GLMM-based modelling of growth in juvenile *Octopus maya* siblings: does growth depend on initial size?

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In most studies on cephalopod growth, variability in initial size is masked by the assumption of a similar growth "starting point" for all hatchlings and by calculating the growth rate (GR) through modelling the average size of individuals through time. Statistical interpretations based on such models are limited because regression assumptions (e.g. homoscedasticity and independence between subjects) are frequently violated. To avoid these limitations, generalized linear mixed modelling was used to model the early growth of two sets of siblings of the holobenthic octopus *Octopus maya* under controlled conditions. The aim was to (i) determine the effect of initial weight (IW) on the GR of individuals grouped in three size categories (small, medium, and large), (ii) obtain statistically reliable estimates of parameters in an exponential growth model for juveniles up to 105 d old, and (iii) evaluate the influence of hatching date on weight at hatching. Using restricted maximum likelihood, linear models were fitted between (i) IW and final weight (FW) for octopuses in each size category, and (ii) the natural logarithm of IW as a function of time. The models were validated by visually inspecting the residuals. Individual FW depended on IW, but GR did not differ between juveniles of different sizes. The exponential growth model for individuals of all size categories was, with $\varepsilon_i \sim N(0,\sigma^2\,[\mathrm{age}_i]^{2\delta})$. Hatching date had no effect on hatching size ($F = 1.93$; $p = 0.11$). The GR value is similar to those reported for other holobenthic species, and one of the first estimates of the magnitude ($\delta = 0.20$) and structure of the increase in variance of individual weight through time is provided.

Keywords: exponential growth phase, GLMM, growth depensation, initial size, *Octopus maya*.

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Introduction

Understanding growth has been a major focus of cephalopod research over the past few decades. This research is important owing to the central role of cephalopods in marine ecosystems as both predators and prey for many other species (Hanlon and Messenger, 1996; Jackson, 2004) and because of the implications in terms of sustainable management of cephalopod fisheries (Leporati *et al.*, 2007). Studies on growth have relied on both indirect and direct methods (Semmens *et al.*, 2004), and they have shown that cephalopod growth is unusual because: (i) its rates are among the highest in metazoans (Calow, 1987; the highest in invertebrate metazoans, higher than those of fish and similar to those of homeotherms, specifically mammals); (ii) it lacks an asymptotic growth phase (Moltschaniwskyj, 2004); (iii) it is highly plastic owing to its strong dependence on abiotic and biotic factors, mainly temperature (Forsythe and Van Heukelem, 1987; Forsythe, 1993; Pecl *et al.*, 2004), the amount and quality of food (Koueta and Boucaud-Camou, 1999; André *et al.*, 2008), and sexual maturation (Semmens *et al.*, 2004); (iv) it follows a biphasic pattern (as it often does in captivity), consisting of an initial rapid exponential phase followed by a second phase, where growth slows down progressively (Semmens *et al.*, 2004; André

et al., 2009); and (v) it is highly variable intraspecifically (Pecl *et al.*, 2004; Leporati *et al.*, 2007).

Heterogeneous growth (HG) among individual cephalopods attributable to age and size being unrelated has been documented at the level of cohorts and microcohorts (Cortez *et al.*, 1999; Markaida *et al.*, 2004; Jackson *et al.*, 2007; Leporati *et al.*, 2008), and in populations of known origin (i.e. cultures; Leporati *et al.*, 2007). HG has important implications for population dynamics, age and size structures, reproduction, larval survivorship, and local abundance (Leporati *et al.*, 2007). Several studies have shown the effect of temperature on the emergence of HG, with small variations during the hatching period resulting in strong differences in individual "growth histories" at an intraspecific level (the "Forsythe effect"; Pecl *et al.*, 2004). In addition, great variability in size at a given age (under controlled temperature and food conditions) has been associated with initial size (Forsythe, 1993, 2004; Leporati *et al.*, 2007), which in turn is highly variable both intra- and interspecifically. High coefficients of variation (*CV*s) in initial weight (IW) have been observed in some octopod species (23% in *Octopus ocellatus*, Segawa and Namoto, 2002; 25% in *Octopus digueti*, DeRusha *et al.*, 1987; and 27% in *Octopus bimaculoides*, Forsythe and Hanlon, 1988).

It is not known whether the growth rate (GR) depends on initial size in cephalopods, but in fish, small differences in size during early life are amplified and accumulated throughout the life cycle (Vigliola and Meekan, 2002). In the first attempts to explore this issue in cephalopods, Pecl et al. (2004) simulated the growth of paralarval Sepioteuthis australis, under the assumption that GR remains constant during a month and rises exactly 1% of body weight per day on the first day of each month. Those authors stressed the importance of empirically validating this assumption and recommended segregating individuals from hatching. Following this advice, Leporati et al. (2007) found a direct relationship between IW and final weight (FW) in juvenile siblings of Octopus pallidus, with larger animals having faster growth than smaller ones. However, those authors did not compare GR as a function of initial size, so the assumption was not corroborated. With this in mind, inter-individual variation in initial size clearly has to be considered in experimental designs and data analyses aimed at understanding the increase in growth heterogeneity through time, as suggested for growth analyses in fish (Gardeur et al., 2001). Analyses of individual growth have commonly involved fitting regression models of weight against time. However, such an approach involves difficulties because the weight vs. time relationship is rarely linear and, when it is, it is only for very short and specific periods. Moreover, repeated measurement of the same individuals violates an indispensible requirement of regression models, namely that each datapoint be independent from others (Zar, 1999; Zuur et al., 2007).

Another methodological approach is fitting a regression model to the weight of each individual at a known fixed time (t_2) against its weight at an earlier point in time (t_1). This method ensures linearity of the $X-Y$ function and independence of datapoints (as long as they are individually labelled). The resulting linear equation describes a type of relative growth, and its slope represents the proportionality of the difference between two individuals at t_2 relative to the difference between them at t_1. In turn, the line's intercept represents the FW reached by the smallest individual in the dataset. In this context, comparing the slopes of different lines gives information on how much inter-individual weight differences change over experimental time. Concomitantly, comparing different line intercepts informs on individual GRs: lines with different intercepts indicate different GRs, because two animals with the same IW reach different FWs within the same period. Although this approach at the study of growth allows indirect corroboration of whether individuals in different size categories (i.e. different lines) within a population have different GRs, it does not permit estimation of those parameters in the equation that describes individual growth over time.

Generalized linear mixed models (GLMMs) are a tool that can complement growth analyses because they allow modelling of the large variability in individual size that can be observed in a population through time. A GLMM can be applied to non-normal data in which random effects are present (Bolker et al., 2008; Zuur et al., 2009). By incorporating components that modify the structure of variance, mixed models yield more-reliable estimators of model coefficients.

Octopus maya is endemic to the Yucatan Peninsula (Solis, 1967), and its culture has received considerable attention (Van Heukelem, 1977; Hanlon and Forsythe, 1985; Domíngues et al., 2007; Rosas et al., 2007). This species provides an interesting biological model to test hypotheses on HG among siblings. Therefore,

we aimed to (i) establish the relationship between hatching date and hatching weight, (ii) evaluate the assumption of Pecl et al. (2004) that GR is the same for all individuals by testing the hypothesis that GRs are independent from IW under controlled temperature and feeding conditions, and (iii) model the exponential growth phase during the early juvenile stage to understand whether variability in IW is amplified through time.

Material and methods

Juvenile O. maya were obtained from the Laboratorio Experimental de Producción de Pulpo of the National Autonomous University of Mexico, at Sisal (Yucatan, Mexico). All were the offspring of a single female captured off the coast of Sisal, induced to spawn by controlling feeding, photoperiod, and temperature. The eggs were held at 28°C ($\pm 1^\circ$C) in an artificial incubator (without maternal care) until hatching.

In all, 197 juveniles hatched over the course of 8 d; their weight was recorded 24 h after hatching (W_1; ± 0.01 g). Octopuses were housed individually in 300 ml containers connected to a recirculation system in which the water was treated with a UV filter, an ozonifier, and a skimmer. Temperature was kept at $27 \pm 1^\circ$C with a heater/cooler. Octopuses were fed live adult brine shrimp (Artemia salina) and pieces of blue crab (Callinectes sapidus) meat ad libitum.

During the 10-d immediately after hatching, O. maya physiology, morphology, and feeding behaviour modifies strongly, their habits changing markedly from the post-hatching to the juvenile phase (Moguel et al., 2010). Because the variability among individuals is markedly greater than the difference in the weight of one individual in such a short time, this period has been recognized previously as one of no net growth (Vidal et al., 2002; Moguel et al., 2010). Therefore, the weight of each individual was recorded 15 d after hatching ($W_{15} \pm 0.01$ g), and individuals were classified as small (S; $W_{15} \leq 0.10$ g; $n = 30$), medium (M; $0.11 \geq W_{15} \leq 0.12$ g; $n = 45$), and large (L; $W_{15} \geq 0.13$ g; $n = 30$). Our aim was to have similar numbers of animals in each category and separations between categories, allowing clear size-based discrimination. Octopuses were weighed again at ages 45, 75, and 105 d (W_{45}, W_{75}, and W_{105}, respectively). Deaths were checked for and recorded during feeding periods. Octopuses between ages 15 and 105 d were fed pieces of blue crab (C. sapidus) meat twice daily. Food leftovers and faeces were siphoned out once daily.

To determine whether W_1 varies depending on hatching date, a one-way ANOVA was carried out after verifying homoscedasticity and normality assumptions through an analysis of residuals.

To establish whether individuals in our three W_{15}-based size categories showed different GRs during their first days of life, a model for a linear relationship between W_{75} and W_{15} was adjusted for each individual, with initial size category (i.e. S, M, or L) as the nominal factor. The slopes and intercepts (ANCOVAR) of individual linear equations were compared between initial size categories. Similar line intercepts would indicate that small, medium-sized, and large O. maya juveniles grow at the same rate. To obtain a curve of weight gain as a function of time, a model was adjusted to the exponential relationship between the W_1, W_{15}, W_{45}, W_{75}, and W_{105} weights of all individuals and their corresponding ages. Before the previous analyses, graphic representations of the data were explored to (i) identify extreme points (point graphs); (ii) assess normality (histograms and percentile graphs); (iii) verify linear relationships ($X-Y$ graphs); and (iv) identify co-linearity between explanatory variables ($X-Y$ graphs;

Zuur *et al.*, 2007). The regressions were fitted with a generalized least-square procedure through restricted maximum likelihood and incorporated correlation and variance structures, using GLMM to ensure that homoscedasticity and independence requisites were met. Models featuring optimal correlation and variance structures were selected by considering values of the Akaike information criterion (AIC) and hypothesis tests based on *F* and likelihood ratio (*L*-ratio) values. Once the significance of regression parameters were established through *F*, *L*-ratio, and *t*-tests, models were validated by visual inspection of residuals (Montgomery and Peck, 1992; Draper and Smith, 1998). We used the parameter δ as an estimator of the tendency of weight variances to increase with age.

Results

The lowest average W_1 was on hatching day 5 (0.103 g, $n = 6$) and the largest on hatching day 6 (0.121 g, $n = 7$; Figure 1). Because most octopuses hatched on days 1 (26.90%), 2 (19.80%), 3 (9.64%), 4 (18.27%), and 8 (15.23%), data from those hatching dates only were used in our ANOVA. The analysis revealed no significant differences in W_1 between these hatching peaks ($F = 1.93$; $p = 0.11$).

Visual inspection of the survival curve (Figure 2) revealed that large individuals suffered greater mortality (>40%) after 20 d during a single peak, after which survival stabilized (64.52%). Octopuses of small and medium size had a similar pattern, with two mortality peaks at 7–32 and 88–95 d, respectively, but just half the animals in both size classes survived to the end of the experiment.

Our ANCOVAR of W_{75} vs. W_{15} regressions and size categories failed to show significant interaction between W_{15} and size category (*L*-ratio = 2.35; $p = 0.36$), indicating that slopes were similar among the three size categories (Figure 3). In addition, our ANCOVAR showed that W_{75} did not depend on size category (*L*-ratio = 0.30, $p = 0.86$) and depended solely on W_{15} ($F = 22.96$; $p < 0.001$). The results indicate that there are no significant differences between the intercepts of the three size categories (intercepts are the same between groups and equal to 0; $t = 1.7$, $p = 0.09$) and show that juvenile *O. maya* classified as small, medium, or large grow at the same rate during their first 75 d. Hence, a single regression model was fitted to all data, regardless of size category. The slope of that model was 5.52 ± 1.14, representing the magnitude of the increase in weight difference between any given pair of siblings between ages 15 and 75 d.

To fulfil the homoscedasticity requirement, we initially fitted our model using different variance structures. We obtained the minimum AIC value using a variance structure of the type $\varepsilon \sim N(0, [\sigma^2 P_{15}])$ (AIC = 113.80). Using that structure improved the model and resulted in a lack of pattern among residuals, so complying with the requirements of regression analysis.

We log-transformed our weight data before modelling the exponential relationship between weight and age. Regression parameters differed significantly from 0 (Table 1). Interdependence of data over time (because we weighed animals repeatedly) resulted in a cyclic residual pattern, so we incorporated an autocorrelation structure (spherical spatial structure) in the random-effects term of the model (ε_i). Following Pinheiro and Bates (2000), we kept this structure in the model, because (i) AIC values indicated that using it improved the model (AIC = 319.45), and (ii) it made the cyclic residual pattern disappear. The estimated rank parameter associated with this correlation structure was 74.3

(Table 1), representing the interval (in days) necessary to avoid correlation between two consecutive weight measurements of the same animal.

Heterogeneity of variances was identified based on an increase in weight variation with age and accounted for by including a variance structure of the type ($\varepsilon_i \sim N(0, \sigma^2 [\text{age}_i]^{2\delta})$) in the model. Including this term significantly improved the model (*L*-ratio = 70.00; $p < 0.001$; AIC = 251.4). Finally, visual inspection of residuals revealed uniform dispersion and no evident patterns, and δ (a constant representing the increase in residual weight variation with age) was estimated to be 0.20 (Table 1).

Discussion

The GLMM presented includes the use of a variance and a correlation structure that enhanced model fit (better AIC values), and successfully explained octopus weight as a function of age. Because the date of hatching was registered for each individual, "age" is fixed in the model (i.e. it has no associated error), and there was no need to back-calculate using hard structures such as otoliths to obtain precise measures of this explanatory variable (Chambers and Miles, 1995; Vigliola and Meekan, 2009). In their paper on fish growth calculated from otolith readings, Vigliola and Meekan (2009) discuss various models and conclude that just one of them (the AE model) generated unbiased estimates of fish length and growth, but was also the least precise, giving low values of r^2 between the predicted and the observed length. They argued that this was possibly a consequence of the increased dispersion of size estimates produced by the AE model, because it is vulnerable to growth effects and highly sensitive to the accuracy and precision of the regression calculated between fish length, age, and otolith radius. Given the correlation and variance structures included in the current model, and the parameters associated with them (δ, range), it is our opinion that the procedures followed to adjust the GLMM detailed here allow a high level of precision in predicting octopus weight from known age, so make the estimates of GR more reliable than previous models.

Great variability in size at hatching has been reported for several cephalopod species under controlled environmental conditions (Van Heukelem, 1976; DeRusha *et al.*, 1987; Forsythe and Hanlon, 1988; Forsythe, 1993; Villanueva, 1995; Domíngues *et al.*, 2002; Segawa and Namoto, 2002; Ortiz *et al.*, 2006; Leporati *et al.*, 2007). In *O. maya*, hatching occurs over 5–8 d, long enough to consider hatching time a potential source of variation in size. This study revealed no significant differences in W_1 as a result of hatching date, but this does not rule out a potential effect of the latter variable on posterior growth.

An influence of hatching date on initial size variation has rarely been reported for cephalopods (Choe, 1966; Ikeda *et al.*, 1999; Steer *et al.*, 2003). Although Minton (2004) reported similar results to the present ones for *Sepia pharaonis*, Ikeda *et al.* (1999) showed that after incubating eggs of a single *Sepioteuthis lessoniana* female at 25°C, the mantle length of the newly hatched paralarvae was directly related to hatching date. Those authors surmised egg position within the clutch to be the mechanism underlying such a relationship. Moreover, the time it takes a female to spawn an entire brood and attach the eggs to the roof of the nest cavity may explain low hatching synchrony among members of that brood (Boletzky, 1987, 1997; Oosthuizen *et al.*, 2002).

The slopes of the linear models of the relationship between IW (W_{15}) and FW (W_{75}) did not differ between size groups. Under the assumption that weight gain through time indicates a capacity to
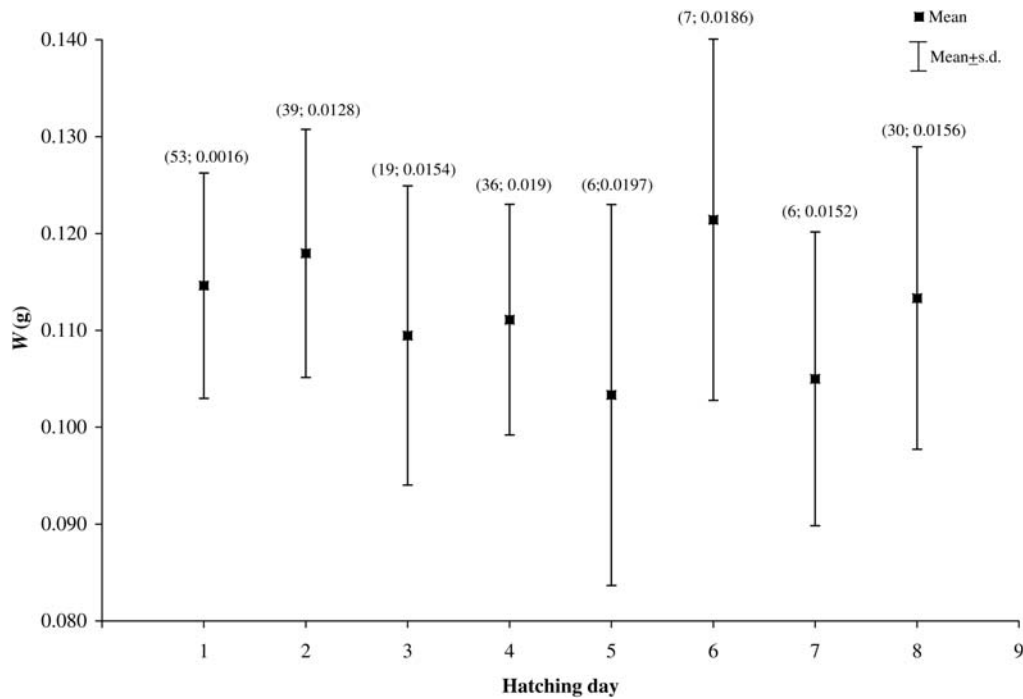
Figure 1. Mean weight ($\pm$ s.d.) of *O. maya* juveniles 24 h after hatching (W_1) throughout the hatching period, under controlled environmental conditions. The first numbers in parentheses are the number of individuals hatched per day and the second numbers the standard deviations.
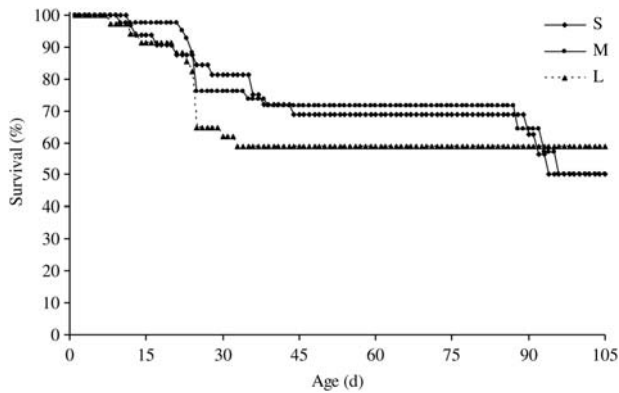

Figure 2. Survival of individually housed small, medium, and large *O. maya* juveniles (size categories defined based on IWs).
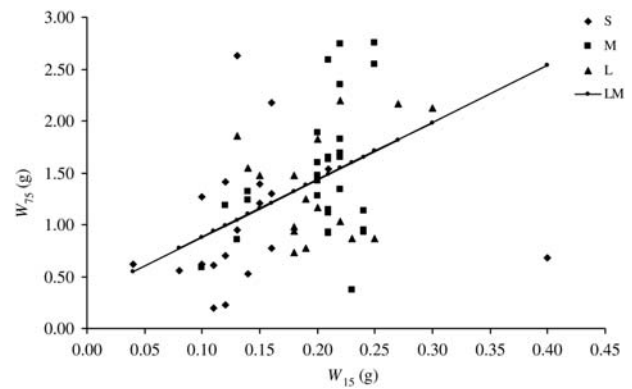

Figure 3. Linear relationship of weights-at-age 15 d (W_{15}) and 75 d (W_{75}) of small (S; $W_{15} \leq 0.10$ g; $n = 30$), medium (M; 0.11 g $\geq$ $W_{15} \leq 0.12$ g; $n = 45$), and large (L; $W_{15} \geq 0.13$ g; $n = 30$) individually housed juvenile *O. maya*. The line is defined by a linear model ($W_{75} = 5.523W_{15} + 0.327$) fitted to all datapoints.

transform biomass and that this capacity is an expression of GR, we conclude that *O. maya* juveniles grow at the same rate, although their FW will always depend on their IW.

Most models of octopus exponential growth in the literature use determination coefficients (R^2) as indirect indicators of the extent of variability in the relationship between weight and age (Table 2) and take high values of R^2 to reflect a goodness-of-fit. However, R^2 is only an indicator of the amount of variation explained by the model, not of how well it fits the data. Additionally, most studies of cultured animals use mean values as a way to identify trends in growth, often ignoring the fact that growth in cephalopods is highly variable. The latter two considerations argue against the use of R^2 as a reference to compare different growth models. The present study offers growth estimates that may be more reliable because they take into account octopus size

variability at a given age. In addition, they provide indications of the way and the magnitude ($\delta = 0.20$) in which variability in weight increases with age, allowing for future comparisons with octopuses kept under different laboratory conditions.

The present linear model of the relationship between IW and weight at different times allowed the behaviour of weight differences in a given period to be analysed. The model was applied to all animals, on the assumption that individual FW was conditioned by IW. Although growth in each individual is influenced by diverse factors (such as temperature and feeding; André *et al.*, 2008), small differences in IW were amplified through time in the same way for all individuals. The latter was confirmed by the fact that variance structures and the slopes of the linear

relationships between initial and FWs were similar among size categories (Figure 3). Quantifying the pattern of variation in the weight of individuals from the same brood is important in predicting their future weight; such information cannot be obtained from most of the studies in which octopus growth has been modelled. Applying the parameter δ in the growth model allowed prediction of how weight would change through time, with a high probability of obtaining mean values that truly represent the population.

The increase in size variation as individuals' age has been referred to as growth depensation (Ricker, 1958; Pfister and Stevens, 2002) and has been well-documented for fish (Smith and Fuiman, 2003) and other taxa (Pfister and Stevens, 2002). In contrast to earlier suggestions (Leporati et al., 2007), however, the results here show that growth depensation is not explained by variability in the IW, but by other biological variables (not considered in the model) which amplify the differences in octopus weight as the animals grow. Although previous workers have reported that some variation could be due to external factors (e.g. temperature, Forsythe, 2004; diet, André et al., 2008), the results here exemplify the reliability of the procedure in estimating the magnitude of residual variation in weight as it increases with octopus age (δ), facilitating comparative studies of average growth and its variability under contrasting external conditions. Other effects, such as those of multiple paternity (Shaw and Boyle, 1997; Shaw and Sauer, 2004; Naud et al., 2005; Voight and Feldheim, 2009), inter-individual variation in feeding and conversion rates (Semmens et al., 2004; André et al., 2008), and the precocity of cephalopod sexual maturation

(Avila-Poveda et al., 2009) should be studied to understand the adaptations of O. maya and other cephalopods to collect the benefits of variable growth.

The model here of exponential growth incorporates weight variability as age increases (Figure 4), which makes it a robust and statistically reliable approach. Previous models for O. maya and other cephalopod species have failed to consider the variability in growth, leading to less reliability and predictive capacity. The data in Table 2 reveal marked differences in the estimated growth parameters for several octopus species (including O. maya). Van Heukelem's (1976) faster GRs were obtained from group-housed animals kept at very low densities, at 25°C, and fed live prey, whereas here the animals were individually housed, held at 27°C, and fed pieces of fresh blue crab meat. This, together with the results presented, suggests that particular culture conditions, as well as different technical approaches during the calculation of exponential equations, might explain some of the reported differences in GRs among and within species (Table 2).

Although more studies are needed to assess whether differences in temperature, food type (live prey vs. fresh frozen meat), and housing space influence growth in O. maya, earlier research has shown that activity patterns, temperature, and sexual maturity influence food conversion, contributing to inter-individual differences in GR even when animals are fed the same diet (Mangold and Boletzky, 1973; Leporati et al., 2007; André et al., 2008). Wells and Clark (1996) showed that high levels of activity affect the GR because more-mobile animals allocate less energy to biomass production. These observations contradict the fast rates of growth reported by Van Heukelem (1976) and others, where group-housed animals have grown faster than individually housed ones. Although there are no studies on how higher activity levels may enhance growth in octopuses, work on halibut (Paralichthys californicus) has shown that the efficiency of muscle mass accumulation increases when animals are kept swimming against moderate water flows (Merino et al., 2007).

Temperature strongly influences growth in cephalopods (Forsythe and Hanlon, 1988; Wood and O'Dor, 2000; Aguado-Giménez and García-García, 2002). GR increases with temperature (Forsythe and Van Heukelem, 1987; Hatfield et al., 2001), and temperature has a stronger effect on the exponential growth phase than on the potential growth phase. Contradicting this trend, Van Heukelem (1976) reported that GR in O. maya

Table 1. Parameters of the exponential growth model of individually housed juvenile O. maya kept at 27 ± 1°C.

Parameter	Value	Significance
α	−2.182 + 0.22[a]	$t = -100.92$[b]
β	0.030 + 0.001	$t = 48.60$[b]
σ	0.209	
δ	0.204	L-ratio = 70.00[b]
Rank	74.3	L-ratio = 114.20[b]
AIC	251.4	

α, intercept; β, slope; σ, residual standard error; δ, variance structure parameter; rank, correlation structure parameter.
[a]Transformed values.
[b]$p < 0.001$.

Table 2. Post-hatching exponential GRs (EGR = b from $Y = e^{bX}$) and their duration in Octopus spp. kept at different temperatures [$T(°C)$] under laboratory conditions.

Species	IW (g)	EGR	R^2	Time (d)	T (°C)	Source
O. digueti[a]	0.040	0.065	0.999	70	25	DeRusha et al. (1987)
O. vulgaris[a] (P)	0.0014	0.081	0.985	60	21.2	Villanueva (1995)
O. joubrini	0.045	0.066	0.992	28	25	Forsythe and Hanlon (1981)
O. briareus	0.065	0.048	0.970	140	25	Hanlon (1983)
O. ocellatus[b]	0.189	0.046	0.916	80	20	Segawa and Namoto (2002)
O. ocellatus[b]	0.179	0.059	0.944	60	25	Segawa and Namoto (2002)
O. pallidus[b]	0.245	0.014	0.784	114	14 → 18	Leporati et al. (2007)
O. pallidus[b]	0.276	0.018	0.896	114	18 → 14	Leporati et al. (2007)
O. maya[a]	0.100	0.062	0.999	105	25	Van Heukelem (1976)
O. maya[a]	0.100	0.040	0.810	129	28	C. Rosas (unpublished data)
O. maya[b]	0.110	0.030	0.889	105	27	This study

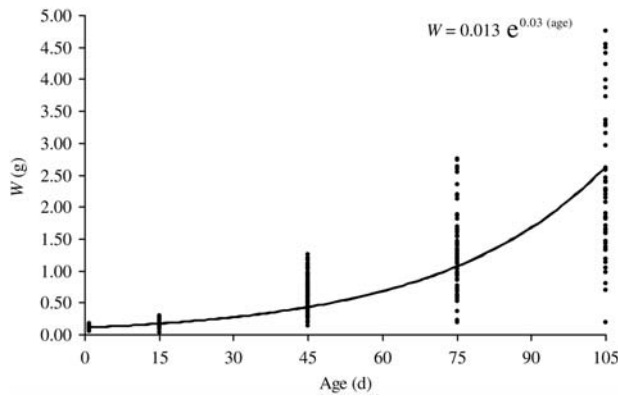P, Paralarvae; R^2, Coefficient of determination.
[a]Group-housed.
[b]Individually housed.

Figure 4. Exponential relationship of weight and age (to age 105 d) in individually housed juvenile *O. maya* kept at 27 ± 1°C.

was faster in animals kept at 20 and 23°C than in the *O. maya* used here, which were individually housed and kept at 27°C. Although optimal temperature intervals for *O. maya* are yet to be established, there is evidence that at temperatures outside the maximum biokinetic rank, energy loss through basal metabolism can compromise energy availability for growth (Díaz *et al.*, 2007). Water temperature in the natural distribution of *O. maya* fluctuates between 22 and 26°C over a year, so it is possible that keeping octopuses at temperatures outside the natural fluctuation range increases their basal metabolism, so diminishing the energy available for growth. In a recent study, Farias *et al.* (2009) observed that biomass production of the subpolar octopus *Enteroctopus megalocyathus* held at 11°C was greater than that of *O. maya* kept at 27°C. Those authors explained this pattern as the consequence of the tropical species having a higher metabolism than the subpolar species.

Variability in cephalopod growth and in particular of *O. maya* is not an error source in measures of growth, but a plastic adaptation that is as yet not well understood (Semmens *et al.*, 2004). Multidimensional interactions determining such variability need to be studied from different angles to understand better the dynamics of populations. This information will be valuable for conservation, fishery, and culture purposes (Domíngues *et al.*, 2007; Rosas *et al.*, 2007, 2008). For example, future studies on the combined effect of biotic and abiotic variables need to consider variability in size-at-age, and the incorporation of statistical tools (such as those used in mixed modelling) may assure more precise representation of octopus population dynamics in the context of environmental change. Moreover, accurate projections of biomass growth under different controlled conditions can now be estimated and used under commercial schemes.

Acknowledgements

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