

## ENERGY BALANCE GROWTH MODELS: APPLICATIONS TO CEPHALOPODS

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**ABSTRACT:** The term 'growth model' in fisheries literature commonly refers to equations predicting size-at-age. Applying statistical goodness-of-fit criteria to such equations measures their capacity to describe populations but implies an unstated corollary that some individuals grow 'wrong'. This 'wrongness' may result from techniques misrepresenting age, but, as cephalopods often exhibit ten-fold variation in growth under controlled conditions and have multiple sub-annual cohorts in nature, it may simply be wrong to try to represent a 'population' with a single equation. This article provides a simple spreadsheet model, adjustable daily, that allows tests of a wide variety of environmental and physiological variables' effects on an individual animal's growth parameters. This allows independent elimination of implausible individual errors from statistical analyses and has important consequences for growth models used in an ecosystem context. Growth efficiency during low food intake can be ten-fold lower than at high intakes, so the cumulative error in estimating a population's energetic impact on an ecosystem may be wrong by a hundred-fold. The standard assumptions of this spreadsheet model can be run with no input except size and age, but all assumptions, except that energy can be created or destroyed, can be adjusted, if real measurements such as temperature or feeding rate are available.

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### INTRODUCTION

The most common approach to modeling growth is to acquire data on size-at-age by rearing animals in the laboratory and then to compare the goodness of fit for a variety of mathematical descriptions of the relationship between these data (Hanlon *et al.* 1989, Lee *et al.* 1994, Nabhitabhata 1997). For species where independent estimates of age are possible (*e.g.* squid statoliths) the best laboratory growth relationships (Forsythe *et al.* 2001) can be compared to size-at-age data for natural populations (Jackson and Moltschanivskyj 2002). For cephalopods, this approach has led to recognition of strong influences of temperature on laboratory growth rates and of seasonal cohorts in nature. Projecting temperature sensitive laboratory growth equations onto natural temperature regimes led to recognition of the Forsythe effect, in which summer spawned animals outgrow those spawned earlier. Thus,

*Loligo pealei* hatched in July could weigh four-times more after 3 months than those hatched in May and reach 10 g weight at half the age (Forsythe 1993). Although field data for laboratory-validated species (Dawe and O'Dor 1998) supports these interpretations, such variation makes it difficult to demonstrate the reliability of independent aging techniques.

Because growth is the result of a series of energy transformations, knowledge of other energetic factors can be used to constrain growth models (O'Dor and Wells, 1987). We have developed an incremental spreadsheet modeling approach to growth energetics that provides a daily 'checksum' to validate various assumptions of models when applying them in the field. Checksums are used in communications to test that packets<sup>3</sup> of digital information are intact and have not lost any elements. The analogy to energy models is not perfect but very close. These incremental models are not generally

convenient for direct inclusion in larger ecological models, but they identify critical transitions in continuous equation models, allow for numerous growth stanzas and provide good graphical representations. This spreadsheet model has been tested on numerous datasets on a range of cephalopods.

**MATERIALS AND METHODS**

An energy balance model allows us to compare diverse types of data in one model. We start with a first generation model making 'standard' assumptions applied to a fitted growth curve for *Sepia apama*. If anything is impossible in the

model, first the assumptions and then the data will have to be examined. Improbable trends suggest where more data is needed.

The model, on an Excel spreadsheet, is available online as an Accessory Publication? As indicated in Table 1 below, the model is driven by a size-at-age regression equation predicting body weights for each day in column 1.

- C1 - Days since hatching
- C2 - Size-at-age regression
- C3 - Daily growth, calculated by difference
- C4 - Assume one gram of tissue contains 1 kcal or 4.19 kJ of energy
- C5 - Routine oxygen consumption can be measured in animals of any size

**Table 1.** The beginning and end of a full life cycle energetic balance model for *Sepia apama* based on the information in the columns as indicated below.

day	bw (g)	growth (g/d)	growth (kJ/d)	oxygen (ml/h)	Mr (kJ/d)	Mr (g/d)	removal (g/d)	cum (g)	remi (g/d)	intake (g/d)	intake (kJ/d)	G+2Mr (kJ/d)	G+2Mr (g/d)	net eff G/(1-2Mr)
0	1.1													
1	1.12	0.016	0.067	0.5955	0.276	0.066	0.6624	0.66236	0.244	1.023	0.6189	0.148	0.14269	
2	1.13	0.016	0.068	0.602	0.279	0.067	0.6696	1.33196	0.247	1.034	0.6259	0.149	0.14321	
3	1.15	0.017	0.069	0.6086	0.282	0.067	0.6769	2.00888	0.25	1.045	0.633	0.151	0.14373	
4	1.17	0.017	0.07	0.6152	0.285	0.068	0.6843	2.6932	0.252	1.057	0.6402	0.153	0.14425	
5	1.18	0.017	0.071	0.622	0.288	0.069	0.6918	3.385	0.255	1.068	0.6474	0.155	0.14477	
6	1.2	0.017	0.072	0.6288	0.291	0.07	0.6994	4.08436	0.258	1.08	0.6548	0.156	0.1453	
7	1.22	0.018	0.073	0.6356	0.294	0.07	0.707	4.79137	0.261	1.092	0.6622	0.158	0.14583	
8	1.24	0.018	0.074	0.6426	0.298	0.071	0.7147	5.5061	0.264	1.104	0.6697	0.16	0.14636	
9	1.25	0.018	0.076	0.6496	0.301	0.072	0.7225	6.22865	0.267	1.116	0.6773	0.162	0.14689	
10	1.27	0.018	0.077	0.6567	0.304	0.073	0.7304	6.95909	0.269	1.128	0.685	0.163	0.14742	
11	1.29	0.019	0.078	0.6639	0.308	0.073	0.7384	7.69751	0.272	1.14	0.6927	0.165	0.14796	
12	1.31	0.019	0.079	0.6711	0.311	0.074	0.7465	8.44401	0.275	1.153	0.7006	0.167	0.14849	
13	1.33	0.019	0.08	0.6785	0.314	0.075	0.7547	9.19867	0.278	1.165	0.7085	0.169	0.14903	
14	1.35	0.019	0.081	0.6859	0.318	0.076	0.7629	9.96157	0.281	1.178	0.7166	0.171	0.14957	
539	2718	39.12	163.8	206.47	95.64	22.82	229.65	21180	84.71	354.7	355.05	84.74	1.00243	
540	2758	39.69	166.2	208.72	96.68	23.07	232.16	21412.1	85.63	358.5	359.53	85.81	1.00607	
541	2798	40.27	168.6	211.01	97.74	23.33	234.7	21646.8	86.57	362.4	364.07	86.89	1.00972	
542	2839	40.86	171.1	213.31	98.81	23.58	237.27	21884.1	87.52	366.4	368.67	87.99	1.01339	
543	2881	41.45	173.6	215.64	99.89	23.84	239.86	22124	88.47	370.4	373.33	89.1	1.01707	
544	2923	42.06	176.1	218	101	24.1	242.48	22366.4	89.44	374.5	378.05	90.23	1.02076	
545	2965	42.67	178.7	220.38	102.1	24.36	245.13	22611.6	90.42	378.6	382.82	91.37	1.02447	

*Energy balance growth models: applications to cephalopods*

Typically metabolic rate scales as  $bw^{0.75}$ , which can be substituted (Aitken and O'Dor, 2004).

$$O_2 \text{ at } 246g = 34.2ml \text{ h}^{-1}$$

$$246^{0.75} = 62.1; 34.2/62.1 = 0.55$$

$$O_2 = 0.55 * bw^{0.75}$$

A  $Q_{10}$  of 2.5 is also typical, so for data at 21°C the factor is:

$$1.096^{21} = 6.86; 0.55/6.86 = 0.080$$

$$O_2 = 0.08 * bw^{0.75} * 1.096^{21}$$

This allows comparisons of data for a variety of sizes and temperatures. The  $Q_{10}$  parameter can vary and temperature could be easily be placed in a separate column and allowed to vary daily. The allometry exponent, 0.75, could be varied in stanzas. C6 - One milliliter of oxygen generates about 20 Joules of metabolic energy

C8 – The amount fed corresponds to the amount removed from the ecosystem

Average at 229g = 36g; calculate scaling and  $Q_{10}$  as for  $O_2$

C9 – The cumulative removal is the sum of daily removals

C10 – Intake is less than amount fed, by wastage and assimilation efficiency

Wells *et al.* 1983 estimate these as 50% and 90%, respectively in octopus

C12 – Models often assume the extra activity metabolism in the field equals the routine metabolic rate, *i.e.* a 100% increase.

C14 – Net efficiency calculates the fraction of intake converted to growth after metabolism is accounted for.

Available data for cephalopods typically show high conversion efficiencies (30–60%),

## RESULTS

The challenge with sparse data on a species that has not been intensively studied is to link it all together with some basic models. A good place to

**Table 2.** The growth and energetic data available for the *Sepia apama* model. (Cronin and Seymour, 2000; K. Hall, R. Hanlon, pers. com.)

Source	Length (m)	Weight (kg)	Age (d)	Feed (kg/d)	Growth (%BW/d)	Routi (mlO <sub>2</sub> )
Hall	0.01	0.000346	1			
Cronin	0.012	0.0005	1			
Hall	0.03325	0.008431	90			
DalA	0.12	0.215	302	0.036	0.71	34.2
DalB	0.125	0.215	304	0.036	0.71	34.2
DalC	0.128	0.2	305	0.036	0.71	34.2
DalA	0.128	0.238	325	0.036	0.71	34.2
DalB	0.13	0.27	329	0.036	0.71	34.2
DalC	0.13	0.236	326	0.036	0.71	34.2
WH	0.087	0.102	270			
WH	0.117	0.23	373			
WH	0.125	0.381	411			
WH	0.11	0.229	414			
WH	0.12	0.276	421			
WH	0.12	0.379	425			
WH	0.12	0.379	426			
WH	0.155	0.525	435			
WH	0.15	0.414	442			
WH	0.115	0.268	435			
LMSC	0.245	2.05	515			

start is a length-weight relationship because lots of field data (especially from live tagged animals) only provides mantle lengths (Fig. 1). Clearly weight at length can be quite variable, but one usually gets a reasonably good predictor of an average animal over a wide range of sizes from a power regression (log weight vs. log length). More detailed models of changing growth allometries can be added if there is interest and data.

Size at age data is much harder to get and to interpret or model. The power curve seems to be the better fit statistically with simple Excel regressions, but it is really way off at very small and very large sizes – the fit and the  $R^2$  term depend largely on the distribution of data points and can be deceptive if the points are not uniformly distributed over the range (Fig. 2).

The log-log plot (Fig. 3) shows that the exponential fit is much more plausible over the whole range of sizes.

An exponential fit to the data for relatively young animals studied at Dalhousie predicts that the largest animal at Lincoln Marine Science Centre (LMSC), Port Lincoln, Australia was 420 days old. Adding the animals reared for longer at Woods Hole (WH), as shown in Figure 4, projects its age to 520 days or about 18 months, which is the best guess from population data in the field. The power curve fit to all of the data predicts its age as 3–4

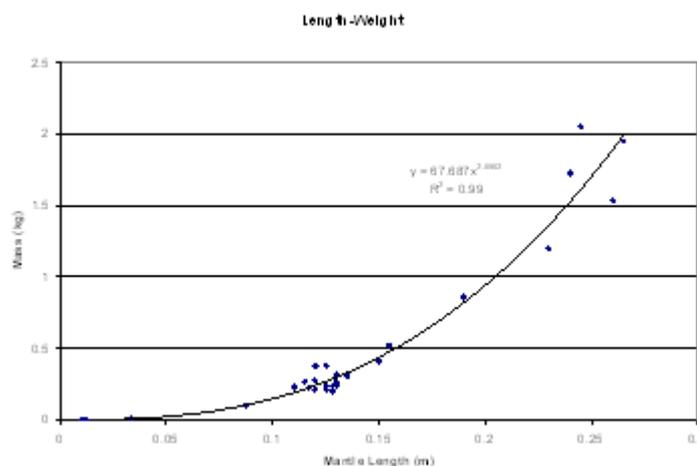
years, which seems improbable for a cephalopod.

Figure 5, provides a graphic representation of the entire life of the cuttlefish based on all of the standard assumptions outlined above. Although these assumptions are a reasonable starting place, they must be adjusted and refined with real observations of particular species and individuals. Aitken *et al.* (submitted), for example, measured the active metabolism for *Sepia apama* as 77% of routine metabolism ( $M_r$ ), so the assumption of 100% (*i.e.*  $2M_r$ ) overestimates energy expenditure for these lazy cuttlefish. Knowing this should improve the next iteration of the model.

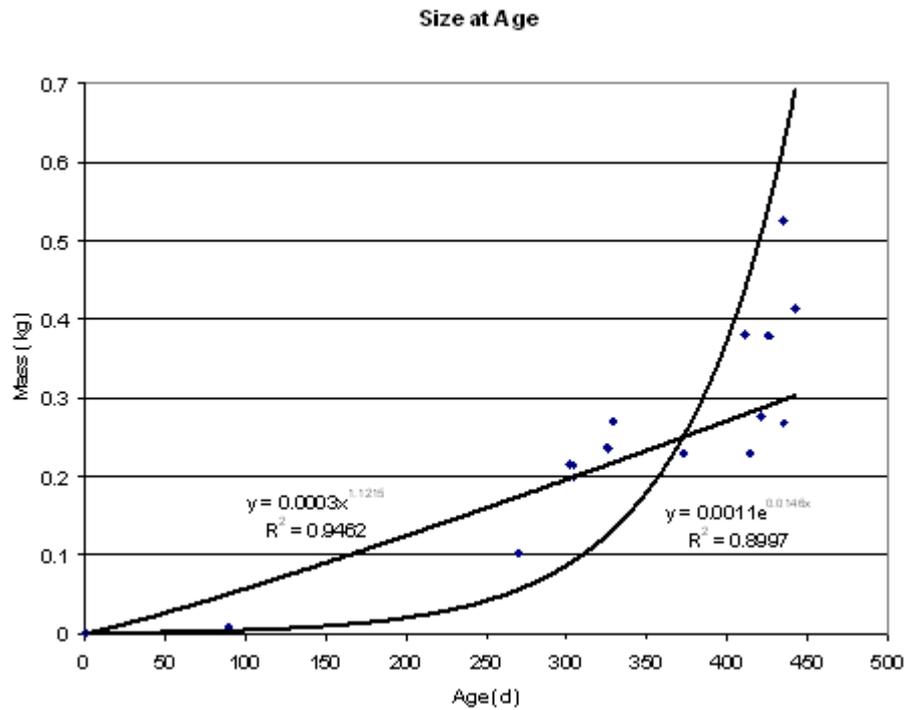
## DISCUSSION

The model in Figure 5 tests many relationships once you learn how to look at it. For example, it suggests that growth begins to exceed metabolism after 400d. This could reflect more efficient predation and declining activity, which could make more energy available for gonad growth. However, efficiency approaches 100%, as the cuttlefish approaches full adult size, which is suspicious. An efficiency of 14% in the first week might be low, but 102% at 18 months is definitely too high!

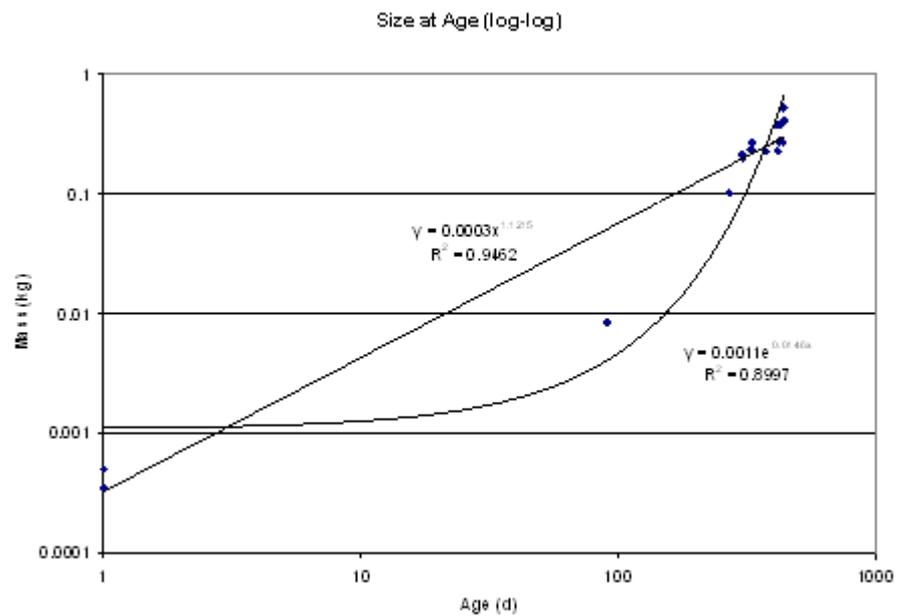
Cephalopods can lose weight during spawning (Moltschaniwskyj and Semmens 2000, Jackson 2000) so this may reflect over-extrapolation of the



**Figure 1.** A regression of log body mass versus log mantle length, providing a power curve to predict the allometry of body growth and reveal questionable measurements.



**Figure 2.** A comparison of power and exponential curves fitted to a limited set of size at age data from cuttlefish at Dalhousie University.



**Figure 3.** The same data and regressions from Figure 2 replotted as a log-log graph to illustrate non-uniform data distribution.

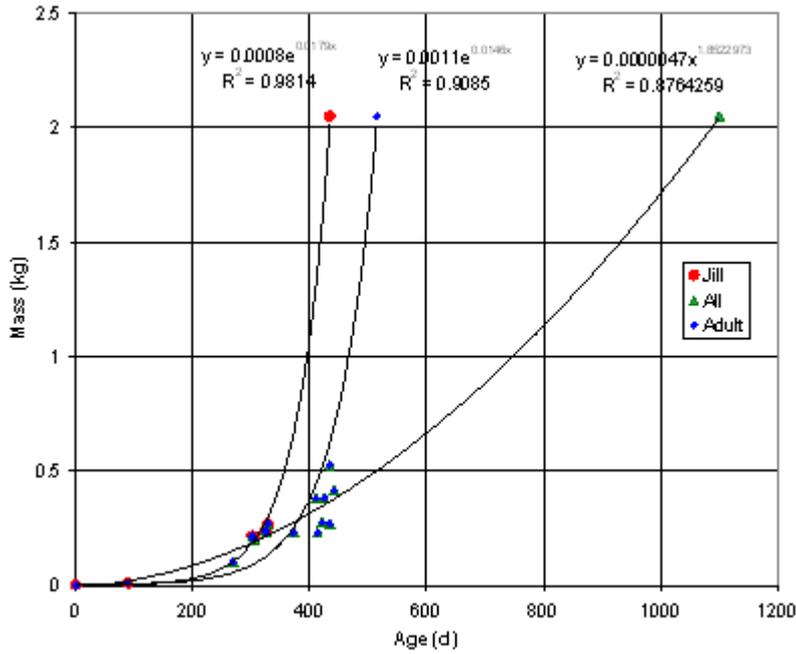


Figure 4. A comparison of exponential and power curve regressions to the larger data set including cuttlefish reared at Woods Hole and extrapolations to wild-caught cuttlefish.

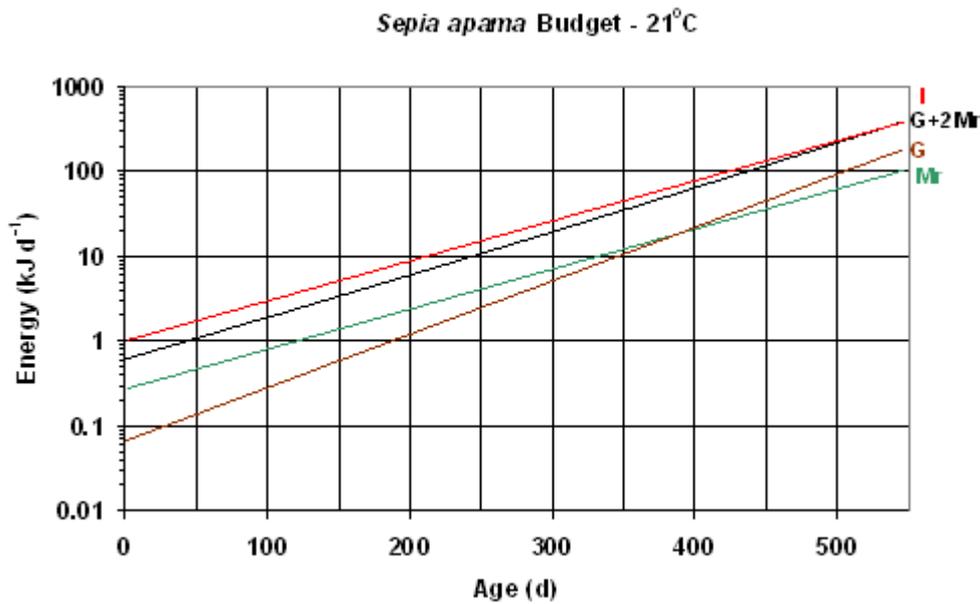


Figure 5. A semi-log graphical representation of the energy budget of a *Sepia apama* over an entire life at 21°C. Growth, as predicted by the size-at-age regression, is indicated by the G-line. Food intake, I, is extrapolated from growth efficiency measurements at a single age and routine metabolic rate, Mr, from oxygen consumption measurements at the same age. The typical assumption that field activity doubles laboratory routine measurements provides the estimate of energy output in nature, G+2Mr.

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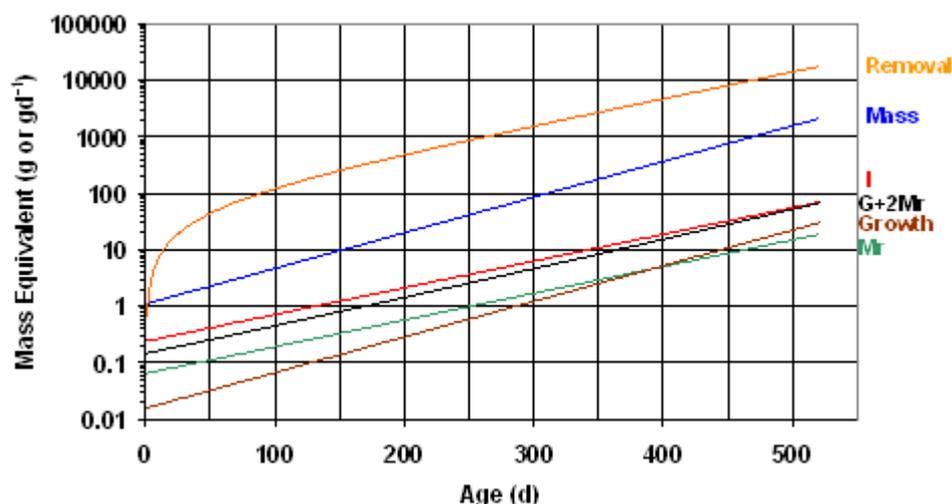
basic growth curve. A stanza of weight loss at the end of life may give a better fit. Few people think in kJ, so Figure 6 is back-calculated to grams and explores the broader implications of this model.

In this format you can also compare body weight and cumulative removal. After 18 months the body mass is about 13% of the mass removed, which is better than the 10% efficiency commonly used in ecological models. You can also see that the growth-metabolism crossover happens at about 300g, which is a reasonable size to start maturation.

One nice feature of spreadsheet modeling is that it can easily accommodate different equations in different life stanza. It would be no trouble to add a new term for egg production, for example. This could give rise to different models for males and females. It is, in fact, possible to run these models for individuals. Daily growth increments from gladius or statolith analyses could be used to

drive the model, and to estimate lifetime food consumption for ecological modeling (Perez and O'Dor 2000, Jackson and O'Dor 2001). Actual temperature records (Forsythe *et al.* 2001) can be used to drive the feeding and metabolic rate estimates. If daily growth patterns fail to fit local temperature regimes it could argue for migrations.

The effects of varying rations in the laboratory (Perez *et al.* 1996, Jackson and Moltschaniwskyj 2001) or prey availability in the wild are little explored in the cephalopod literature, but are a key alternative to temperature as growth limiting factors. Such data could play a powerful role in understanding how cephalopods use the ecosystem and the role they play in buffering seasonal and annual match-mismatch problems of long-lived marine species (Rodhouse 2001, Anderson and Rodhouse 2001, Jackson and Domeier 2003).



**Figure 6.** The energy balance model from Figure 5 transformed to mass equivalents with cumulative estimates of body mass from G and total removal of biomass from the environment from I.

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