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Chick growth in albatrosses: curve fitting with a twist

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We present a new type of equation to describe the growth patterns of procellariiform seabirds and other species whose chicks characteristically lose mass towards the end of the rearing period. Our equation is based on the Gompertz curve; our principles are also applicable to logistic and von Bertalanffy curves. From our model, five coefficients can be derived to characterise the patterns of growth. These are: growth rate, peak mass and age at which it is attained, loss rate and an index describing the overall shape of the curve. We illustrate the use of this new equation with data collected, using automated weighing platforms, on six years of chick growth of Black-browed *Diomedea melanophris* and Grey-headed *D. chrysostoma* albatrosses at Bird Island, South Georgia. In comparison with Grey-headed Albatross, Black-browed Albatross chicks grow at a faster rate and to a higher peak mass; they also reach their peak mass at an earlier age, and lose mass at a faster rate in the mass recession period. However, in both species, chicks reached peak mass when 72% of the rearing period had elapsed; within species, only this did not vary between years. This new equation not only enables the period of mass recession to be incorporated into growth analysis, but, because it does not require assumptions about asymptotic mass, greatly facilitates inter-species comparisons.

Patterns of growth in birds are an important component of their life history traits. Furthermore, there is great variability in patterns of growth between species (Ricklefs 1968a, O'Connor 1984). Knowledge of development patterns can be useful in understanding ecological differences among similar species.

Analysis of growth rates has been achieved by fitting different types of equation to growth curves. These equations allow the extraction of key parameters of chick growth in an objective and repeatable manner, instead of relying on raw data which can be highly variable. This is especially true for species with protracted growth, such as Procellariiformes, where chicks are fed irregularly (Warham 1990). As a consequence, individual growth curves are irregular with numerous fluctuations, making it difficult to ascertain in a reliable manner the exact timing and corresponding mass of the different phases of growth. The most commonly used equations belong to the Richards family of sigmoid curves (Richards 1959). Three special cases are known as the logistic, Gompertz and von Bertalanffy curves (Ricklefs 1968a, Brown and Rothery 1993). Although these curves can be used to describe the pattern of growth of birds whilst they gain mass, they cannot incorporate or describe the period of mass recession prior to fledging that is characteristic of many species of birds (Ricklefs 1968b), particularly seabirds of the order Procellariiformes (albatrosses, petrels, shearwaters, etc.).

In this paper we present a new type of equation that is capable of incorporating this later period of chick growth when chicks, after being heavier than their parents, lose mass until fledging. We describe and illustrate its properties and advantages by comparing chick growth in Black-browed Albatrosses *Diomedea melanophris* and Grey-headed Albatrosses *D. chrysostoma* at Bird Island, South Georgia.

Black-browed Albatross and Grey-headed Albatross are similar in both size and mass but their chicks grow at different rates, with Black-browed Albatross chicks growing faster and to a heavier mass (Prince and Ricketts 1981), leading to Grey-headed Albatross chicks taking longer to rear (Tickell and Pinder 1975). Even within species, the growth patterns of these two species are highly variable between years but it has proved difficult adequately to characterise the nature of this variation (Huin et al. 2000).

Methods

Data collection and preparation

Data were collected between January and June of 1990 and 1992–1994 for the Black-browed Albatross and of 1993–1996 for the Grey-headed Albatross at Bird Island, South Georgia (54°S, 38°W). Chick mass was measured every 10 min from the day chicks were left unattended (25–30 days old) until the day they fledged, using a maximum of 10 automatic weighing platforms (accurate to the nearest 10 g) per year and per species, as described by Prince and Walton (1984) and Huin et al. (2000). Prior to the deployment of the weighing platforms, chicks were weighed daily using either a 500 g Pesola spring balance or a 5 kg Salter pan balance.

Only chicks that survived to fledge were used in this analysis, which included 23 and 24 chicks for Black-browed Albatross and Grey-headed Albatross, respectively. Because the sampling frequency of chick mass was set to detect and measure the mass of meals delivered, we obtained some 13 000–18 000 mass values per chick per year. To simplify these data for fitting growth curves we applied a running average to each 24 h of data (144 values). We then extracted four values per day (at 00.00, 06.00, 12.00 and 18.00 hours), giving 350–500 values per chick per year in total.

Equations

Of the variety of curve equations available, the three most commonly used all belong to the Richards family (for more details see Richards 1959, Ricklefs 1968a and Brown and Rothery 1993) and are as follows:

1. The logistic curve:

$$W(t) = \frac{A}{[1 + e^{-k(t-t_1)}]} \tag{1}$$

This curve is a symmetrical sigmoid curve, with chicks growing to an asymptotic mass A and having their fastest growth rate at exactly the midpoint in mass at A/2 and in time at t_1, k being a constant growth rate factor.

2. The von Bertalanffy curve:

$$W(t) = A[1 - e^{-k(t-t_1)}]^3 \tag{2}$$

This curve is no longer symmetrical, with most of the mass gain occurring later but at a faster rate and taking longer to complete the final growth to the asymptotic mass.

3. The Gompertz curve:

$$W(t) = A\, e^{-e^{-k(t-t_1)}} \tag{3}$$

This curve lies somewhat in between the two preceding ones with the fastest growth rate occurring at a mass of A/e at time t_1.

However these equations possess only one positive growth rate, namely k, and therefore cannot be used for the later parts of albatross growth when chicks, after reaching a peak mass greater than that of their parents, lose mass until fledging. Thus a new type of equation must be created, to take into account this last phase of chick growth. The period of chick growth in albatrosses leading to the chicks attaining peak mass is best described by the Gompertz curve (Ricketts and Prince 1981). We apply this to the first part of the chick growth by using equation (3), where A is the asymptotic mass, t_1 the time at which the growth reaches its maximum rate at mass A/e and k_1 being the slope of log(W(t)) at t_1 (Fig. 1a). The requirements of an equation describing the mass recession part of the chick growth would be that the majority of the mass loss has to occur towards the end of the chick growth period. These requirements can be met by a negative Gompertz curve (Fig. 1b) described by the following equation:

$$W(t) = e^{-e^{k2(t-t2)}} \tag{4}$$

In this equation, after an initial period of relative stability, mass loss becomes more important, with the maximum loss rate occurring at t_2 at mass 1/e; at that point t_2, k_2 is the slope of log (W(t)). A combination of these two equations should thus be able to describe the full pattern of chick growth in albatrosses. This is achieved by creating a final equation that is the product of equations (3) and (4) and by taking into consideration the properties of the exponential function (Fig. 1c). The final equation is of the form:

$$W(t) = A\, e^{[-e^{-k(t-t1)} - e^{k2(t-t2)}]} \tag{5}$$

New equation coefficients

This new equation (5) possesses five coefficients: A, k_1 and t_1 from the original equation (3) and k_2 and t_2 from equation (4). However, the two parts of equation (5) interact with each other in such a way that the asymptotic mass A is never reached and both inflection points no longer occur at t_1 and t_2. Thus five other, more meaningful, coefficients need to be extracted. The most useful such coefficients are: (a) the peak mass W_{max}; (b) the time t_{max} at which the curve reaches its maximum; (c) an estimate of the mass growth rate; (d) an estimate of the loss rate and; (e) a measure of the shape of the growth curve.

Only at t_{max} will the growth rate be null, being always positive before and always negative afterwards. This can be mathematically expressed by calculating the time at which the derivative of equation (5) is equal to zero. It can be proved that the unique solution occurs at:

$$t_{max} = \frac{\ln\left(\frac{k_1}{k_2}\right) + k_1 t_1 + k_2 t_2}{k_1 + k_2} \tag{6}$$

W_{max} is then calculated by replacing t by t_{max} in equation (5). To extract mass growth and mass loss rates that could be compared to existing values, we followed the method described by Ricklefs (1968a) and calculated the average growth rate as being the mass gained divided by the amount of time needed for chicks to grow between masses of 10% and 90% of W_{max}. However, as the recession period is now included, there are two possible times when chicks have a mass of 90% of W_{max}. The first occurrence of t_{90} was used in the calculation of this growth rate. Because the recession period can be short in time and because we still wanted the coefficients to be expressed by values corresponding to times when data were available, a corresponding loss rate was calculated as being the amount of mass lost from peak mass to fledging mass divided by the amount of time between these two events. The ratio between the two times when chicks have a mass of 90% of W_{max} was used as a dimensionless measure of the shape of the curve (t^2_{90}/t^1_{90}). That is, when the shape value is small the curve will be pointed and when the shape value is big, the curve will be flatter around peak mass.

Statistical analysis

Growth curves were fitted using a weighted least squares technique with the help of the SigmaPlot v. 4.01 software. This implements the Marquardt-Levenberg algorithm (Marquardt 1963) to find the coefficients of equation (5). Following Ricketts and Prince (1981) and SigmaPlot documentation, weights were applied to the least squares technique to counteract the tendency of the variance in mass to increase with chick age. This involved the use of $1/W(t)^2$ as a weighting factor in the case of individual chick curves and of $\sqrt{N}/W(t)^2$ in the case of multiple chick curves, where N is the sample size used to determine each mass, hence according more importance to the more accurate points.

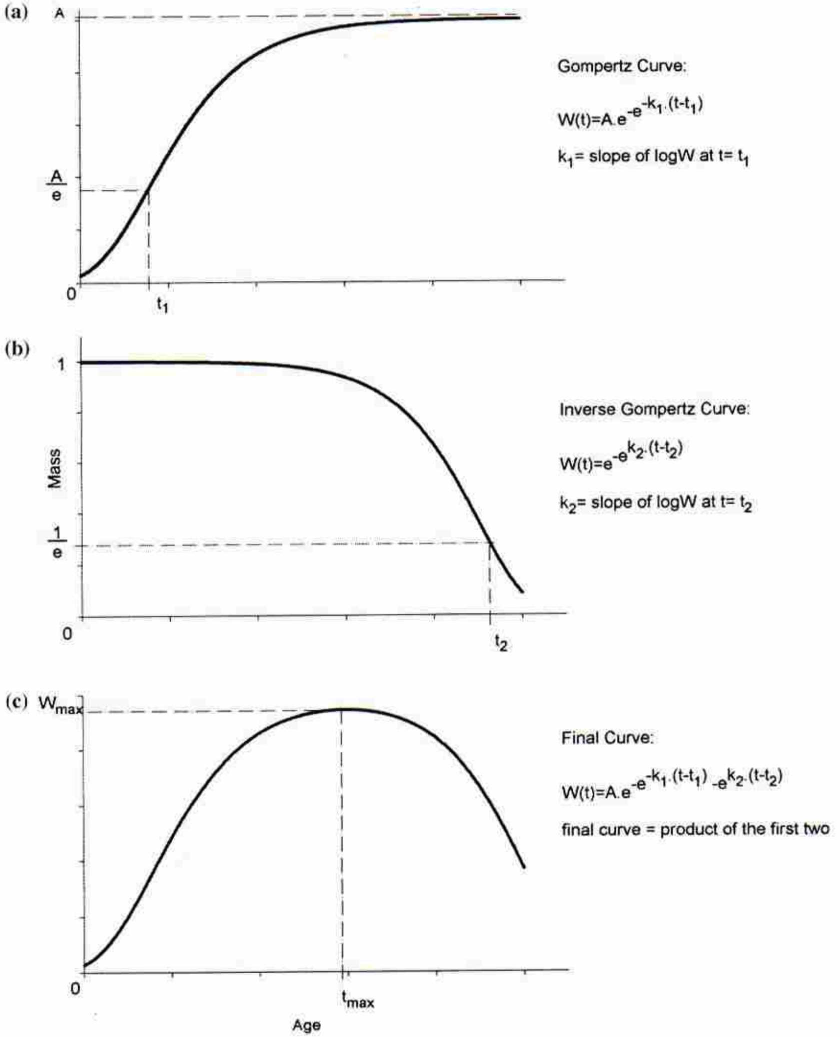

Fig. 1. Steps taken to modify an original Gompertz curve (a) by the production of a delayed inverse Gompertz curve (b) to produce a new final curve (c). See Methods for details of the curve coefficients.

Table 1. Coefficients extracted from equation (5) describing the growth patterns of successful Black-browed Albatross and Grey-headed Albatross chicks at Bird Island, South Georgia. Annual means ± 1 S.E. (and sample size in brackets) are presented. See Methods for explanations.

		Peak age (d)	Peak mass (kg)	Shape	Growth rate (g d^{-1})	Loss rate (g d^{-1})
(a)	Black-browed Albatross					
	1990	80.65 ± 6.76 (5)	3.23 ± 0.21 (5)	2.05 ± 0.09 (5)	56.87 ± 3.52 (6)	29.48 ± 4.86 (5)
	1992	86.51 ± 2.54 (6)	4.57 ± 0.28 (6)	1.64 ± 0.07 (6)	63.79 ± 2.98 (6)	37.94 ± 8.57 (6)
	1993	87.36 ± 1.98 (6)	4.04 ± 0.19 (6)	1.66 ± 0.05 (6)	57.73 ± 3.97 (6)	34.47 ± 8.81 (6)
	1994	94.59 ± 1.10 (5)	5.09 ± 0.07 (5)	1.42 ± 0.04 (5)	61.29 ± 2.16 (5)	74.05 ± 9.65 (5)
	Mean	87.25 ± 1.94 (22)	4.24 ± 0.17 (22)	1.69 ± 0.06 (22)	59.86 ± 1.66 (23)	43.28 ± 4.95 (22)
(b)	Grey-headed Albatross					
	1993	104.54 ± 4.44 (8)	4.05 ± 0.24 (8)	1.85 ± 0.06 (8)	49.32 ± 2.51 (8)	20.02 ± 5.66 (8)
	1994	103.03 ± 2.35 (4)	3.36 ± 0.43 (5)	1.80 ± 0.27 (4)	38.63 ± 5.49 (5)	26.56 ± 9.27 (4)
	1995	94.72 ± 4.46 (3)	4.77 ± 0.16 (3)	1.62 ± 0.05 (3)	60.92 ± 3.29 (3)	31.76 ± 4.13 (3)
	1996	94.37 ± 2.22 (8)	4.22 ± 0.12 (8)	1.97 ± 0.08 (8)	56.87 ± 2.14 (8)	16.23 ± 2.61 (8)
	Mean	99.46 ± 2.04 (23)	4.05 ± 0.15 (24)	1.86 ± 0.06 (23)	51.06 ± 2.19 (24)	21.37 ± 2.80 (23)

Table 2. Correlation matrix of the five parameters from equation (5) for both Black-browed and Grey-headed Albatross chicks at Bird Island, South Georgia. Significance levels are $P<0.005$ in bold, $0.005<P<0.05$ in italics, and n.s. in normal characters.

		T_{max}	W_{max}	Growth rate	Loss rate
a)	Black-browed Albatross				
	W_{max}	−0.180			
	Growth rate	**−0.620**	**0.846**		
	Loss rate	−0.081	**0.669**	0.370	
	Shape	0.036	**−0.571**	−0.242	**−0.798**
b)	Grey-headed Albatross				
	W_{max}	*0.479*			
	Growth rate	−0.295	**0.599**		
	Loss rate	*0.505*	**0.705**	0.180	
	Shape	*−0.548*	**−0.820**	−0.196	**−0.710**

One of the pitfalls of employing such an equation with many parameters is that some of the parameters might be superfluous and/or that the parameters are highly intercorrelated. SigmaPlot software also gives a measure of the utility of the parameters used by calculating a dependency value of all the parameters. If too many parameters are used, several of those will have a dependency value close to one. Another approach to estimate the intercorrelation of the parameters used was to calculate the correlation matrix of these parameters.

Another difficulty of using this type of equation is in trying to estimate the confidence limits of the five coefficients described above. Firstly, as these coefficients are all a function of the original five parameters of equation (5), the calculation of the standard error of each coefficient in each individual growth curve should take account of this due to the propagation of errors from one parameter to the next. Furthermore, the data used are not independent because of our high sampling rate and because of our subsequent use of running averages as a smoothing tool. This results in underestimating further the confidence limits of the fitted parameters which is again reinforced by using a weighting factor to stabilise the variance throughout chick growth. Estimation and then comparison of individual chick growth coefficients would then be seriously impaired. One remedy would have been to use jackknife confidence intervals, as described by Bradley et al. (1984). However, because we restricted our comparisons to those between different populations but did not compare individual chicks one to another and because a similar sampling method was used for all chicks, ordinary statistical computation of confidence intervals around the mean for each coefficient is acceptable (comparison of strict longitudinal data as mentioned by Bradley et al. (1984)). Comparisons of the different coefficients obtained between species (two) and years (six) were performed by two-way analyses of variance using Minitab v. 10 statistical software.

Results

Using this new equation (5) on individual chick, we were able to describe accurately all chick growth data (R^2 ranging from 97.0 to 99.9%) except for one Black-browed Albatross chick in 1990 and one Grey-headed Albatross chick in 1994, neither of which possessed a mass recession period. Means of the curve coefficients for each year and species are presented in Table 1.

In all but the two cases above, the dependency values given to the parameters were less than one, thus validating the use of an equation with five parameters. A correlation matrix of the five parameters for each species is given in Table 2. For Black-browed Albatross, five out of ten correlations were highly significant and in Grey-headed Albatross, four were highly significant and an additional three were significant. Furthermore, none of the correlation values exceeded 0.90. This suggests that, although there is a degree of redundancy between the five different equation parameters (and especially for peak mass), the overall equation did not possess too many parameters.

Black-browed Albatross chicks reached a higher peak mass (190 g heavier) at an earlier age (12 days earlier) than Grey-headed Albatross chicks ($F_{1,39} = 7.28$, $P < 0.01$ and $F_{1,38} = 13.9$, $P < 0.001$ respectively). Although the variation between years in peak mass for both species was significant ($F_{5,39} = 4.43$, $P < 0.005$), the age at which they attained that peak mass remained constant between years ($F_{5,38} = 2.4$, $P = 0.06$). Similarly, the growth curves of Black-browed Albatross chicks were more steep-sided than the flatter and broader curves of Grey-headed Albatross chicks, as indicated by the significant difference in their shape index ($F_{1,38} = 8.13$, $P < 0.01$). The shape of the curves also varied significantly between years ($F_{5,38} = 5.10$, $P < 0.001$). Black-browed Albatross chicks gained mass at a faster rate (by 8 g d^{-1}) than Grey-headed Albatross chicks ($F_{1,40} = 17.8$, $P < 0.001$) but also lost mass at a faster rate (by 22 g d^{-1}) during the recession period ($F_{1,38} = 16.6$, $P < 0.001$). In both cases there were significant differences between years in mass gain and loss rates ($F_{1,40} = 3.60$, $P < 0.01$ and $F_{1,38} = 4.29$, $P < 0.005$ respectively).

The mean values of the coefficients presented in Table 1 are very similar to the ones calculated when fitting growth curves to the average chick mass for each

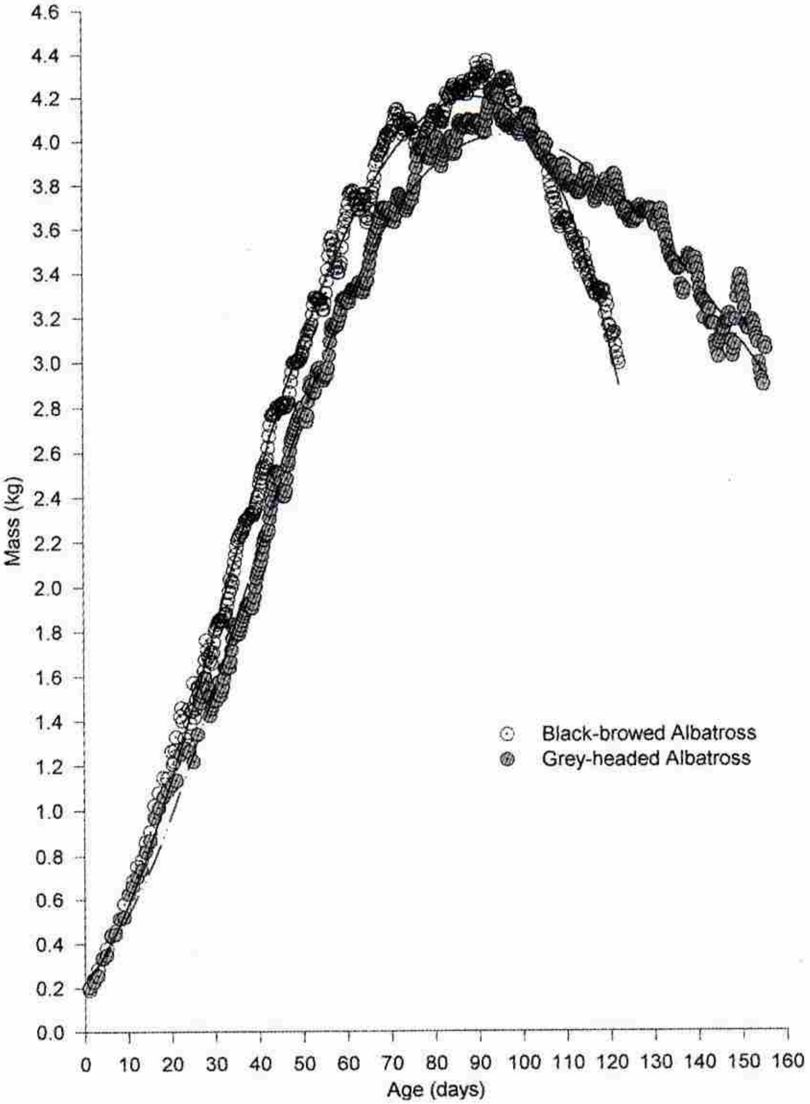

Fig. 2. Four-year average growth curves and their fitted model for Black-browed Albatross and Grey-headed Albatross at Bird Island, South Georgia.

Table 3. Coefficients of regression, degrees of freedom, F value, probability (P) and R^2 of the regression analysis of chick provisioning rate up to 100 days old on peak age and mass, shape index and growth rate and of chick provisioning rate between peak age and fledging age on mass loss rate for all Black-browed Albatross chicks at Bird Island, South Georgia.

	Coefficient	df	F	P	R^2
Peak age	0.0026	26	0.02	0.876	0.1%
Peak mass	0.0049	30	16.09	<0.001	35.7%
Shape	-5×10^{-6}	21	0.001	0.993	<0.001%
Growth rate	0.0463	30	24.6	<0.001	45.9%
Loss rate	−0.0618	28	9.67	<0.005	26.4%

Table 4. Coefficients of regression, degrees of freedom, F value, probability and R^2 of the regression analysis of chick provisioning rate up to 100 days old on peak age and mass, shape index and growth rate and of chick provisioning rate between peak age and fledging age on mass loss rate for all Grey-headed Albatross chicks at Bird Island, South Georgia.

	Coefficient	df	F	P	R^2
Peak age	−0.0254	28	0.64	0.429	2.3%
Peak mass	0.00669	33	39.62	<0.001	55.1%
Shape	−0.001	23	2.21	0.152	9.1%
Growth rate	0.102	33	46.45	<0.001	59.2%
Loss rate	−0.0294	27	2.76	0.109	9.6%

species, combining all years (Fig. 2). In the latter case, Black-browed Albatross chicks attained a peak mass of 4.20 kg at the age of 89.11 days with a growth rate of 56.93 g d^{-1} and a loss rate of 39.43 g d^{-1}, giving the growth curve a shape index of 1.65 ($R^2 = 99.5\%$). Grey-headed Albatross chicks, in contrast, attained a peak mass of 4.03 kg at the age of 96.51 days with a growth rate of 50.85 g d^{-1} and a loss rate of 18.38 g d^{-1}, giving the growth curve a shape index of 1.85 ($R^2 = 99.9\%$).

Discussion

The successful use of a new type of growth equation has enabled us to compare more objectively and in more detail the growth patterns of chicks of the Black-browed Albatross and Grey-headed Albatross and to identify differences more precisely. In accordance with the findings of Prince and Ricketts (1981), we found that Black-browed Albatross chicks grow at a faster rate and to a higher maximum mass. Furthermore, the growth curves of the Grey-headed Albatross chicks have a higher shape index, indicating that their curves are broader; that is, they have a slower growing phase, are then flatter around peak age and have a less accentuated recession phase. In addition we showed that in Black-browed Albatross peak mass is attained at an earlier age and the loss of mass during the recession period occurs at a faster rate. However, as Black-browed Albatross chicks fledge when 119 days old, around 20 days earlier than Grey-headed Albatross chicks (Prince et al. 1994), peak mass is attained in both species when 72% of the chick rearing period has elapsed. Thus the age at which peak mass is attained might be determined by intrinsic mechanisms. In contrast, growth and loss rates, as well as peak mass and thus shape index, showed variations between years. Huin et al. (2000) demonstrated that at least growth rate and peak mass were significantly affected by chick provisioning rate. Thus when the amount of food delivered to the chicks was low, their growth rate was slower and their peak mass was lower. We can now re-examine the influence of chick provisioning rate on the five new growth coefficients for both species (Tables 3 and 4). For chicks of both species, provisioning rate during the first 100 days has a positive effect on peak mass and especially growth rate. This relationship is identical (i.e. same coefficients of regression and same differences between species) to the previous results presented by Huin et al. (2000). The only difference between the two methods is that the amount of variation in growth rate explained by provisioning rate is greater than previously: nearly 50% the variation in Black-browed Albatross and 60% of the variation in Grey-headed Albatross growth rates, compared with 21% and 47% obtained previously. This reflects the greater accuracy of our method for estimating growth rate. However, both the age at which chicks attain their peak mass and the shape of their growth curve are uninfluenced by provisioning rate. Provisioning rate between peak age and fledging age has a negative effect on the loss rate for Black-browed Albatross chicks (the more chicks are provisioned, the less they lose mass), but the much lower loss rate of Grey-headed Albatross chicks does not seem to be affected.

Our new equation describes accurately the full patterns of growth in albatrosses. This was achieved by integrating into an original Gompertz model a component that allowed for the loss of mass in the late part of the chick-rearing period. There is thus no longer a need to truncate the full chick-rearing period to an arbitrarily chosen final age to satisfy the restriction of previous models which did not allow for any mass loss. From this new equation we utilised five coefficients to describe the biological processes involved in chick growth of albatrosses. These coefficients were growth rate, peak mass and the age at which it was attained, loss rate and an index describing the overall shape of the curves. Although one might be tempted to compare growth rate and peak mass with the previous results of Ricketts and Prince (1981) on the same species at the same locality, extreme care should be taken as comparisons of similar coefficients calculated by different types of equation can only be made on a broad basis (O'Connor 1984). This is mainly due to the fact that the previous growth equations used are very sensitive to the asymptotic mass selected (Croxall 1984). This problem does not exist with our new growth model because the asymptotic mass is not used, but a true peak mass (and its timing) can be calculated from the equation itself.

We believe that this new equation will be very useful for describing growth patterns in other bird species, not just Procellariiformes, which possess a mass recession period and to which the Gompertz curve has already been applied successfully (Ricklefs 1973). Hirundines and swifts are particularly appropriate candidates but preliminary work (Huin, unpubl.) has successfully applied the technique to over 60 bird species, including albatrosses, petrels, shearwaters, auks, terns and gulls, gannets and boobies, tropicbirds, hirundines, Merlin *Falco columbarius* and Barn Owl *Tyto alba*. In fact, the greatest restriction is finding published growth curves describing in full the mass recession period.

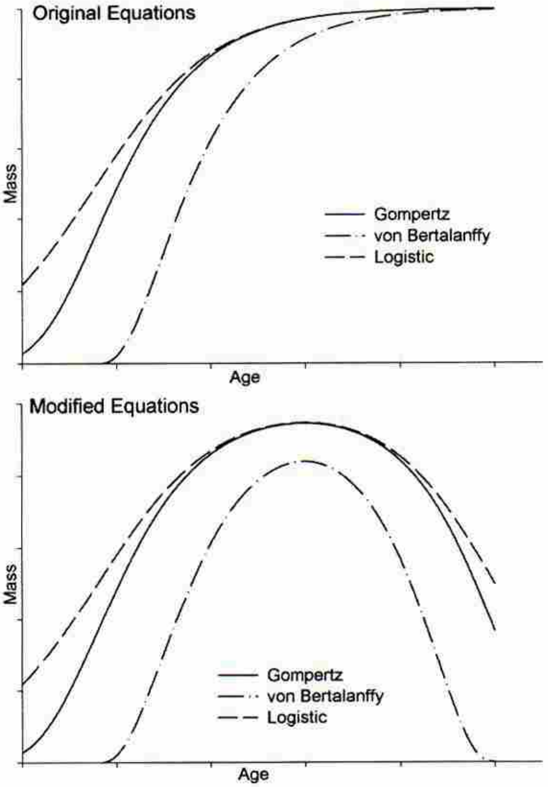

Fig. 3. Original and modified Gompertz, von Bertalanffy and logistic curves fitted with the same values for their coefficients.

Our new equation is derived from the original Gompertz curve, but the same principle can also be applied to the von Bertalanffy and logistic curves (Fig. 3a,b), thus creating a new set of equations:

1. from equation (1):

$$W(t) = \frac{A}{[1 + e^{-k_1(t-t_1)} + e^{k_2(t-t_2)}]} \qquad (7)$$

2. from equation (2):

$$W(t) = A[1 - e^{-k_1(t-t_1)} - e^{k_2(t-t_2)}]^3 \qquad (8)$$

3. and as already mentioned from equation (3):

$$W(t) = A\, e^{[-e^{-k_1(t-t_1)} - e^{k_2(t-t_2)}]} \qquad (5)$$

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