

Energy demand during exponential growth of *Octopus maya*: exploring the effect of age and weight

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Recent work has reported changes associated with physiological, morphological, and behavioural adaptation during the absorption of yolk reserves. The holobenthic endemic species *Octopus maya* was used to explore the energy supply needed from the food intake (I ; $J \text{ animal}^{-1} \text{ d}^{-1}$) to supply the rate of production energy needed for body mass (P ; $J \text{ animal}^{-1} \text{ d}^{-1}$) and respiration rate (R ; $J \text{ animal}^{-1} \text{ d}^{-1}$) as a function of weight and age during the exponential early growth phase of the animal. Individually housed juveniles from hatching (1 d) to 105 d after hatching (DAH) were used, with the age and weight known, and the relationship between oxygen consumption (VO_2 ; $\text{mg O}_2 \text{ animal}^{-1} \text{ d}^{-1}$) and weight (g) was established. Projections of I , R , and P as a function of age (Z) were made. The food intake destined to supply body mass production ($\%P/I$) and respiration rate energy ($\%R/I$) was analysed for an extended age range of 1–150 DAH. When *O. maya* juveniles hatched, they had a greater requirement for R than for P from the food intake, 61% ($\%R/I$) and 13% ($\%P/I$), respectively, suggesting high metabolic cost associated with post-hatching (during yolk absorption). Within the period where $Z_R > Z_P$ (1–105 DAH), there was sufficient metabolic energy to satisfy the demands for sustaining exponential body mass production. The age at which $\%R/I = \%P/I$ delimits the point where P cannot increase for reasons of metabolic constraint.

Keywords: assimilated energy, exponential growth phase, *Octopus maya*, partial energy balance, post-hatching juvenile.

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Introduction

The growth of an individual is the result of a series of energy transformations undergone by ingested food, and of the balance between the uses and destinations of the energy contained in that food (Lucas, 1993; Rosas *et al.*, 2007). The manner in which this process is expressed over time (the growth curve) is a product of physiological and energy demands (O'Dor and Wells, 1987; Pauly, 1998) at differing levels of biological organization, i.e. body size, organs, tissue, and cells (Moltschanivskyj, 2004).

Energy balance is estimated from the equation (Lucas, 1993) $I = H + U + R + P$, where I is the ingested energy, H and U the energy lost in faeces and products from protein metabolism, respectively, and R and P the energy invested in metabolic processes producing tissues and gametes (body mass), respectively. The difference between the energy from I and the loss in H and U is the assimilated energy (A_s) which, according to Lucas (1993), can be defined as $I - (H + U)$ or as $R + P$, and it represents (Rosas *et al.*, 2007) the amount of physiologically useful energy (PUE) available to maintain homeostasis (R) and growth (P).

Bioenergetic models for cephalopods are rare (Rosas *et al.*, 2007; André *et al.*, 2009a, b). Available research can be divided into two forms: (i) studies of ecological adaptation, such as those carried out on *Octopus maya* (Van Heukelem, 1976; Farías *et al.*, 2009), *Octopus vulgaris* (O'Dor and Wells, 1987; Wells and Clarke, 1996; Katsanevakis *et al.*, 2005a, b), *Pareledone charcoti*

(Daly and Peck, 2000), *Enteroctopus megalocyathus* (Farías *et al.*, 2009), *Sepia apama* (Grist and Jackson, 2004), *Octopus pallidus* (André *et al.*, 2009a), and *Octopus ocellatus* (Segawa and Namoto, 2002; André *et al.*, 2009a); and (ii) nutritional evaluation focusing on determining artificial diets for aquaculture (*O. vulgaris*: Petza *et al.*, 2006; *E. megalocyathus*: Pérez *et al.*, 2006; *O. maya*: Aguila *et al.*, 2007; Rosas *et al.*, 2007, 2008). Another aspect of these studies is that most have been limited to subadult and/or adult phases because of their relatively easy maintenance compared with earlier phases, particularly in species whose cycles begin with a planktonic stage (e.g. *O. vulgaris*). From studies carried out on species with benthic hatchlings such as *O. maya*, *O. pallidus*, and *O. ocellatus*, it has been possible to develop scaling models that describe the ratio between body size and food ingestion rate, metabolism, and ammonia excretion (Van Heukelem, 1976; Segawa and Hanlon, 1988; Segawa and Namoto, 2002; André *et al.*, 2009a; Farías *et al.*, 2009).

Some recent studies have used bioenergetic models to shed further light on the factors giving rise to the biphasic growth pattern characteristic of cephalopods (Forsythe and Van Heukelem, 1987; Semmens *et al.*, 2004). Grist and Jackson (2004) formulated a bioenergetic model based on the principle of energy conservation, which theoretically suggests that the shift to a slower growth phase in *S. apama* may be associated with a body mass and age threshold at which the energy derived from food (I) can no longer satisfy the physiological demands

associated with metabolism (R) and production of biomass (P), thereby producing an energy disequilibrium ($I < R + P$). It is suggested that such disequilibrium could bring a switch from a faster (exponential) to a slower growth phase, described as a power function by some authors (see Grist and Jackson, 2004), and which is more common among marine organisms in which the physiological demands of body mass production remain biologically possible (Grist and Jackson, 2004, 2007; André et al., 2009a). Age and body mass thresholds associated with the transition between the two growth phases under diverse temperature scenarios have also shown how variations in that parameter modulate the use and function of energy, allowing better understanding of the effect that it may have on the life cycle of cephalopods (André et al., 2009b).

Since the end of the 19th century, the use of the term physiological useful energy (PUE) has become more common, because it is known to be related to weight, mainly because the energy demand changes in synchrony with the body mass of an organism (Andrews et al., 1972; Storey and Storey, 1978; Clarke and Johnston, 1999; Gillooly et al., 2001, 2002; Clarke, 2004; Clarke and Fraser, 2004; Pörtner et al., 2005; Fariás et al., 2009).

In a recent study, Moguel et al. (2010) characterized the post-hatching development of *O. maya*. Morphometric changes revealed that juveniles have a “non-growth phase” during the first 10 d after hatching (DAH). Histological analysis revealed that the digestive gland of octopuses changes with age, from a simple tubular gland 2 DAH, to a tubulo-acinar and vacuolar structure with digestive cells characterized by vacuoles 45 DAH. Digestive enzyme activity showed erratic activities until 14 DAH, but thereafter, it started to stabilize. *Octopus maya* 2 and 3 DAH rarely attacked or showed any response to visual or combined visual and chemical stimuli from a prey organism. In contrast, octopuses 4 DAH responded to visual stimuli from crabs and palaemonids, but they did not display a preference for attacking either prey type. Based on these results, we defined two phases within the early life history of *O. maya*: a post-hatching phase and a juvenile phase. The period 10–15 DAH was defined as the transition time for *O. maya* before animals reached the real juvenile stage. Moreover, in the immediate post-hatching period, octopuses showed clear lipid metabolism related to the uptake of yolk. That condition provides a greater opportunity to survive during the first days of life, when food might be limited, mainly when the arms of the animal are insufficiently developed. Evaluation of the rate of energy transferred to carry out basic functions and to growth as an age function could be useful in understanding the physiological adaptations of octopuses to satisfying the energy demands after hatching, during transition to the juvenile stage, and during the juvenile stage itself (Moguel et al., 2010). The exponential growth phase in *O. maya* has been modelled by a generalized linear mixed model (GLMM), using animals individually housed from hatching to 105 DAH, allowing a more accurate growth rate to be determined alongside greater precision in the predictions of octopus weight from known ages (Briceño et al., 2010). At the same time, other recent studies have increased the knowledge of *O. maya* physiology, with special attention paid to the relationship between size, ingested food, and oxygen consumption, within a wide range of weights (0.5–1350 g; Fariás et al., 2009).

Given the information above, the current work focused on establishing the relationships between the energy supply from food (I) and the energy demands associated with body mass

production (P) and respiration (R), using a partial energy model during the exponential growth phase of sibling juvenile *O. maya* individually housed from hatching date. Applying the model proposed, we estimated how energy demands change as a function of age and body mass during the fastest growth phase of the species, contributing new information on the physiology of early-stage cephalopods.

Material and methods

Juvenile *O. maya* were obtained from Laboratorio Experimental de Producción de Pulpo of the National Autonomous University of Mexico, in Sisal (Yucatán, México). The experiments were conducted with two juvenile sibling populations obtained from two wild females induced to spawn by controlling feeding, photoperiod, and temperature. Eggs were incubated artificially (without maternal care) at $28 \pm 1^\circ\text{C}$ until hatching. Juveniles were weighed after hatching (at 1 d old) and housed individually in 300 ml plastic containers connected to a recirculating water system. Water was UV-treated, ozonified, and skimmed to maintain optimal water quality with O_2 levels $>5.0 \text{ mg l}^{-1}$, $\text{pH} > 8$, and ammonia $<0.1 \text{ mg l}^{-1}$. Temperature was maintained at $27 \pm 1^\circ\text{C}$ using a heater/cooler. The octopuses were fed *ad libitum* with pieces of crab blue (*Callinectes sapidus*) to 105 DAH. Juveniles were weighed individually again at 15, 45, 75, and 105 DAH. Daily growth rate (DGR), expressed as $\% \text{BW d}^{-1}$, where BW is body weight, was calculated for each octopus over the age ranges 1–15, 15–45, 45–75, and 75–105 DAH. DGR was calculated using the equation of Forsythe and Van Heukelem (1987):

$$\text{DGR} (\% \text{BW d}^{-1}) = \frac{\ln \text{BW}_2 - \ln \text{BW}_1}{t} \times 100, \quad (1)$$

where BW_2 is the final body weight, W_1 the initial body weight, and t the number of days in the range. Mortality was checked daily when the octopuses were fed, and unconsumed food and faeces were siphoned out daily.

Food intake energy rate (I)

Values of the food intake energy rate (I : $\text{J animal}^{-1} \text{ d}^{-1}$) as a function of weight were estimated using the food intake model of Fariás et al. (2009) for *O. maya*:

$$I = 0.064W^{0.84}, \quad (2)$$

where W is the weight in g. A value of 17 kJ g^{-1} crab was used to transform food intake rate to energy equivalents. We considered the Fariás et al. (2009) food intake energy rate model as representative during the exponential growth phase because it was developed (i) with an extensive dataset of weights of *O. maya* from the juvenile (0.5 g) to the adult stage (1350 g), covering the exponential growth phase, and (ii) with the same food source (fresh crab) provided.

Body mass production to growth (P)

The energy invested in producing body mass (P) was estimated from the weight differences over the age ranges listed above (e.g. $\Delta W_{1-15} = W_{15 \text{ DAH}} - W_{1 \text{ DAH}}$). The value 10.01 kJ g^{-1} dry weight was used to convert each ΔW into its energy equivalent (Rosas et al., 2007). It was determined for groups of 10 animals in a Parr® calorimeter pump.

Oxygen consumption and respiratory rate energy (R)

Oxygen consumption (VO_2) was measured using a continuous flow respirometer comprising respirometric chambers connected to a recirculating system (Rosas *et al.*, 2007). Juveniles were placed in 125 and 110 ml chambers, depending on size, with an approximate flow rate of 0.1 l min^{-1} . All animals were acclimatized into the chambers for 6 h before measurements were made. Empty shells (*Melongena corona bispinosa*) and pieces of PVC tube were used as shelter. A chamber without an octopus (with a shelter) was used as a control. Measurements of dissolved oxygen (DO) were made for each chamber (inlet and outlet) every 15 s with oxygen sensors attached to flowcells that were connected by optical fibre to an Oxy 10 mini-amplifier (PreSens©, Germany). The sensors were calibrated at 27°C with saturated seawater (100% DO) and with a 5% sodium sulphate solution (0% DO). All measurements were taken at night from 18:00 to 09:00 local time, a period of quiet and little movement in the laboratory, to reduce stress of the experimental animals. Values of oxygen consumption obtained from 42 juvenile *O. maya* were used in estimating the body mass function.

We integrated our VO_2 dataset within the Farías *et al.* (2009) oxygen consumption model for *O. maya* by weight to attain a more reliable metabolic coefficient during the exponential growth phase. The factor 14.3 J mg^{-1} was used to transform VO_2 values into metabolic rate energy (R), expressed in $\text{J animal}^{-1} \text{ d}^{-1}$ (Lucas, 1993).

Partial energy balance

The energy demands of respiration (R : $\text{J animal}^{-1} \text{ d}^{-1}$) and body mass production (P : J d^{-1}) were estimated as a function of body mass (W) from

$$R = \alpha_1 W^{\beta_1}, \quad (3)$$

$$P = \alpha_2 W^{\beta_2}, \quad (4)$$

where α_1 and α_2 are constants, and β_1 and β_2 the power exponents, respectively. We have assumed that body mass production energy (P) can be expressed as a power function of body mass with an exponent $\beta_2 = 1$. The constants α_1 and α_2 , and the power exponents β_1 and β_2 were obtained by linear adjustment performed through least squares, before logarithmic transformation of all variables. In both analyses, data were explored with (i) point graphics to identify extreme data, (ii) histograms and quantile graphics to ensure a normal distribution, and (iii) X - Y plots to ensure a linear relationship. Once the significance of the regression parameters had been established by t -test, model validation was carried out by visually inspecting the residuals (Montgomery and Peck, 1992; Draper and Smith, 1998).

Energy values as a function of age

The exponential growth model for *O. maya* of Briceño *et al.* (2010) was used to predict octopus weight (W) at known age (t), growing at 0.03 g d^{-1} , using the equation

$$W = 0.113e^{0.03t}. \quad (5)$$

Replacing weight as a function of age [Equation (5)] within Equations (2)–(4) allowed us to estimate food intake (I),

respiration (R), and body mass production (P) rate energies (J d^{-1}) throughout the exponential growth phase from 1 to 105 DAH. The supply and usage of energy can be estimated as a function of age by the models (Z in J d^{-1} ; Z_I , Z_R , and Z_P):

$$Z_{(k)} = \alpha' [0.113e^{0.03t}]^{\beta'}, \quad (6)$$

where k is I , R , or P , the α' value is a constant, t represents the age in days, and β' is a power exponent. We estimated how much intake food rate energy is necessary to cover body mass production ($\%P/I$), respiratory energy ($\%R/I$), and assimilated energy ($As = P + R$) under conditions of exponential growth over an extended range of ages from 1 to 150 DAH, to investigate energy usage in older animals.

Results

DGR varied between 3.39 and $2.89\% \text{ BW d}^{-1}$ from 1 to 105 DAH, with an average of $2.23 \pm 1.62\% \text{ BW d}^{-1}$. Maximum and minimum values were observed from 15 to 45 DAH and from 1 to 15 DAH, respectively (Table 1). A rate of survival close to 100% was observed until 45 DAH, decreasing subsequently to 28% at 105 d (Table 1).

Food intake rate energy (I)

This increased as a power function of body mass (W). Once those values were converted to energy equivalents, the equation (Figure 1) was

$$I (\text{J animal}^{-1} \text{ d}^{-1}) = 1071.5W^{0.84}. \quad (7)$$

Table 1. DGR and survival of individually housed juvenile (sibling) *O. maya* between 1 and 105 days after hatching (DAH) at $27 \pm 1^\circ\text{C}$.

Juvenile age range (d) and parameter	Mean	s.d.	n
1–15 DAH			
Weight (g) at 1 DAH	0.11	0.02	53
Weight (g) at 15 DAH	0.18	0.05	53
DGR (%BW d^{-1}) (ΔW_{1-15})	2.89	1.29	53
Survival (%)	100		
1–45 DAH/15–45 DAH			
Weight (g) at 45 DAH	0.58	0.26	52
DGR (%BW d^{-1}) (ΔW_{15-45})	3.63	1.41	51
DGR (%BW d^{-1}) (ΔW_{1-45})	3.39	0.98	51
Survival 1–45 DAH (%)	98.1		
Survival 15–45 DAH (%)	98.1		
1–75 DAH/45–75 DAH			
Weight (g) at 75 DAH	1.22	0.59	32
DGR (%BW d^{-1}) (ΔW_{1-75})	2.59	0.74	31
DGR (%BW d^{-1}) (ΔW_{45-75})	3.04	0.66	31
Survival 1–75 (%)	60.4		
Survival 45–75 (%)	61.5		
1–105 DAH/75–45 DAH			
Weight (g) at 105 DAH	2.65	1.34	15
DGR (%BW d^{-1}) (ΔW_{1-105})	2.23	1.62	14
DGR (%BW d^{-1}) (ΔW_{75-105})	2.90	0.56	14
Survival 1–105 (%)	28.3		
Survival 75–105 (%)	46.8		

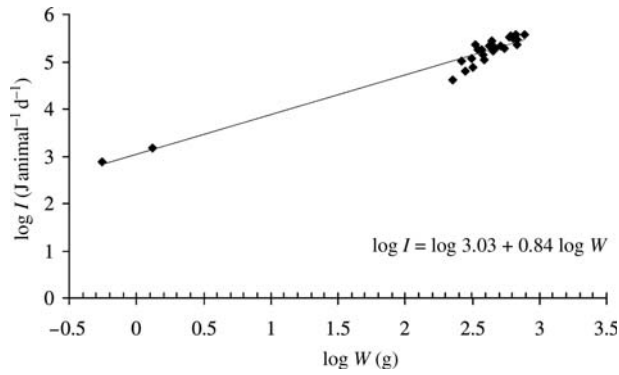


Figure 1. Linear relationship between the food intake energy (I) and weight (W ; g) in juvenile *O. maya*. Data calculated from Farías et al. (2009) at 28°C.

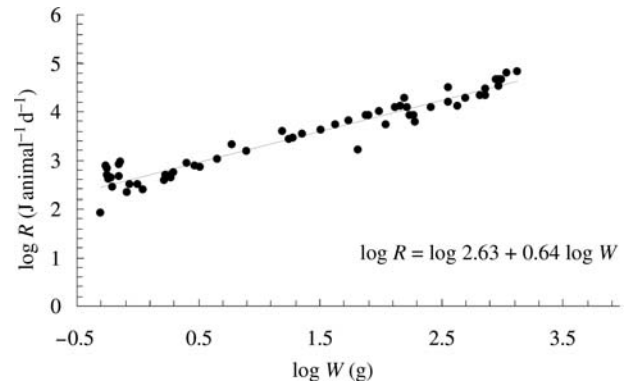


Figure 3. Linear relationship between respiration energy (R) and weight (W ; g) for *O. maya* (0.2–1350 g) maintained at 27°C. The oxygen consumption (VO_2) dataset of this study was integrated onto the *O. maya* VO_2 model of Farías et al. (2009).

Table 2. Coefficients of equations resulting from linear adjustments between respiration rate energy (R ; $J d^{-1} animal^{-1}$) and body mass production rate energy (P ; $J d^{-1}$), as a function of wet weight (g) of *O. maya* from 1 to 105 DAH.

Equation	Parameter	Values \pm s.e.	p -value
log P vs. log W	α	2.29 ± 0.02	$t = 147.5^{***}$
	β	0.98 ± 0.03	$t = 31.7^{***}$
	σ	0.153	
	AIC	-128.8	
log R vs. log W	α	2.63 ± 1.05	$t = 250^*$
	β	0.64 ± 0.02	$t = 28.4^{***}$
	σ	0.1995	
	AIC	-7.16	

Corresponding values of Akaike information criterion (AIC) and σ are also shown.

* $p < 0.05$.

*** $p < 0.001$.

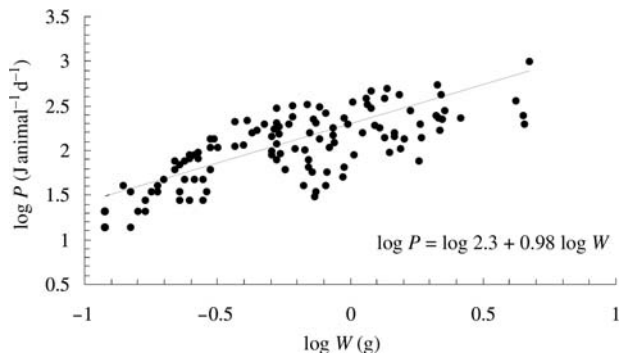


Figure 2. Linear relationship between body mass production energy (P) and weight (W ; g) for juvenile *O. maya* individually housed from hatching.

Body mass production rate energy (P) and respiratory rate energy (R)

Constants and power exponents estimated using linear adjustments of respiration (R ; $J animal^{-1} d^{-1}$) and body mass production (P ; $J animal^{-1} d^{-1}$) as a function of body mass (g) showed that both energy parameters increased as a power function

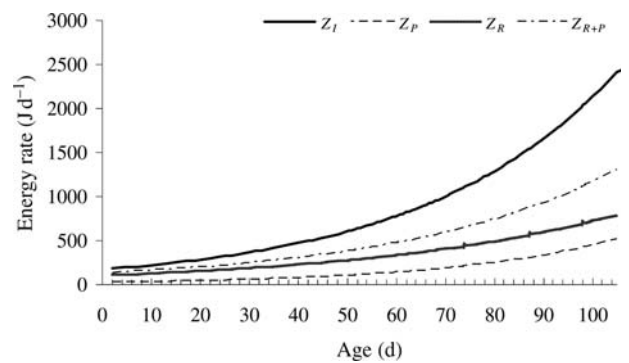


Figure 4. Projections of food intake rate energy (Z_I), body mass production (Z_P), and respiration rate energy (Z_R) as a function of age in the exponential growth phase (1–105 DAH) in *O. maya*. Projections were obtained using the model $Z = \alpha[0.113e^{0.03t}]^\beta$ for Z_I , Z_R , and Z_P (for detail see text).

of body mass (Table 2, Figures 2 and 3):

$$P (J animal^{-1} d^{-1}) = 199.5W^{0.98} \tag{8}$$

$$R (J animal^{-1} d^{-1}) = 426.6W^{0.64} \tag{9}$$

Partial energy balance

Once we had obtained constants and exponents for each energy parameter [I , R , and P ; $J d^{-1}$; Equation (5)] along with their corresponding log-transformations, we developed models to predict supply and usage of energy as a function of age [Equation (6)]:

$$Z_I = 1071.5(0.113e^{0.03t})^{0.84}, \tag{10}$$

$$Z_P = 199.5(0.113e^{0.03t})^{0.98}, \tag{11}$$

$$Z_R = 426.6(0.113e^{0.03t})^{0.64}. \tag{12}$$

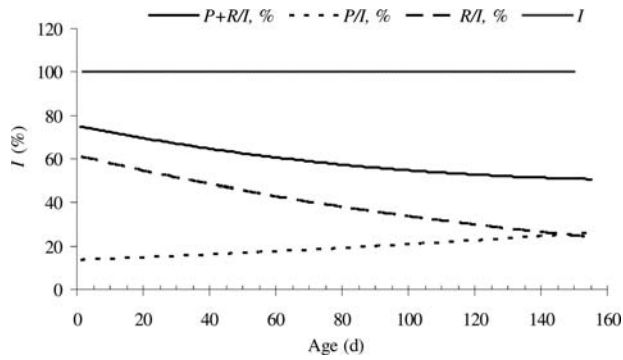


Figure 5. Relationship between body mass production (P), respiration (R), and assimilated ($P + R$) energy as a percentage of the food intake rate energy ratio I and age in juvenile *O. maya*. Values were calculated up to 150 DAH using the model $Z = \alpha[0.113e^{0.031t}]^\beta$ for Z_p , Z_R , and Z_p (for detail see text).

Table 3. Required food for body mass production energy and food conversion ratio of *O. maya* juveniles from different age ranges during the exponential growth phase.

Age (DAH)	Required food		Body mass production		
	kJ	Food (g)	kJ	Body mass (g)	Food conversion ^a
0–15	3.17	0.19	0.45	0.04	4.18
16–30	4.62	0.27	0.70	0.07	3.92
31–60	16.59	0.98	2.78	0.28	3.55
61–90	35.34	2.08	6.72	0.66	3.13
91–120	75.27	4.43	16.22	1.61	2.76
Total	134.99	7.94	26.87	2.66	2.99

^aFood (g) required to produce 1 g of body mass.

Using these models, changes with age of I , P , and R were calculated, and values of A_s were determined $A_s = P + R$ (Figure 4). According to the calculations of Z_k , the energy channelled to P was less than that to R until day 105. The invested energy ($\%R/I$ and $\%P/I$) was projected from 1 to 150 DAH. Animals >105 DAH showed a reduction in $\%R/I$. In contrast, there was an increase in $\%P/I$ with age; that increase meant that values of $\%P/I$ were higher than $\%R/I$ when octopuses reached 150 DAH (Figure 5). Interestingly, the reduction in $(A_s = P + R)/I\%$ stabilized when the animals attained 150 d, maintaining values $\sim 50\%$ and showing similar proportions in both $\%P/I$ and $\%R/I$.

According to the model, the energy needed to produce an octopus of 2.66 g is 135 kJ, equivalent to 7.9 g of crab meat. An animal can reach such a weight 120 DAH. The conversion factor is therefore 3 (3 g of food for 1 g of octopus; Table 3).

Discussion

The food intake rate (I) and respiratory rate (R) energy modelled here for *O. maya* during its exponential growth phase revealed a means of diverting ingested energy to body mass production (P). The results showed that, besides the transition between embryonic and juvenile stages reported for *O. maya* by Moguel *et al.* (2010), juveniles pass through metabolic changes that constrain the way they can grow. Between 1 and 100 DAH, juveniles

invest more energy in respiration ($\%R/I$) than in body mass production ($\%P/I$), showing that the costs associated with nutrient movement and tissue synthesis during morphological, physiological, and behavioural changes at such stages are greater than body mass production (Wells and Clarke, 1996). Taking this into account, the extension of the initial growth phase observed in species with benthic hatchlings, such as *O. pallidus* and *O. maya*, may be explained by the high metabolic requirements at the beginning of the life cycle (Leporati *et al.*, 2007; Briceño *et al.*, 2010; Moguel *et al.*, 2010). Several explanations are possible for these metabolic constraints: (i) culture conditions can stunt growth through the increment on metabolic rate for instance as a stress response by animals housed individually, resulting in a slower growth rate than expected for cephalopods during fastest growth phase; (ii) the nutritional property of the food provided under culture conditions is not sufficient to satisfy the requirements for high rates of body mass production; (iii) the efficiency of octopuses in transforming energy into biomass after hatching is poor; (iv) artificially maintaining octopuses in isolation included some animals that, in open tanks or in nature, are not part of the population, except through their role as food via cannibalism (Ibañez and Keyl, 2010). In the last case, cannibalism provides an extra bonus of energy to a population that can be transformed into body mass and reflected in a faster growth rate than observed when animals are isolated.

The integration of our VO_2 dataset within the VO_2 model of Farias *et al.* (2009) at 27°C presented here allows us to obtain more accurate oxygen consumption estimates for *O. maya* over an extended weight range (82 animals measured under the same experimental conditions). A new constant and new power exponent (metabolic exponent) have been calculated as $\alpha = 1.25$ and $\beta = 0.64$, rather than $\alpha_f = 0.93$ and $\beta_f = 0.69$, respectively (see Farias *et al.*, 2009). The metabolic exponent obtained ($\beta = 0.64$) was lower than reported by Segawa and Hanlon (1988) for *O. maya* ($\beta = 0.9$), but similar to the values reported for other species of octopus: *O. vulgaris* (0.70–0.95; Cerezo-Valverde and García-García, 2004; Katsanevakis *et al.*, 2005a, b); *O. ocellatus* (0.78–0.84; Segawa and Namoto, 2002); and *E. megaloclyathus* (0.69; Farias *et al.*, 2009). These results suggest that the relationship between size and metabolic rate in octopuses, such as in some fish species and aquatic invertebrates (Clarke and Johnston, 1999), is close to an exponent ~ 0.75 proposed as a generalized value under the power law (3/4; Gillooly *et al.*, 2001). On the other hand, Wells and Clarke (1996) stated that cephalopods use between 60 and 80% of assimilated energy for body mass production, and that the balance (20–40%) is lost in thermodynamic costs associated with the movement of nutrients and tissue synthesis. Unfortunately, those values were obtained from late juveniles or subadults of several octopus species without taking into account possible changes in the metabolic rate associated with age (Cerezo-Valverde and García-García, 2004; Katsanevakis *et al.*, 2005a, b). The results obtained here reveal that the proportion of ingested energy available for body mass production and metabolism changes with age. When *O. maya* hatched (1 DAH), R consumed 61% of the ingested energy and P 13%, suggesting that, at that point, the efficiency with which an octopus transforms energy to body mass is poor. That condition is inverted with age, according to the models, and during maturation, there are metabolic changes.

Recent studies carried out on *O. maya* and other species (Vidal *et al.*, 2002) demonstrated that octopuses and cephalopods in

general pass through a transitional post-embryonic stage in which the digestive processes and the use of nutrients are rather inefficient. Those authors reported zero growth in *Loligo opalescens* during the first few days of life, a period when the animals change from endogenous to exogenous food, once the yolk has been absorbed. That period has been identified as critical in squid, because survival can be severely compromised by an energy disequilibrium arising from the high metabolic demand attributable to hatching and the exponential absorption of yolk. Depending on the temperature, this period may last from 10 to 15 d in *L. opalescens*, and it has been recognized as a time at which most of the energy content of the yolk is lost through respiration (Vidal et al., 2002). In our study, *O. maya* hatched with a yolk reserve that was absorbed rapidly over the first 10 DAH (Moguel et al., 2010), when the digestive gland of the octopus passes through a maturation stage similar to that reported for *Sepia officinalis* (Yim and Boucaud-Camou, 1980; Nixon and Mangold, 1998). This stage is accompanied by changes in the activity of digestive enzymes during the multiplication phases (0–8 DAH) and cellular maturation (10–20 DAH). Changes in the proportion of arm length relative to total length were also observed, suggesting that, besides digestive maturation, octopuses also complete their development and acquire the morphology characteristic of their juvenile phase (20 DAH; Moguel et al., 2010). Taking into account the period of yolk absorption reported for cephalopods and digestive and morphological changes, we suggest that the high metabolic rate observed during the first days of life is a reflection of the low efficiency of these organisms during the early transitional period between post-embryonic life and the juvenile phase. Segawa and Hanlon (1988) demonstrated great variability in VO_2 values at 18 DAH (0.17–0.19 g), an age at which they suggested that individuals undergo certain changes associated with lipid metabolism during yolk absorption. Such low efficiency seems to be common among cephalopods. The no-net-growth period after hatching to 15 DAH is followed by an exponential growth phase, in which a rapid transformation of ingested energy into biomass takes place. In *L. opalescens*, this process begins when squid feed for the first time and compensate for the low efficiency associated with yolk absorption. For *O. maya*, Moguel et al. (2010) stated that exponential growth begins between 10 and 15 DAH, when prey selection has started. Moreover, recent histological studies carried out by López-Ripoll (2009) on *O. maya* during the first days of life showed that juveniles 15 DAH had completely developed digestive gland cells in which the nutrients and food are transported to the blood.

In this study, either P or R was modelled as a power function of age (Z_R or Z_P), with differences in the way that energy usage is scaled ($\beta_2 > \beta_3$). This suggests that during exponential growth, the energy demand for body mass production is greater than for respiration, at least from 1 to 149 DAH. These differences in values of β suggest a disequilibrium between the supply (β_1) and uptake of energy (β_2), which should not extend beyond the limits imposed by thermodynamic laws (Wells and Clarke, 1996). The results obtained show that within the period when $Z_R > Z_P$ (between 1 and 149 DAH), there would be sufficient metabolic energy to satisfy the demands to sustain body mass growing exponentially, which would reach a limit once $\%R/I = \%P/I$. The age at which $\%R/I = \%P/I$ is when the body mass production demand cannot increase faster than that of metabolic energy, and it could be associated with a transition between exponential and slower growth phases, as suggested by Grist and

Jackson (2004) and André et al. (2009a) for other cephalopod species. Briceño et al. (2010) provided an exponential growth model based on a GLMM using animals from 1 to 105 DAH, from known-age juveniles taken on hatching. No weight data have been published under the same experimental design proposed by those authors (initial size categories) for *O. maya* between 105 and 165 DAH, showing that a decreased growth rate could be a consequence of growth deceleration associated with a second growth phase (Semmens et al., 2004). That supports the notion that as a consequence of the disequilibrium resulting from maintaining exponential growth, octopuses >150 DAH reduce their growth rate simply because they cannot obtain an adequate energy supply.

Using data from partial energy models, we have calculated the energy required for body mass production in different age ranges of *O. maya*. From these models, body mass (g) and food quantity can be estimated to support culture (Rosas et al., 2009; Table 3). For example, the quantity of food necessary to attain a body mass of 2.66 g is 7.94 g (for crab meat). Therefore, a conversion factor close to 3 and a ratio of one-third of ingested energy would be needed to attain this body mass. These values were similar to those reported by Mangold (1983) for *Eledone moschata* (18–70%), *Eledone cirrhosa* (37%), *Octopus cyanea* and *O. maya* (40%), *Octopus joubini* (40%), and *Octopus tetricus* (47%).

Our results represent a contribution to better understanding the way in which octopuses exchange and transform energy during their fast growth phase. As age is the factor that constrains the differences in efficiency of food assimilation, perhaps management techniques accounting for these differences will facilitate optimal weight gain and growth of *O. maya* under culture conditions. Allowing cannibalism as a strategy to improve the growth rate of culture populations could be valuable in future, but more work is needed first. The asymmetry in size between cannibalizing animals and their victims needs to be explored by searching for the “cannibalistic window” through an intra- and inter-cohort approach, and evaluating its consequences in cultured and wild populations (Ibañez and Keyl, 2010). Such studies could alter the growth models developed with animals in isolation that could not take into account the energy value of a victim to the growth of the cannibal. The incorporation of temperature in future studies would also allow exploration of how the metabolic processes associated with respiration can be altered by varying the environmental conditions. Further analyses integrating other factors, such as sex, the metabolic cost associated with transportation, and prey selection, will be needed to contribute to an even better understanding of the physiological demands of *O. maya*, to continue gathering information required to determine the source of the great variability in growth of cephalopods.

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