ELASMOBRANCHS

Evidence of two-phase growth in elasmobranchs

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Abstract It is often assumed that the von Bertalanffy growth model (VBGM) is appropriate to describe growth in length-at-age of elasmobranchs. However, a review of the literature suggests that a two-phase growth model could better describe growth in elasmobranchs. We compare the two-phase growth model (TPGM) with the VBGM for 18 data sets of elasmobranch species, by fitting the models to 36 age-length-at-age data pairs available. The Akaike Information Criteria (AIC) and the difference in AIC between both models revealed that in 23 cases the probability that the TPGM was true ≥50%. The VBGM tends to estimate larger L_∞ values than the two-phase growth model, while the k parameter tends to be underestimated. The growth rate in length-at-age appears tends to decrease near the age at first maturity in several species of elasmobranch. The importance of the TPGM lies in that it may better describe this aspect of the life history of many elasmobranchs. In this context, we conclude that the TPGM should be used along with other growth models in order to precisely estimate elasmobranch life history parameters.

Keywords Elasmobranchs · von Bertalanffy · Two-phase growth · Sharks · Skates

Introduction

Knowledge of the age structure of a population and the k parameter of the von Bertalanffy growth model (VBGM, von Bertalanffy 1938) are central to understanding the responses of an exploited elasmobranches population. In fact, k has been used as an index of the vulnerability of a stock subject to excessive mortality and is useful for comparing life history strategies and limitations among species (Pratt and Casey 1990; Musick 1999). Those groups having a k coefficient value of <0.1 seem to be particularly vulnerable. Most elasmobranchs fall under that category (Cailliet and Goldman 2004).

The VBGM is one of the most used models to describe growth in elasmobranchs. It is based on the premise that an organism is analogous to a chemical reaction that obeys the mass action law and is described by the familiar equation:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right)$$

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where L_∞ is the asymptotic length-at-age, which represents the average length-at-age of individuals in a stock would attain if they grew indefinitely, k is a curvature parameter determining the rate at which the fish reach the asymptotic length-at-age, and t_0 is a position parameter defining the initial condition on the time axis when mean fish length-at-age is zero.

Caillet et al. (1992) proposed a variant of the VBGM replacing t_0 by L_0 because length-at-age at-birth is generally more easily obtainable in elasmobranchs. This model is expressed as:

$$L_t = L_\infty - (L_\infty - L_0)e^{kt}$$

where L_0 is the length-at-age-at-birth.

Other models used to describe growth in elasmobranchs include the generalized VBGM (Pauly 1981) and Schnute's model (Schnute 1981) used by Goosen and Smale (1997) for *Mustelus mustelus* and a seasonal growth model for *M. lenticulatus* (Francis and Francis 1992). A modification of the VBGM known as the two-phase growth model (TPGM, Soriano et al. 1992) has recently been used to describe the growth of *Isurus oxyrinchus*, *Prionace glauca*, and *Lamna nasus*[1]. The importance of this TPGM resides in that the model predicts the decrease in growth rate observed for different species between the ages of four and seven. Natanson et al. (2002) also observed a decrease in growth rate when male and female *Lamna nasus* from the Northeast Atlantic Ocean first reached sexual maturity, but they fitted the VBGM to the data when a TPGM might have been more appropriate. Similarly, Natanson and Caillet (1990; see their Fig. 4) identified a change in growth between 800 and 1000 mm TL (approximately 28 bands) in *Squatina californica*, which was coincident with the length-at-first maturity of this species, but they did not fit any model to describe the growth. Skomal and

Natanson (2003) described a two-phase growth for *Prionace glauca* by using a non-parametric fit (LOESS), whose change in phase was coincident with the age-at-maturity of females, but suggested that it could have been a problem due to low sample size for females.

A review of published papers on age and growth of elasmobranchs, reveals that in many of the figures in which length-at-age is plotted against age, a decrease in growth rate in length-at-age is observed, coinciding with the attainment of the age at first maturity. This pattern in growth is evident in several elasmobranch species, but it is usually ignored because the VBGM is adopted when the TPGM might be more appropriate, for example; *Carcharhinus obscurus* (Natanson and Kohler 1996), *Dasyatis chrysonota chrysonota* (Cowley 1997), *Squalus acanthias* (Avsar 2001), and *Prionace glauca* (Skomal and Natanson 2003). The problem is compounded in some studies that have fitted growth curves to back-calculated data, which tends to obscure the decrease in growth rate when first reaching maturity. Other studies do not present the distribution of observed length-at-age against age at all (Natanson et al. 1995; Sminkey and Musick 1995).

It seems warranted to propose that elasmobranchs may follow a pattern of growth in length-at-age different from that predicted by the VBGM. The most appropriate growth model for elasmobranchs (or groups of elasmobranchs) has not been clearly established, and no studies have yet attempted to explain the decrease in growth rate near the age at first maturity within a growth model. Walker et al. (1998) and Walker (1998) provide evidence of length-at-age selective fishing mortality as a cause for distorting von Bertalanffy growth curves. These authors also stress the potential effects of length-at-age selective sampling bias and overestimation of age for distorting growth curves. Is two phase growth a common characteristic in the growth of elasmobranchs? We addressed this question by comparing the fit of the TPGM and the VBGM to 36 length-at-age data sets available for 18 populations of elasmobranchs.

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[1] Acuña, E., L. Cid, E. Pérez, I. Kong, M. Araya, J. Lamilla & J. Peñaililllo. 2001. Estudio biológico de tiburones (marrajo dentudo, azulejo y tiburón sardinero) en la zona norte y central de chile. Informe FIP N° 2000-23. Subsecretaría de Pesca. 128 pp. Available from the Internet URL http://www.fip.cl/pdf/informes/inffinal%202000-23.pdf

Materials and methods

Data and growth models

Length-at-age data were requested and made available by several authors that previously had published their results in peer-reviewed journals. In a few cases, data was extracted directly from published figures. In other cases, we used unpublished data[1]. Data based in the analysis belonged to 16 species and 4 orders of elasmobranches (Table 1). Depending on the available information, the analyses were carried out for male, female, or combined sexes.

Growth parameters of both the VBGM and the two-phase growth model were estimated by fitting the model to the observed data through non-linear regression by considering an additive error structure. In the case of the VBGM, this is expressed as:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) + \varepsilon_t$$

where ε_t is the random error, which is assumed normally distributed.

The TPGM of Soriano et al. (1992), which consists of a modified version of the VBGM, is expressed as:

$$L_t = L_\infty(1 - e^{-kA_t(t-t_0)}) + \varepsilon_t$$

This equation is the second variant in Soriano et al. (1992), where A_t is a factor that modifies k when the age is increased, and can be defined by:

$$A_t = 1 - \frac{h}{(t - t_h)^2 + 1}$$

where t_h is the age at which the transition between the two phases occur, and h determines the magnitude of the maximum difference in length-at-age between the VBGM and the TPGM in the point t_h. The loss-function in both models used was least-squares.

Model selection

A maximum likelihood method was used to select the model that best fitted elasmobranch growth (Burnham and Anderson 2002; Motulsky and Christopoulos 2003). The objective of the method is to evaluate the relative power of the evidence supporting a given model. Relative support was evaluated by considering likelihood theory combined with Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). A single AIC

Table 1 Elasmobranchs species considered in the present study

Species	Order	F	M	Both	Source
Squalus acanthias	Squaliformes	X	X	X	Avsar (2001)
Deania calceus	Squaliformes	X	X		Clarke et al. (2002)
Raja clavata	Rajiformes	X	X		Holden (1972)
Raja batis	Rajiformes			X	Du Buit (1976)
Raja naevus	Rajiformes			X	Du Buit (1976)
Rhinobatos productus	Rajiformes		X	X	Timmons and Bray (1997)
Dasyatis chrysonota chrysonota	Rajiformes	X	X		Cowley (1997)
Leucoraja ocellata	Rajiformes	X	X	X	Sulikowski et al. (2003)
Dipturus chilensis	Rajiformes	X	X	X	Araya et al.[1]
Alopias vulpinus	Lamniformes			X	Cailliet et al. (1983)
Lamna nasus	Lamniformes	X	X	X	Natanson et al. (2002)
Lamna nasus	Lamniformes			X	Acuña et al. (2001)
Isurus oxyrinchus	Lamniformes	X	X	X	Acuña et al. (2001)
Negaprion brevirostris	Carcharhiniformes	X	X	X	Brown and Gruber (1988)
Triakis semifasciata	Carcharhiniformes			X	Kusher et al. (1992)
Carcharhinus leucas	Carcharhiniformes			X	Cruz-Martínez et al. (2002)
Prionace glauca	Carcharhiniformes	X			Skomal and Natanson (2003)
Prionace glauca	Carcharhiniformes	X	X	X	Acuña et al. (2001)

F: females; M: males

[1] M. Araya, H. Arancibia & P. Ortiz (Unpublished data)

value does not have an interpretation by itself, but comparisons between different values of AIC allow evaluation of the relative support of the data for two or more models. The AIC penalizes the complexity of the model, given by the number of parameters, by attaining an optimum between parsimony and accuracy. The expression used is:

$$\text{AIC} = n \ln(\hat{\sigma}^2) + 2p$$

where p is the number of estimated parameters, n is the number of observations, and σ^2 is given by:

$$\hat{\sigma}^2 = \frac{\sum \hat{\varepsilon}_i^2}{n}$$

where $\hat{\varepsilon}_i$ are the residuals for a given model. The model with the lowest AIC value is selected as the most probable and true model for the data. How much more probable? According to Burnham and Anderson (2002) and Motulsky and Christopoulos (2003) the difference between the AIC with the higher number of parameters and the model with fewer parameters, ΔAIC, allows computation of the AIC weight (w), which corresponds to the probability of choosing the true model, i.e., in this case the TPGM:

$$w = \frac{e^{-0.5\,\Delta AIC}}{1 + e^{-0.5\,\Delta AIC}}$$

Results

The values of AIC's, ΔAIC and w, were obtained for the different species (Table 2). There were significant differences between models in the L_∞ parameter estimates as suggested by the slope of the regression (=0.866), which was significantly different from unity ($p < 0.0001$; Fig. 1a). The VBGM tends to estimate larger values of L_∞ than the TPGM. In 15 cases, the difference in L_∞ values between the two models was between 10 and 141 cm, in 19 cases the difference was between 9.4 and 9.7 cm, and in only two cases the difference was less than –26 cm (Fig. 1b).

The opposite occurred in the case of the k parameter, i.e., the VBGM tends to estimate a lower k compared with the TPGM. The slope of

the regression (=0.866) was not significantly different from unity ($p = 0.318$), but the intercept (=0.036) was significantly different from zero ($p < 0.01$). The majority of k values estimated by the TPGM was above the based or line of 45° (Fig. 2a). In 13 cases, the difference in k values was between –0.026 and –0.165 year^{-1}, while in 23 cases the difference ranged between –0.017 and 0.018 year^{-1} (Fig. 2b).

Length-at-age L_{th} of different species at age t_h when the difference between the models is maximum was always higher for the VBGM than for the TPGM (Fig. 3). This means that there is a time in the life history of elasmobranchs when the rate of change in growth in length-at-age tends to decrease. In fact, in 23 of 36 cases, the probability that the TPGM is true was ≥50% (Fig. 4), representing 16 species (9 cases were females, 7 males, and 7 sexes combined).

Discussion

The AIC is a good criterion for selecting the most parsimonious model for explaining the observed variation in the data while using fewer parameters (Burnham and Anderson 2002). However, which model is better or worse will always depend on the context. Wang et al. (1995) pointed out that choosing a growth curve is often subjective and recommend that in some cases a pragmatic decision based on previous studies and experience rather than goodness-of-fit of the data should be used. In contrast, Haddon (2001) stated that the model best explaining the growth process should be used, but unfortunately it is not so simple to decide what the "better" description of the process is since statistical results and biological interpretation can sometimes conflict (see Cailliet et al. this issue). Generally, it is not possible to maximize all of the attributes of a particular model simultaneously, because often parsimony, precision, accuracy, and biological realism are not independent attributes.

Ricker (1979) considered that growth may be divided into a series of stages in the life history of a fish, and the changes between stages are characterized by some crisis or discontinuity in development, such as maturity, changes in behavior, or changes in habitat. This is in agreement

Table 2 Values of AIC for the two models (AIC$_{VB}$: von Bertalanffy model growth; AIC$_{TP}$: two-phase model); ΔAIC: difference between the AIC with the higher number of parameters and the model with fewer parameters; w_{TPGM}: AIC weight corresponds to the probability of the TPGM being correct

| Species	Female				Male				Both			
	AIC$_{VB}$	AIC$_{TP}$	ΔAIC	w_{TPGM}	AIC$_{VB}$	AIC$_{TP}$	ΔAIC	w_{TPGM}	AIC$_{VB}$	AIC$_{TP}$	ΔAIC	w_{TPGM}
S. acanthias	42.35	43.04	0.68	41.5%	27.11	30.51	3.39	15.5%	38.52	38.89	0.38	45.3%
D. calceus	337.21	341.08	3.87	12.6%	235.46	237.56	2.10	25.9%				
R. clavata	105.45	101.85	–3.60	85.8%	48.34	46.36	–1.97	72.9%				
R. batis									275.85	269.31	–6.54	96.3%
R. naevus									96.00	95.96	–0.04	50.5%
R. productus					103.77	100.16	–3.61	85.9%	179.76	181.49	1.73	29.6%
D. ch. chrysonota	74.82	73.67	–1.15	64.0%	47.69	37.39	–10.30	99.4%				
L. ocellata	892.36	892.30	–0.07	50.8%	682.64	681.45	–1.19	64.5%	1576.19	1578.76	2.57	21.6%
D. chilensis	228.18	222.47	–5.71	94.6%	136.70	140.41	3.71	13.6%	368.30	371.18	2.88	19.1%
A. vulpinus									949.06	952.85	3.79	13.1%
L. nasus	1485.81	1487.28	1.47	32.4%	1412.45	1408.85	–3.59	85.8%	2981.25	2977.23	–4.02	88.2%
L. nasus									313.66	312.86	–0.80	59.8%
I. oxyrinchus	1373.13	1345.83	–27.30	100.0%	1537.23	1534.70	–2.52	77.9%	3110.73	3133.11	22.38	0.0%
N. brevirostris	183.44	178.66	–4.78	91.6%	187.70	186.45	–1.25	65.2%	360.25	370.79	10.54	0.5%
T. semifasciata									1519.49	1516.22	–3.27	83.7%
C. leucas									124.31	121.84	–2.47	77.5%
P. glauca	603.23	592.51	–10.72	99.5%								
P. glauca	993.23	992.88	–0.35	54.4%	553.97	560.07	6.08	4.6%	1584.36	1593.63	9.27	1.0%
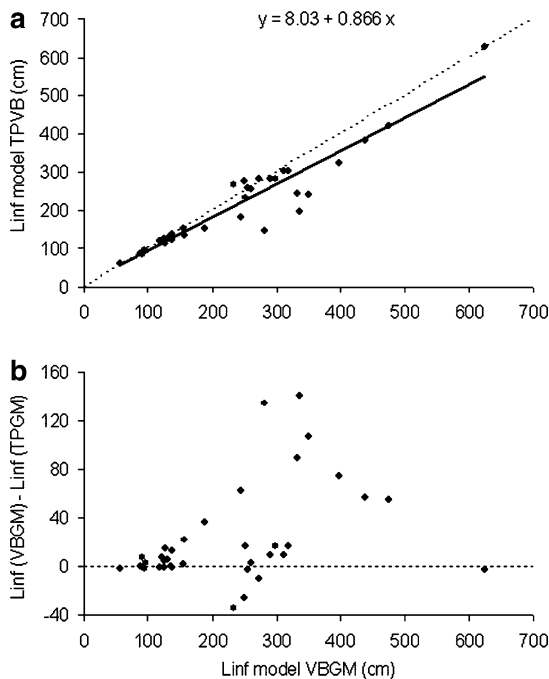
Fig. 1 (a) Relationship between parameter L_∞ (Linf) estimated by the models. The dotted line corresponds to 1:1. (b) Relationship between Linf estimated by VBGM and the difference between both models. VBGM: von Bertalanffy growth model; TPGM: two-phase growth model
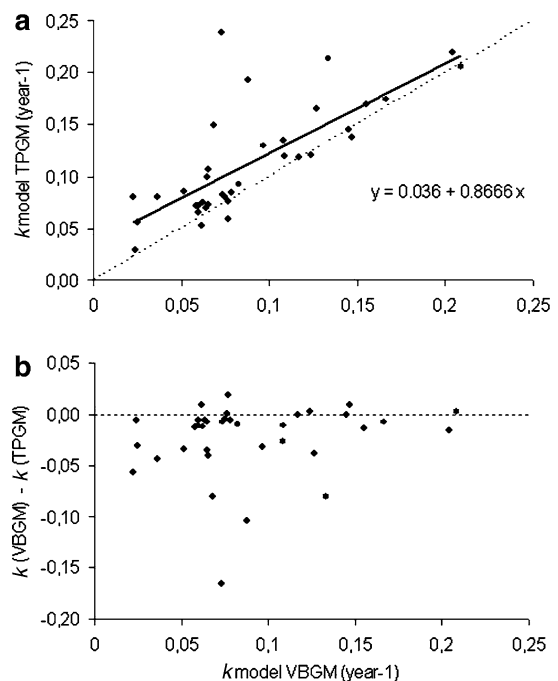

Fig. 2 (a) Relationship between parameter k estimated by both models. The dotted line corresponds to 1:1. (b) Relationship between k estimated by VBGM and the difference between both models. VBGM: von Bertalanffy growth model; TPGM: two-phase growth model
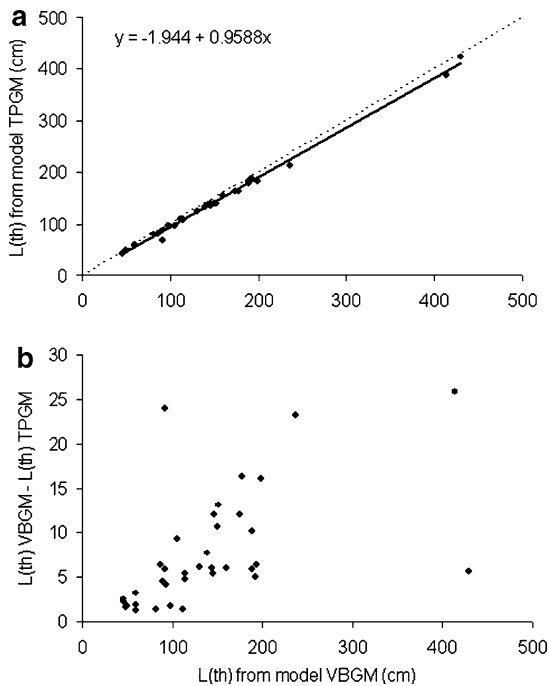
Fig. 3 (a) Relationship between the length-at-age at age t_h, $L(t_h)$ as estimated by both models. The dotted line corresponds to 1:1. (b) Relationship between $L(t_h)$ estimated with VBGM and the difference between both models

with the suggestion of Day and Taylor (1997), who stated that the growth trajectory should be specified by two separate equations: one describing pre-maturity, in which essentially no surplus energy is destined to reproduction and post-maturity equation, in which all (determinate growth) or some (indeterminate growth) surplus energy is used for reproduction. These authors in fact suggested that there are not reasons for the use of the VBGM when studying the relationship between growth and maturity because growth in pre- and post-maturity seems to be different. The maturity principle involves a reduction in the energy destined to growth because the energy is allocated to reproduction (Jensen 1985). Consequently, the growth trajectory should exhibit a fundamental change at the onset of maturity, and growth models should be able to distinguish between the process of growth before and after maturity (Day and Taylor 1997).

Attaining maturity would likely be recognized as a new growth phase if individual growth data were available, but growth in wild populations is inferred by using averages of individuals from different year classes (Ricker 1979). As such, changes in growth rate at the onset of maturity are obscured by data from fish that come from different year classes.

According to Soriano et al. (1992), the two-phase growth would be apparent when individuals are sampled only in a single episode and the average length-at-age is computed from various annual classes. If one-year class has had a lower growth rate, then a decline will appear in the growth curve. However, most elasmobranch growth studies surveyed here had samples collected during one or more years, so lower growth rates at intermediate ages should not be related to the sampling procedure. Conversely, when the two-phase models fitted to length-at-age data pairs of combined sexes is considered, e.g., *Leucoraja ocellata, Negaprion brevirostris, Isurus oxyrinchus, Prionace glauca*, the probability (w) in choosing the TPGM is very low. However, when we take into account male and female individually the conclusion is completely different. There is a higher probability favoring the TPGM. This situation could be because usually female and male attain their first maturity at different ages, and therefore the reduction in the length-at-age growth rate predicted by the two-phase model for both sexes could be masked, affecting the fit of the model when both sexes are combined. Of course, this explanation is right only if the reduction in the length-at-age growth rate is related to the age at first maturity.
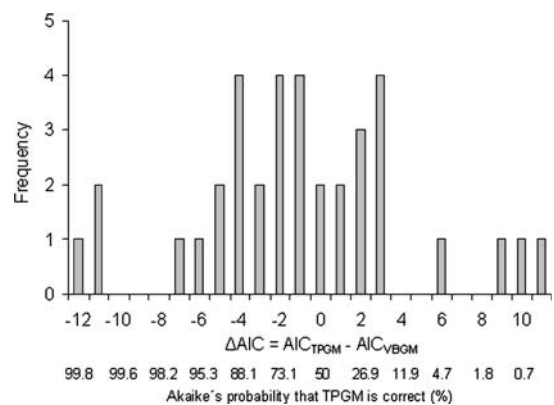

Fig. 4 Frequency distribution of the differences in the AIC between models VBGM and TPGM (ΔAIC) and corresponding Akaike's probability that the TPGM is true
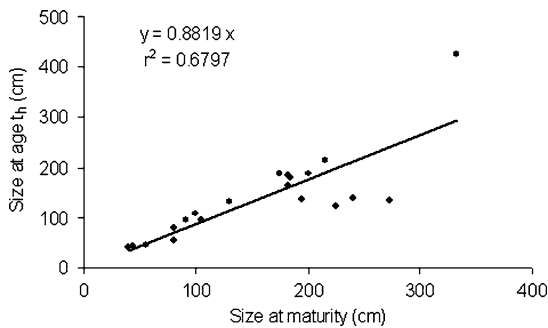
Fig. 5 Relationship between the size at maturity and size at age t_h. The slope is not significantly different from one. The size at maturity of Lamniformes and Carcharhiniformes was obtained from Cortés (2000) and size of Squaliformes and Rajiformes from Froese and Pauly (2004)

The TPGM could be related to the age at first maturity in elasmobranchs. Indeed, length at first maturity of most elasmobranchs coincides with the average length-at-age (i.e. t_h in Fig. 5), where the slope was not significantly different from the unity. In 7 of 10 species, t_h of females was higher than that of males, since females reach maturity at a larger size than males (Cortés 2000).

According to our results, growth in elasmobranchs should be analyzed carefully because the VBGM does not always apply (Cailliet et al. 2006). Many of the elasmobranchs considered in this study seem to follow a different growth pattern, characterized by a decrease in the growth rate in length-at-age at a time that apparently coincides with the onset of maturity. This could result in errors in stock assessments that make use of growth parameters derived from the VBGM, as well as in age-structured models that take into account the average weight and length-at-age.

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