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On the growth patterns of the cephalopod *Sepia officinalis* under long-term culture conditions

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1 Introduction

Cephalopods are considered to attain fast growth, generally showing two phases, the first one being exponential (Forsythe, 1993; Semmens et al., 2004; Jolly et al., 2022). Researchers dealing with growth patterns of cephalopods usually present two types of plots: i) body weight (BW) vs. time plot and, ii) the specific growth rate (SGR) vs. time plot (Iglesias et al., 2014). The conclusions about the growth pattern derived from both types of plots should be the same. For example, the exponential model implies a curvilinear/concave increasing line in the BW vs. time plot. However, other models of growth, e.g. the power model (Cho, 1992; Iwama and Tautz, 1981), also generate a curvilinear/concave pattern in the plot BW vs. time, thus it is convenient to check the SGR vs. time plot since, by definition, the exponential model implies the constancy of SGR over time (Forsythe, 1993), this constancy being a diagnostic feature for that type of growth.

The European cuttlefish *Sepia officinalis* is a remarkable case among cephalopods. It is a model organism that can be successfully acclimated and reared under culture conditions (Sykes et al., 2006, 2014, Capaz et al., 2020). For this reason, a number of authors have explored the growth of the species for a long period of time under captivity, even from hatching to the reproductive age (Domingues et al., 2001a, 2002; Sykes et al., 2006). Researchers studying *S. officinalis* growth usually report temporal changes in BW or SGR (Domingues et al., 2001a, 2002; Correia et al., 2005; Sykes et al., 2006; Capaz et al., 2020). As previously explained, the only inspection of the BW vs. time plot can be misleading when assessing growth patterns, whereas the SGR vs. time plot adds important details. For all these reasons, the main goals of this study are: i) contributing to the interpretation of growth patterns in cultured *Sepia officinalis*, ii) explore the effects of culture variables on cuttlefish growth through multivariant statistics, and iii) proposing recommendations to recognize growth patterns during a given growth trial.

2 Methods

To determine growth patterns in *Sepia officinalis* under captivity, we selected articles reporting data on body weight and/or specific growth rate for more than 6 samplings during the whole life cycle, or for a long time of culture (usually several months) (Table 1). For each article, SGR values in the plot SGR vs. time, were extracted by measuring ordinate height (mm) of each point with the pdf tool "Measurement", and comparing ordinate values to the length of the Y axis. In the study by Domingues et al. (2001a), the authors provided a table with SGR values over time; thus, those values were taken for the statistical analysis. Generally, sampling times were easily recognized from the X axis since they were conducted on a periodical basis but, when necessary, they were calculated in a way similar to that applied to SGR data. SGR were calculated as $\ln(BW_{final}/BW_{initial})$ (time increment)$^{-1}$.

After determining SGR values and sampling times, the plot SGR vs. time was inspected to disclose temporal stretches with conspicuous SGR trends. At last, trends of SGR for each of those temporal stretches were evaluated using the Spearman coefficient of correlation (Pearson coefficient produced similar results). The exponential model was discarded whenever the Spearman coefficient was significantly positive or negative. On the contrary, when the values of SGR seem to be approximately constant, or fluctuate, and the Spearman coefficient was not significant, then a stretch of exponential growth was assumed. Since temperature is a factor clearly affecting growth in ectotherms, data in Table 1 was revised for a potential correlation between temperature and growth rates. After examining data, the 18 culture conditions were cross-tabulated according to the following variables (Supplementary Material): i) "presence of a period with constant SGR", ii) "presence of a long period with temperature below 20°C". Subsequently, the association between both variables was tested with a χ^2 test (with Yates correction), setting the significance level at 0.05. In addition, we performed a multidimensional scaling analysis (MDS, Euclidean distance, proxscal method) based on 6 variables: temperature pattern, presence of a long period with temperatures below 20 °C, initial cuttlefish density, initial cuttlefish weight, experiment duration, and presence of a period of exponential growth (= constant SGR). Since several variables were of categorical nature, all of them were similarly converted into numerical codes with an ordinal meaning (Supplementary Material). The case corresponding to Domingues et al. (2001b) were discarded from the MDS analysis due to differences in the experimental design. MDS analysis calculates several coordinates (MDS dimensions related to the original variables) for each case. Typically, the first two dimensions are used to represent studied cases in a bidimensional plot where distances among points can be interpreted as similarities.

3 Results

Seventeen different long-term growth experiments, with culture times between 90 and 220 days, and initial body weights between 0.17 and 33 g were found (Domingues et al., 2001a, 2002, 2003; Correia et al., 2005; Sykes et al., 2006; Capaz et al., 2020). An additional work (Domingues et al., 2001b) was included despite reporting culture times of 40 days, and a different design for growth assays, because animals of a wide weight range (0.05 – 65 g) were reared in isolation, this experiment being another way of exploring the shape of growth trajectories throughout the life cycle.

After checking SGR vs. time plots, four growth patterns were initially proposed (Table 1), and one case was classified as an irregular pattern. Pattern A (6 cases) consisted in a continuous decrease of SGR that, sometimes, can be preceded by a very short period of SGR increase (Domingues et al., 2001a, b; Sykes et al., 2006). Pattern B (6 cases) comprised a phase of decreasing SGR (also preceded or not by a short period of increasing SGR) plus a phase of constant or fluctuating SGR (Domingues et al., 2001a, 2002; Sykes et al., 2006; Capaz et al., 2020). Pattern C (3 cases) consisted in the constancy or fluctuation of the SGR over all the experimental time. Pattern D (2 cases) can be described as an early period of constant SGR plus a late period of decreasing SGR (Correia et al., 2005).

In 7 out of 18 culture conditions, there was no clear evidence of any period with constant/fluctuating SGR: the 3 last experiments in Domingues et al. (2001a), the experiment by Domingues et al. (2001b), and cultures F3, F5 and F6 in Sykes et al. (2006). When the 18 culture conditions were considered, the χ^2 statistic (with Yates correction) showed that the presence of an exponential period was associated with the existence of a long period of temperatures below 20 °C ($\chi2 = 6.45$, df = 1, $p = 0.011$). A correlation analysis showed that MDS dimension 1 was mainly and inversely related to long periods below 20 °C, and the presence of a period of exponential growth, whereas dimension 2 was mainly and directly related to temperature pattern (Supplementary Material). Consequently, MDS analysis confirmed the importance of low temperatures over other variables, such as temperature trend or cuttlefish initial density. In addition, the MDS plot drew a distinction between cases previously included in pattern A, and cases included in pattern B. It also showed a separate group for cases with pattern D but in close proximity to pattern B, whereas cases with pattern C did not stand in close proximity. Thus, MDS analysis supports at least three of the patterns previously defined by checking SGR vs. time plots, more clearly for patterns A and B.

4 Discussion

The most interesting finding in the present work is probably the infrequency, in *Sepia officinalis*, of the commonly accepted growth pattern for cephalopods, which comprises an early exponential phase and a late non-exponential period (Jolly et al., 2022; Forsythe, 1993). Moreover, one frequent pattern in *S. officinalis* consists just in nearly the opposite sequence, i.e. an early SGR-decreasing phase, followed by a period of nearly constant or fluctuating and low SGR. This last period can be defined as exponential or very close to the exponential model. In any case, growth patterns here proposed should not be considered as categories with neat boundaries. MDS analysis (Supplementary Material) showed a continuous variation among cases in terms of MDS dimensions and culture variables, that mainly supports patterns A and B. However, growth categories or patterns can be useful simplifications to classified variations among

TABLE 1 Patterns of growth of *Sepia officinalis* cultured during long periods.

Article	Temp. pattern	Temp.	Initial weight	Duration	SGR pattern	Pattern type
Domingues et al., 2001a	Daily variation	25-30	0.23	120	↑↓=	B
	Daily variation	25-30	0.22	120	↑↓↓	A
	Daily variation	25-30	0.18	90	↑↓	A
	Daily variation	25-30	0.17	90	↓	A
Domingues et al., 2001b	Daily variation	25-30	0.05 - 65	40	↓	A
Domingues et al., 2002	~ Constant	~ 15	0.074	220	↓=	B
Domingues et al., 2003	~ Constant	~ 18	17	110	=	C
	~ Constant	~ 18	19	140	=	C
Correia et al., 2005	Increasing	18-25	1.4	99	=↓	D
	Increasing	18-25	1.4	99	=↓	D
Sykes et al., 2006	~ Constant	~ 17	Newly hatched	220	↑↓=	B
	~ Constant	~ 23	Newly hatched	90	↑↓	A
	Increasing	12-20	Newly hatched	210	==	C
	Decreasing	25-17	Newly hatched	115	↑↓	A
	Incr./constant	21-25	Newly hatched	90		Irregular
Capaz et al., 2020	Seasonal	22-12-27	32.7	150	↓=	B
	Seasonal	22-12-27	32.7	165	↓=	B
	Seasonal	22-12-27	32.7	165	↓=	B

SGR patterns are indicated by the sequence of temporal stretches with increasing (↑), decreasing (↓), and constant (=) trends.
Temp., temperature in °C. Initial weight of animals in g. Duration of the experiment in days.

growth trajectories, and to understand the most important variables shaping those trajectories.

The most probable growth rate trend during the first months of culture consists in a decreasing pattern (11 out of 18 cases), although it can be preceded by short increase during the first weeks. This transient increase could be explained by the maturation of the digestive tract (Boucaud-Camou et al., 1985), because it appears when the culture was initiated with hatchlings. The subsequent and consistent decreasing trend can stop to give rise to a period of SGR without trend in approx. 50% of the cases. The causes for this change need further research but it was accompanied by a stabilization of the feeding rate in Capaz et al. (2020). Finding indicators pointing to the next transition from SGR decrease to SGR stability will help the researcher or producer to plan feeding rates. In this regard, temperatures below 20 °C plus a mean SGR below 0.02 day^{-1} indicate the proximity of the stabilization phase. Interestingly, patterns similar to patterns A and B herein described have been reported for *Sepia pharaonis*, *Sepiella inermis* (Nabhitabhata, 2014a, 2014b) and the Sepiolid *Euprymna hyllebergi* (Nabhitabhata and Nishiguchi, 2014).

Regarding the associations of growth with culture variables, temperature seems to be an important one according to the χ^2 test, and the association between MDS dimension 1 and temperatures below 20 °C. Pattern A (decreasing SGR) occurs under conditions of constant or fluctuating temperatures, but preferably when temperature is high, above 20 °C (Domingues et al., 2001a, b; culture F3 in Sykes et al., 2006), and cultures last up to 120 days. Pattern B (decreasing and stabilization) tends to appear at temperatures below 20 °C (Domingues et al., 2002; F2 in Sykes et al., 2006) or when the temperature regime includes a long period below 20 °C (Capaz et al., 2020), those cultures usually lasting more than 120 days. An MDS analysis supports that a long period of low temperatures shape more clearly the growth model than other variables, such as temperature trend or animal density.

Long-term cultures are particularly convenient to study animal growth because many sampling points are reported. Nevertheless, there are short-term cultures pointing to the inadequacy of the exponential model in juvenile *S. officinalis*. For example, in the work by Forsythe et al. (2002), juveniles of 1.5 g were reared for 5 weeks according to two-factors: temperature (17 vs. 25 °C) and animal density (100 and 400 m^{-2}). Under those conditions, the exponential model fitted weights of cuttlefish grown at 17 °C very well but, the exponential line was clearly overestimating body weights for the last sampling at 25 °C. Although the authors did not show the SGR vs. time plot, they reported a decrease of the feeding rate over time at 25 °C, whereas the conversion rate remained nearly constant (low density) or peaked at the first week and then underwent a steep drop (high density). Therefore, the combination of these two zootechnical variables made it clear that the SGR was not constant over time at 25 °C.

We propose several recommendations when assessing the growth of a group of captive *S. officinalis*:

i. whenever a series of weight samplings is available, plot not only the weight vs. time graph, but also the SGR vs. time graph,

ii. when animals are reared at temperatures below 20 °C, consider that SGR can stabilize when it is below 0.02 day^{-1},

iii. whenever possible, plot the temporal patterns of ingestion rate and food conversion rate, and compare them to the SGR vs. time plot. By taking into account several zootechnical variables, it will be improbable to assign a mistaken growth model.

Author contributions

LM: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft. AH: Writing – review & editing. ML: Data curation, Visualization, Writing – review & editing. EA: Conceptualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1475556/full#supplementary-material

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