maturity maintenance rate coefficient | 0.002 | 0.002 |
| $T_A$ | K | Arrhenius temperature | 9000 | 9000 |
| $T_{REF}$ | K | Reference temperature | 293.1 | 293.1 |
| Estimated model parameters | | | | |
| $\dot{v}$ | cm/d | Energy conductance | 0.001574 | 0.001696 |
| $\kappa$ | – | Allocation fraction to soma | 0.9911 | 0.991 |
| $[\dot{p}_M]$ | J d$^{-1}$.cm$^{-3}$ | Volume-specific somatic maintenance rate | 3399 | 2697 |
| $\{\dot{p}_{Am}\}$ | – | Surface-area-specific maximum assimilation rate | 185.3194 | 159.3723 |
| $[E_G]$ | J cm$^{-3}$ | Volume-specific costs for structure | 4444 | 4443 |
| $E_H{}^b$ | J | Maturity level at birth | 0.0002397 | 0.0002524 |
| $E_H{}^j$ | J | Maturity level at metamorphosis | 0.6672 | 0.693 |
| $E_H{}^P$ | J | Maturity level at puberty | 21.19 | 21.78 |
| $\ddot{h}_a$ | d$^{-2}$ | Weibull aging acceleration | 2.037e$^{-06}$ | 2.037e$^{-06}$ |
| $\delta_M$ | – | Shape coefficient | 0.06192 | 0.06691 |
| $\{\dot{p}_{Am}\}_{GC2}$ | J d$^{-1}$ cm$^{-2}$ | Surface-area-specific maximum assimilation rate for male GC2 | 209.3862 | – |
| $\{\dot{p}_{Am}\}_{GC1}$ | J d$^{-1}$ cm$^{-2}$ | Surface-area-specific maximum assimilation rate for male GC1 | 197.0236 | – |
| $\{\dot{p}_{Am}\}_{CC}$ | J d$^{-1}$ cm$^{-2}$ | Surface-area-specific maximum assimilation rate for male CC | 149.3563 | – |
| $\{\dot{p}_{Am}\}_{TC}$ | J d$^{-1}$ cm$^{-2}$ | Surface-area-specific maximum assimilation rate for male TC | 130.0562 | – |
| $[\dot{p}_M]_{GC2}$ | J d$^{-1}$ cm$^{-3}$ | Volume-specific somatic maintenance rate for males GC2 | – | 2303 |
| $[\dot{p}_M]_{GC1}$ | J d$^{-1}$ cm$^{-3}$ | Volume-specific somatic maintenance rate for males GC1 | – | 2498 |
| $[\dot{p}_M]_{CC}$ | J d$^{-1}$ cm$^{-3}$ | Volume-specific somatic maintenance rate for males CC | – | 3627 |
| $[\dot{p}_M]_{TC}$ | J d$^{-1}$ cm$^{-3}$ | Volume-specific somatic maintenance rate for males TC | – | 4352 |

## 3.3. Physiological characteristics

The models have the completeness of the data in 2.5, indicating the model has information about growth and age, in morphotype-specific assimilation and morphotype-specific somatic maintenance models also include reproduction as a function of length. Even with low completeness data, both models were able to predict physiological characteristics and demonstrate that females and male morphotypes have distinct physiologies, which were, in turn, consistent with observed measurements (Figures 3.2 and 3.3).

### 3.3.1.Mass gained and daily growth

The heterogeneous growth of this species is extremely diverse, with different reports of maximum length and weights depending on the environment and population density (Moraes-Riodades & Valenti, 2004; Moraes-Riodades, 2005). The Figures 3.4 and 3.5 compare the results from both models with the results obtained by Augusto & Masui (2014) and Augusto & Valenti (2016). Figure 3.4 compares the results of mass gained and Figure 3.5 compares the results of daily growth, within 30 days after puberty. The models presented similar results with the mass gained at 30 days being similar between morphotypes, but the daily growth showed that females and males morphotypes have different growth rates.

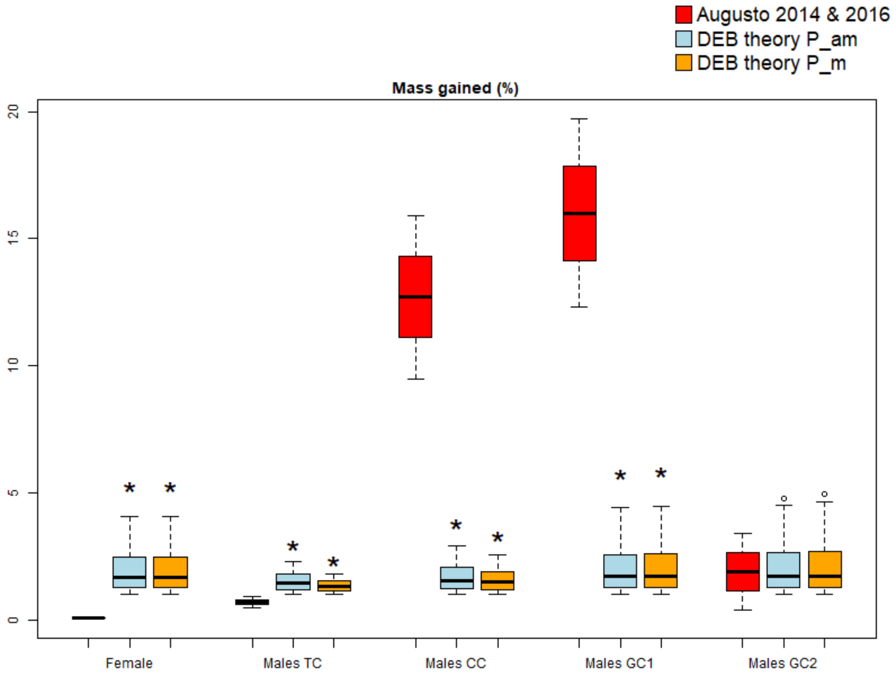

Figure 3.4: Boxplot graph comparing Augusto & Masui (2014) and Augusto & Valenti (2016) results (red) with morphotype-specific assimilation (blue) and morphotype-specific somatic maintenance (yellow) models for mass gained (%) for non-ovigerous females and male morphotypes. Asterisks (*) indicate significantly different results.

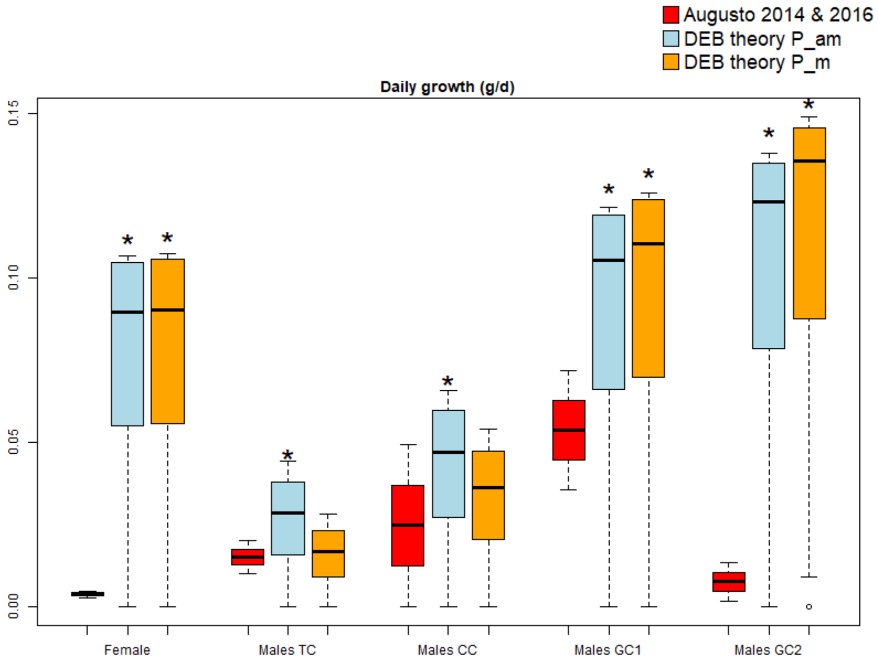

Figure 3.5: Boxplot graph comparing Augusto & Masui (2014) and Augusto & Valenti (2016) results (red) with morphotype-specific assimilation (blue) and morphotype-specific somatic maintenance (yellow) models for daily growth (g/d) for non-ovigerous females and male morphotypes. Asterisks (*) indicate significantly different results.

The models displayed similar results, but the morphotype-specific somatic maintenance model came closest to the experimental results. According to the results of Augusto & Valenti (2016), the morphotypes that grow most are CC and GC1, but predictions based on the models indicated that GC1 and GC2 may grow even more. This difference can be explained by the fact that the models do not consider the transformation from one morphotype to another. Due to this characteristic, the morphotypes CC and GC1 are considered as a reserve of individuals, therefore, if the number of GC2 individuals declines, these individuals quickly transform into the subsequent morphotype (Moraes-Riodades & Valenti, 2004).

Another factor that may influence the differences in the results, is the methodology used in the experiments by Augusto & Masui (2014) and Augusto & Valenti (2016), which cultivated the individuals separately, whereas the data used to parameterize the models was obtained from the article by Moraes-Riodades (2005) who cultivated the animals together. This difference likely influenced the growth of animals. Individuals that live isolated, without the dominant morphotype grow more until they change morphotype (Moraes-Riodades & Valenti, 2004).

### 3.3.2.Ingestion and Faecal

Figure 3.6 and 3.7 compare the ingestion and faecal rates, respectively, from Augusto & Masui (2014) and Augusto & Valenti (2016) with the results from the morphotype-specific assimilation and morphotype-specific somatic maintenance models. Morphotypes GC1 and GC2 present the highest rates of ingestion and faeces in the models, as well as in the experiments compared. In the case of females, models did not predict the high rates presented in the experiment, and the results obtained are similar to the GC1 morphotype results.

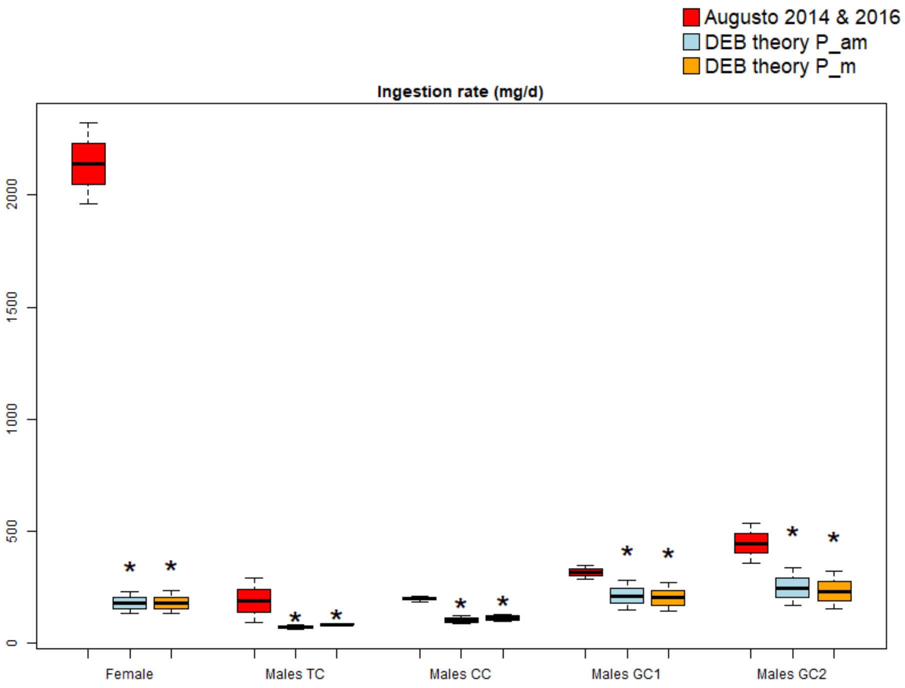

Figure 3.6: Boxplot graph comparing Augusto & Masui (2014) and Augusto & Valenti (2016) results (red) with morphotype-specific assimilation (blue) and morphotype-specific somatic maintenance (yellow) models for ingestion rate (mg/d) for non-ovigerous females and male morphotypes. Asterisks (*) indicate significantly different results.

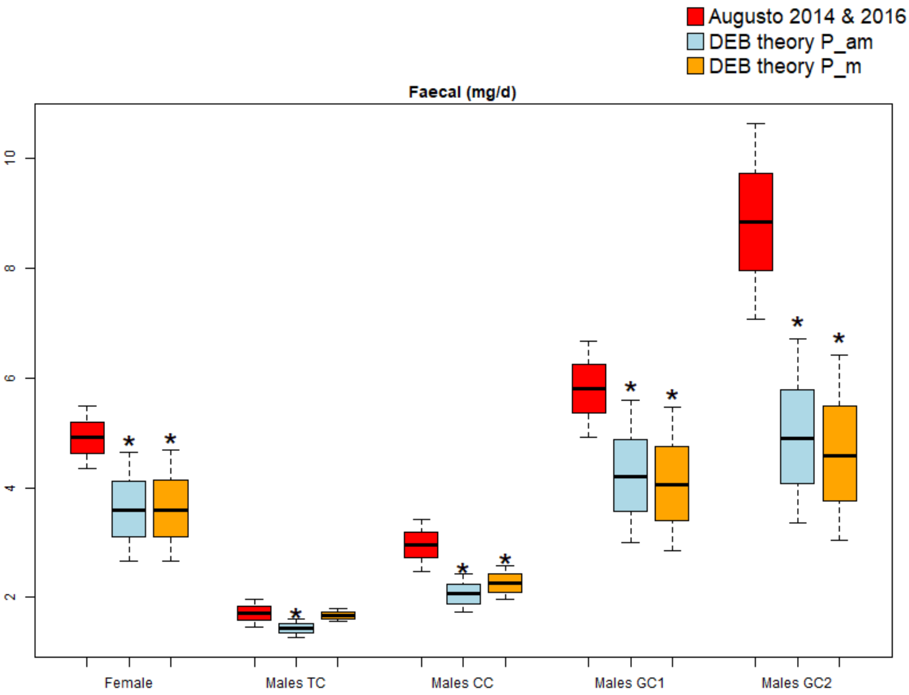

Figure 3.7: Boxplot graph comparing Augusto & Masui (2014) and Augusto & Valenti (2016) results (red) with morphotype-specific assimilation (blue) and morphotype-specific somatic maintenance (yellow) models for faecal (mg/d) for non-ovigerous females and male morphotypes. Asterisks (*) indicate significantly different results.

Although the results of the models were statistically different from the experiments, both models showed the same pattern as the experiments between male morphotypes. In the case of females, the article by Augusto & Masui (2014), discusses that the rates of ingestion and faeces may be due to the poor quality of the feed provided. Mantoan *et al.* (2021) demonstrated that diets with different percentages of crude protein influence the energy budget of the animals.

### 3.3.3.Excretion and Respiration

Figures 3.8 and 3.9 compare the model's estimates with the results of the experiments for excretion, production of $NH_3$, and respiration, consumption of $O_2$, respectively. The models predicted very similar results. In both cases the estimates present similar patterns to the experiments.

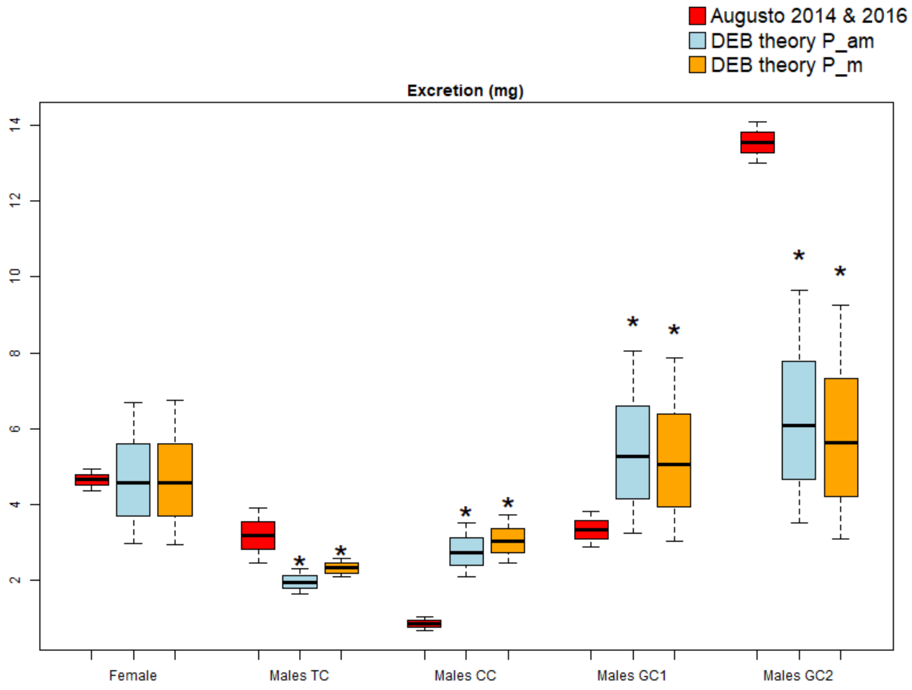

Figure 3.8: Boxplot graph comparing Augusto & Masui (2014) and Augusto & Valenti (2016) results (red) with morphotype-specific assimilation (blue) and morphotype-specific somatic maintenance (yellow) models for excretion (mg) for non-ovigerous females and male morphotypes. Asterisks (*) indicate significantly different results.

As in the experiments, the larger males presented higher excretion rates. Estimates for the CC morphotypes resulted in higher rates, while in the experiments this morphotype had the lowest excretion rate. In the case of females, both models were able to estimate the excretion rate obtained in the experiments.

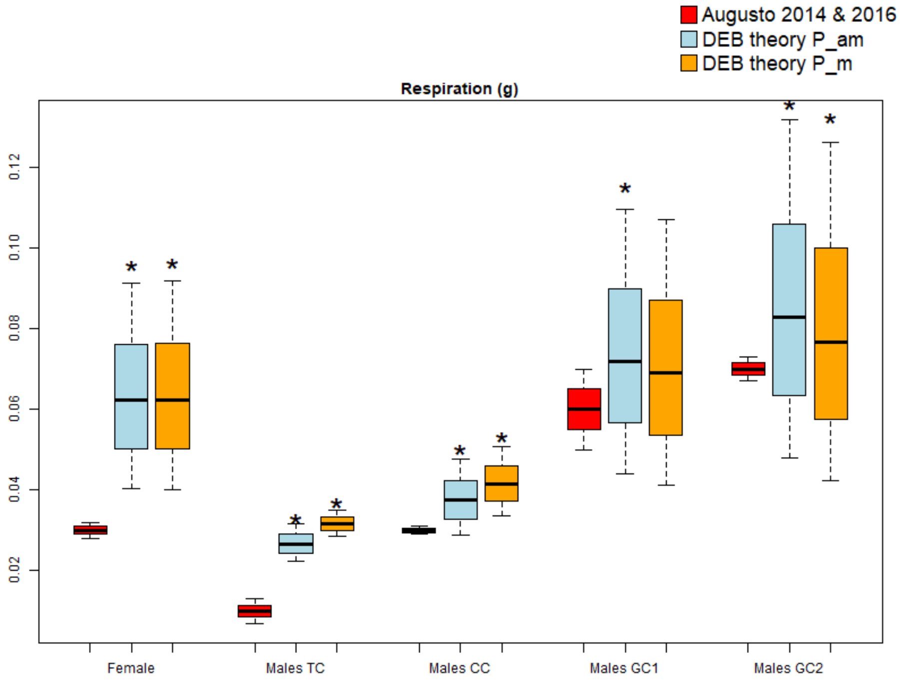

Figure 3.9: Boxplot graph comparing Augusto & Masui (2014) and Augusto & Valenti (2016) results (red) with morphotype-specific assimilation (blue) and morphotype-specific somatic maintenance (yellow) models for respiration (g) for non-ovigerous females and male morphotypes. Asterisks (*) indicate significantly different results.

The respiration presented a pattern with respect to the body size of the individuals. Larger animals exhibited higher respiration rates. Although the models presented similar results, for males TC and CC the morphotype-specific assimilation model was closer to the experiment data and for males GC1 and GC2 the morphotype-specific somatic maintenance model, for females the models estimated equal results. Augusto & Valenti (2016) have demonstrated that there is a relationship between respiration rates and body size. This relationship may explain the high respiration rates for females and the differences between the respiration rates of males, in the models we considered animals reaching an ultimate length of 12.66 cm for females and ultimate length of 14 cm for males (Table 3.1).

## 4.Conclusion

Both models showed similar results and similar patterns considering the experimental data. This demonstrates that DEB models parameterized with growth data can predict other physiological characteristics. Between the models, the morphotype-specific somatic maintenance model presents smaller MRE and SMSE when compared to the growth data and presents closest results to the physiological characteristics data, but the morphotype-specific assimilation model should be considered for future studies due to the low errors presented.

Models with more diverse data representing different stages and aspects of the life cycle are more complete models, but even with few data of the species it is possible to obtain results approximating those observed in experiments.

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# CONCLUSÕES

A diversidade nos usos para a teoria DEB é enorme, podendo ser uma ferramenta para estudos em diferentes áreas como evolução, ecologia, fisiologia e aquicultura. O uso desta teoria permite compreender eventos que dificilmente poderiam ser recriados em laboratório, e pode ser uma ferramenta complementar para estudos fisiológicos. A teoria DEB pode auxiliar em estudos sobre polimorfismo em diversas áreas. Os modelos desenvolvidos neste estudo conseguiram descrever o crescimento de cada morfotipo de duas espécies polimórficas: *Macrobrachium rosenbergii* e *M. amazonicum,* o que demonstra suas utilidades para compreender aspectos evolutivos e fisiológicos. Para a primeira espécie a interpretação feita sobre os modelos desenvolvidos focaram nos mecanismos evolutivos, e para a segunda, aspectos fisiológicos.

Neste trabalho desenvolvemos quatro modelos, dois para cada espécie. Os modelos de assimilação morfotipo-específica utilizaram diferentes taxas de assimilação para diferenciar as fêmeas e os morfotipos dos machos após a puberdade e os modelos de manutenção somática morfotipo-específica se baseou em diferentes taxas de manutenção somática para diferenciar as fêmeas e os morfotipos dos machos.

No artigo *"Two dynamic energy budget models and the evolution mechanisms for polymorphic prawns Macrobrachium rosenbergii"*, desenvolvemos dois modelos utilizando diferentes parâmetros para estimar o desenvolvimento das fêmeas e dos morfotipos dos machos. O modelo "*morphotype-specific somatic maintenance model*", com diferentes taxas de manutenção somática $\left[\dot{p}_M\right]$ para os morfotipos dos machos conseguiu prever as diferentes curvas de crescimento dos machos.

O modelo "*morphotype-specific assimilation model*", com diferentes taxas assimilação máxima $\left\{\dot{p}_{Am}\right\}$ também previu as diferentes curvas de crescimento para os morfotipos dos machos. Apresentando erros menores tanto nos dados zero variados como nas curvas de crescimento obtidas. Os resultados desse modelo se adequam melhor aos dados, indicando que esse modelo pode representar melhor a espécie.

Cada modelo representa um grupo de hipóteses formuladas para a compreensão dos mecanismos evolutivos que levam ao polimorfismo. Os resultados deste trabalho corroboram as hipóteses de hierarquia social e agressividade e eficiência alterada na absorção de alimento, podem explicar a diferenciação dos morfotipos. Como as dinâmicas populacionais são baseadas na hierarquia social, a hipótese de hierarquia social e agressividade se adequa melhor ao *Macrobrachium rosenbergii.*

No artigo *“Can a DEB model based on growth data predict physiological characteristics of polymorphic species?”*, desenvolvemos dois modelos, um com diferentes taxas de manutenção somática $\left[\dot{p}_M\right]$, “*morphotype-specific somatic maintenance model*”, e outro com diferentes taxas de assimilação máxima $\left\{\dot{p}_{Am}\right\}$, “*morphotype-specific assimilation model*”, para os morfotipos dos machos. Comparamos os resultados dos modelos com os dados fisiológicos publicados por Augusto & Masui (2014) e Augusto & Valenti (2016). e ambos modelos apresentaram resultados similares e com padrões semelhantes aos resultados empíricos obtidos por meio de experimentos. Isso sugere que modelos DEB parametrizados apenas com dados de crescimento podem predizer outras características fisiológicas e morfológicas. Entre os modelos desenvolvidos, o modelo “*morphotype-specific somatic maintenance model*” apresentou erros menores e resultados fisiológicos mais próximos, indicando que esse modelo pode corresponder melhor aos dados experimentais. Porém “*morphotype-specific assimilation model*” apresentou erros baixos e resultados fisiológicos semelhantes aos experimentais e não deve ser desconsiderado para estudos futuros.

Modelos mais realistas, com dados de diferentes estágios e aspectos do ciclo de vida, podem descrever melhor as espécies, mas mesmo com poucos dados é possível obter resultados próximos dos observados em experimentos.

No futuro, modelos DEB podem ser desenvolvidos para demonstrar a transição dos morfotipos dos machos, transições que influenciam muito nas dinâmicas populacionais e nos fluxos de energia de cada indivíduo. O desenvolvimento desses modelos pode auxiliar na compreensão da relação entre as densidades populacionais e as estratégias evolutivas estáveis nas espécies. Tais modelos podem servir também para observar como as densidades populacionais podem influenciar nos fluxos de energia, acelerando ou desacelerando o crescimento dos indivíduos - muitos estudos mostram uma relação entre a densidade populacional e o crescimento dos animais. No caso do *M. amazonicum* um modelo que inclua as diferentes populações da espécie poderia ajudar a compreender a sua distribuição e as diversas características apresentadas entre essas populações.

No geral, este trabalho demonstrou que o desenvolvimento de modelos com um único parâmetro estimado para diferentes grupos pode descrever diferentes morfotipos naturalmente observados em espécies polimórficas. E a diversidade nos usos desses modelos permite estudos em diferentes áreas, revelando a grande versatilidade que uma ferramenta como a teoria DEB pode representar no campo da biologia.

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