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Kwang-Ming Liu[1,2,3*], Chiao-Bin Wu[1], Shoou-Jeng Joung[3,4], and Wen-Pei Tsai[5]

[1] Institute of Marine Affairs and Resource Management, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224, Taiwan.

[2] George Chen Shark Research Center, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224, Taiwan.

[3]Center of Excellence for the Oceans, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224, Taiwan.

[4]Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224, Taiwan.

[5]Department of Fishery Production and Management, National Kaohsiung Marine University, 2 Haitzuan Road, Kaohsiung 811, Taiwan

*: corresponding author

E-mail: kmliu@mail.ntou.edu.tw

Tel: +886-2-24622192 ext. 5018. Fax: +886-2-24620291

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ABSTRACT

Age and growth information is essential for accurate stock assessment of fish, and growth model selection may influence the result of stock assessment. Previous descriptions of the age and growth of elasmobranches relied mainly on the von Bertalanffy growth model (VBGM). However, it has been noted that sharks, skates and rays exhibit significant variety in size, shape, and life-history traits. Given this variation, the VBGM may not necessarily provide the best fit for all elasmobranches. This study attempts to improve the accuracy of age estimates by testing four growth models—the VBGM, two-parameter VBGM, Robertson (Logistic) and Gompertz models—to fit observed and simulated length-at-age data for 37 species of elasmobranches. The best growth model was selected based on corrected Akaike's Information Criterion (AIC_c), the AIC_c difference, and the AIC_c weight. The VBGM and two-parameter VBGM provide the best fit for species with slow growth and extended longevity ($L_\infty > 100$ cm TL, $0.05 < k < 0.15$ yr^{-1}), such as pelagic sharks. For fast-growing small sharks ($L_\infty < 100$ cm TL, k_r or $k_g > 0.2$ yr^{-1}) in deep waters and for small-sized demersal skates/rays, the Robertson and the Gompertz models provide the best fit. The best growth models for small sharks in shallow waters are the two-parameter VBGM and the Robertson model, while all the species best fit by the Gompertz model are skates and rays.

INTRODUCTION

Most elasmobranches are characterized by a K-selection life history; slow growth, late maturation, extended longevity, few offspring, and low mortality (Hoenig & Gruber, 1990; King & McFarlane, 2003; Winemiller & Rose, 1992). Elasmobranches also take a long time to recover when subjected to high fishing pressure. Three reproductive strategies, oviparity, viviparity, and aplacental viviparity, have been identified for elasmobranches, and a variety of external morphologies, sizes, and life histories have been found. In short, the life history traits, particularly the reproductive traits of elasmobranches, are more complex than those of teleosts, which are mostly oviparous.

Similar to many marine mammals, elasmobranches are among the ocean's top predators, and their life history characteristics make them vulnerable to overexploitation. A collapse of the elasmobranch population could result in imbalances in marine ecosystems (Stevens et al., 2000). Age, growth, and reproduction parameters are crucial for accurate stock assessment and evaluation of their population dynamics (Cailliet et al., 1986, Cailliet & Goldman, 2004). Information on age and growth can be used in natural mortality, longevity, and yield-per-recruit estimates (Ismen, 2003). In the 1950s, Beverton & Holt (1957) first applied the von Bertalanffy growth model (VBGM) to fish population dynamics. However, VBGM may not necessarily provide the best fit for all elasmobranches (Cailliet & Goldman, 2004). Therefore, selecting the most appropriate growth model is important in stock assessment and fishery management of elasmobranches (Gelsleichter et al., 1998).

Four growth models are commonly used in description of age and growth of elasmobranches: the VBGM, the two-parameter VBGM, the Robertson (Logistic) model, and the Gompertz model (Cailliet et al., 2006). Numerous examples exist that used VBGM to estimate the age and growth of elasmobranches. These include studies on the bonnethead shark *Sphyrna tiburo* (Carlson & Parsons, 1997), smalltail shark *Carcharhinus porosus* (Lessa & Santana, 1998), pelagic thresher *Alopias pelagicus* (Liu et al., 1999), whiskery shark *Furgaleus macki* (Simpfendorfer et al., 2000), undulate ray *Raja undulate* (Coelho & Erzini, 2002), Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Carlson & Baremore, 2003), winter skate *Leucoraja ocellata* (Sulikowski et al., 2003), thorny skate *Amblyraja radiate* (Sulikowski et al., 2005), yellownose skate *Dipturus chilensis* (Licandeo et al., 2006), common guitarfish *Rhinobatos rhinobatos* (Ismen et al., 2007), and deepwater lantern shark *Etmopterus spinax* (Coelho & Erzini, 2008).

Although the VBGM is the most commonly-used growth model, others have also been employed. The two-parameter VBGM has been successfully applied in describing growth of the bull shark *Carcharhinus leucas* (Neer et al., 2005) and the female shortfin mako shark *Isurus oxyrinchus* (Chang & Liu, 2009; Semba et al., 2009), for which size-at-birth data are available. An S-sharp model (Gompertz model) has been used to estimate the growth of the Pacific electric ray *Torpedo californica* (Neer & Cailliet, 2001), pelagic stingray *Dasyatis violacea* (Mollet et al., 2002) and Alaska skate *Bathyraja parmifera* (Matta & Gunderson, 2007), while the Robertson (Logistic) model has been used to fit the size-at-age data for the spinner shark *Carcharhinus brevipinna* (Carlson & Baremore, 2005) and the dusky shark *Carcharhinus obscures* (Natanson et al., 2014; Joung et al., 2015).

In some cases, particularly in recent years, a variety of models have been used in age and growth studies of sharks. These include studies on the tiger shark *Galeocerdo cuvier* (Kneebon et al., 2008; Wintner & Dudley, 2000), bull shark *C. leucas* (Wintner et al., 2002), blue shark *Prionace glauca* (Lessa et al., 2004), sandbar shark *C. plumbeus* (Romine et al., 2006), shortfin mako (Natanson et al., 2006), whitespotted bamboo shark *Chiloscyllium plagiosum* (Chen et al., 2007), smooth skate *Malacoraja senta* (Natanson et al., 2007), scalloped hammerhead *S. lewini* (Piercy et al., 2007), sharpspine skate *Okameiei acutispina* (Joung et al., 2011), dusky shark (Simpfendorfer et al., 2002; Natanson et al., 2014; Joung et al., 2015), and spinner shark (Geraghty et al., 2014). The use of different models in fitting length-at-age data is considered preferable. Araya & Cubillos (2006) stated that a two-phase growth model provides a better estimate of elasmobranch growth than the VBGM. This finding was later supported by Braccini et al. (2007) in their study of the piked spurdog *Squalus megalops*.

Chen (pers. comm., 2004) applied several growth models to a variety of teleost species and concluded that the Richards and Robertson models best fit fish with slender and long lateral profiles, while the VBGM and Gompertz model best fit other species. Romney & Campana (2009) examined four skate species and concluded that the VBGM best fit the winter and thorny skate *Amblyraja radiata*, while the Robertson model best fit the little skate, *Raja erinaceian*, and the Gompertz model best fit the smooth skate. Ebert et al. (2007) concluded that the VBGM provided the best fit for the Aleutian skate *Bathyraja aleutica* but that the Bering skate *B. interrupta* was more accurately described by the Robertson model. Katsanevakis

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(2006) also concluded that different growth models best described the growth of different chondrichthyan fish.

Given the influence of growth model selection on the results of stock assessment, in particular, age-structured models, the objectives of this study were twofold: first, to fit the length-at-age data using different growth models, selecting the best model for each species; and second, to group species on the basis of the best-fit model, examine the life history traits for each of these groups, and discuss the possible factors involved. We hope that our findings can provide an important future reference for the selection of the most appropriate growth model for elasmobranches.

MATERIALS AND METHODS

Source of data

This study collected and analyzed the length-at-age data of 37 species, including the observations of vertebral band counts of 7 species in Taiwanese waters and the age-length key data of 30 species from the literature (Table 1). These species fell into 6 orders and 12 families (Table 2). Two species were from Hemiscylliidae and Rhincodontidae (Orectolobiformes), 2 were from Odontaspididae, and Alopiidae (Lamniformes), 19 were from Triakidae, Carcharhinidae, and Sphyrnidae (Carcharhiniformes), 2 were from Etmopteridae (Squaliformes), 11 were from Rhinobatidae and Rajiformes (Rajidae), and 1 was from Dasyatidae (Myliobatiformes). Life history parameters and ecological information, including habitat information, reproductive strategy, fecundity, reproductive cycle (R_c), and size at maturity (L_{mat}), were collected through literature searches in FishBase (http://www.fishbase.net/) as well as from published scientific articles and gray literature.

Data process

In addition to observed length-at-age data, age-length key data adopted from the literature comprised the following data sets: (1) detailed age-specific length distribution data that can be directly fitted by the growth models, (2) age-specific mean length with standard deviation, and (3) age-specific length interval. For data sets 2 and 3, a simulation process was used to generate (mimic) individual observations. For data set 2, a normal random number generator was used to generate 100 sets of observations based on the sample size, mean length, and standard deviation for each age. The simulated data set was adopted when its mean length and standard deviation were equal to the observed values. For data set 3, the length distribution of each age was assumed to be a uniform distribution, and a total of 100 sets of observations were generated from a uniform random number generator based on the sample size and the maximum and minimum length of each age. The simulated data set was adopted when its mean length (the average of the maximum and the minimum length) was equal to the observed value.

The literature reveals an inconsistency in the way that body length is measured. Total length (TL) of 26 species, fork length (FL) of 3 species, precaudal length (PCL) of 7 species, and disc width (DW) of 1 species have all been used. Size-at-birth data were available for 21 of the 37 species (Table 1). Our analysis converted all length data to TL using linear relationships between TL and other measurements.

Data analysis

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Growth models

Three commonly used growth models, the VBGM (von Bertalanffy, 1938), the Robertson (Logistic) (Robertson, 1923) and the Gompertz (Gompertz, 1825), were fitted to the length-at-age data for all species. For those species where size-at-birth data were available, an additional model, the two-parameter VBGM (Fabens, 1965), was also used. The NLIN procedure of the statistical package SAS ver. 9.0 (SAS Institute, 2008, Cary, NC, USA) was used to estimate the parameters of each model. The four growth models are described as follows:

(1) VBGM (von Bertalanffy, 1938)

$$L_t = L_\infty(1-\exp(-k(t-t_0)))$$

(2) Two-parameter VBGM (Fabens, 1965)

$$L_t = L_\infty(1-((L_\infty - L_0)\exp(-kt))/L_\infty)$$

(3) Robertson (Logistic) model (Robertson, 1923)

$$L_t = L_\infty(1+\exp(c_r - k_r t))^{-1}$$

(4) Gompertz model (Gompertz, 1825)

$$L_t = L_\infty \exp(-c_g \times \exp(-k_g t))$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is the growth coefficient, t is the age (year from birth), t_0 is the age at length 0, c_r and k_r are the parameters of the Robertson model, and c_g and k_g are the parameters of the Gompertz model.

Model selection

The goodness of fit of the four growth models was compared based on the corrected Akaike's Information Criterion (AIC_c), the AIC_c difference (ΔAIC_c), and the AIC_c weight (w_i) (Burnham & Anderson 2002). AIC_c was expressed as:

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1},$$

$$AIC = n \times \ln(MSE) + 2K \quad \text{(Akaike 1973)},$$

where n is the total sample size, MSE is the mean square of residuals, and K is the number of parameters estimated in the growth model. The AIC_c difference (ΔAIC_c) of each model was calculated as the difference between $AIC_{c,i}$ and the lowest observed AIC_c value (AIC_{cmin}). Models with ΔAIC_c less than 2 have good support, while those with greater than 10 have no support. The corrected Akaike weight (W_i) is expressed as a percentage, which is useful when there are only minor differences in AIC_c values among the growth models (Burnham & Anderson 2002). AIC_c weights with higher values (indicating a better fit) can be expressed as follows:

$$W_i = \frac{\exp(-0.5\Delta_i)}{\sum_{m=1}^{4}\exp(-0.5\Delta_m)},$$

where m is the number of growth models being analyzed.

RESULTS

VBGM as the best growth model

The VBGM provided the best fit for 4 shark species: the pelagic thresher, blue shark, night shark *Carcharhinus signatus*, and tiger shark; and 2 skates: roundel skate, and blue skate *R. batis* (Table 3). All are large-size sharks or skates except the roundel skate and blue skate. The tiger shark had the highest L_∞ (L_∞ = 364.3 cm TL), while the blue skate had the lowest (L_∞ = 47.6 cm TL). The blue skate had the slowest growth rate (k = 0.024 yr^{-1}), while the roundel skate had the fastest (k = 0.194 yr^{-1}).

Two-parameter VBGM as the best growth model

The two-parameter VBGM provided the best fit for 16 species, of which 13 were sharks and 3 were skates/rays, comprising 52% and 25% of the 25 species of sharks and 12 species of skates/rays, respectively (Fig. 1).

Only the smooth lantern shark, the Atlantic sharpnose shark, and the cuckoo ray *R. naevus* had an L_∞ < 100 cm TL. The remaining species had an L_∞ > 100 cm TL. The silky shark had the highest L_∞ (L_∞ = 315.2 cm TL), while the smooth lantern shark had the lowest (L_∞ = 53.1 cm TL). The Atlantic sharpnose shark had the fastest growth rate (k = 0.582 yr^{-1}), while the gummy shark had the slowest (k = 0.072 yr^{-1}). The exceptionally large-sized whale shark also fell into this group, with L_∞ = 1580 cm TL and k = 0.020 yr^{-1} (Table 4).

Robertson model as the best growth model

The Roberson model provided the best fit for 12 species (Table 5), including 8 sharks and 4 skates/rays, comprising 32% and 33% (Fig. 1) of the sharks and skates/rays in this study, respectively. Five species (42%) were large sharks, 3 species (25%) were small sharks, and 4 species (33%) were skates/rays (Fig. 2).

The thorny skate, blacknose shark *Carcharhinus acronotus*, spinner shark, daggernose shark *Isogomphodon oxyrhynchus*, school shark *Galeorhinus galeus*, and dusky shark fell into the large-size category (L_∞ > 100 cm). The remainder fell into the small-size category (L_∞ < 100 cm). The dusky shark had the largest L_∞ (L_∞ = 362.9 cm), while the deepwater lantern shark had the smallest (L_∞ = 42.3 cm). The little skate had the fastest growth rate (k_r = 0.665 yr^{-1}), while the dusky shark had the slowest (k_r = 0.131 yr^{-1}).

Gompertz model as the best growth model

The Gompertz model (Table 6) provided the best fit for three species, including yellownose skate, winter skate, and Kwangtung skate *Dipturus kwangtungensis* (Fig. 1).. One species was a small skate (33%), and 2 species (67%) were large skates (Fig. 2).

The Kwangtung skate fell into the small-size category (L_∞ < 100 cm). While the yellownose skate and winter skate fell into the large-szie category (L_∞ > 100 cm). as The yellownose skate had the fastest growth rate (k_g = 0.192 yr^{-1}), while the Kwangtung skate had the slowest (k_g = 0.114 yr^{-1}).

In summary, sharks were best fitted by the two-parameter VBGM (52%), while skates/rays were best fitted by the Robertson model (33%). Large sharks were best fitted by the two-parameter VBGM (44%), small sharks were best fitted by the Robertson model (60%), and skates/rays were best fitted by the Robertson model (33%) (Fig. 3). The species best fitted by the Gompertz model were all skates and rays (100%).

DISCUSSION

Cailliet & Goldman (2004) intensively reviewed 115 publications on the age and growth of 91 species of chondrichthyans, and Cailliet et al. (2006) presented updated information on 28 new studies. However, most of these studies did not provide either length-at-age or age-length key data. Thus, only 37 species with either observed length-at-age or age-length key data were used in this study.

Uncertainties

As mentioned above, observed length-at-age data were available for only 7 of 37 species. For the remaining 30 species, figures were generated (simulated) from age-length key data. Because such simulations may not be representative of real observations, there may be inaccuracies in the growth parameter estimates. Some species were represented by a small sample size - the common stingray, sand tiger shark, cuckoo skate, etc. Because of this, and due to a lack of small or large specimens, the size-at-age data may not cover the whole life history of the fish. As a result, estimated parameters might not accurately describe the growth over the entire life history. Cailliet & Goldman (2004) stated that growth parameter estimates are greatly influenced by a lack of very young or old individuals. The existence of length-at-birth information may therefore have a significant effect on the choice of growth model. In this study, the simulated observation data set was adopted only when its mean length and standard deviation were equal to observed values. Several simulations were made for each species and although minor variations in growth parameter estimates were noted, this had no effect on the selection of best-fit growth model.

The basic theory of growth equation

Derived from the allometric relationship between metabolic rate and body weight, the VBGM has been widely used to describe the growth of fish (Haddon, 2001). The ideas underpinning this model are that energy transformation during growth can be expressed as the difference between anabolism and catabolism and that the growth rate decreases exponentially with age (Pütter, 1920). Beverton & Holt (1957) were the first to apply the VBGM to the study of fisheries. The Gompertz model was originally developed to estimate human mortality rates (Gompertz, 1825), while the Robertson model was based on the logistic model used to describe population dynamics and individual growth over time. Both models are S-shaped curves with inflection points occurring at an intermediate age when the growth rate starts to decrease (Wang & Zuidhof, 2004). The inflection point of the Robertson model occurs at 50% of L_∞, but it occurs at approximately 37% of L_∞ for the Gompertz model (Winsor, 1932). Under these two models, growth rates increase with age to a maximum at the inflection points and then decrease thereafter (Ricker, 1975, 1979). Discrepancies in life history among elasmobranch species are likely to affect the result of selecting the best-fit growth model.

Energy allocation in animals can be expressed as $C=R+G+S+W$, where C is energy consumption, R is the catabolic rate, G is growth, S is spawning, and W is waste (Winberg, 1960). Catabolism includes both standard and active forms (e.g., energy consumption when feeding). When more energy is allocated to reproduction and growth, less can be allocated to catabolism and waste, and vice versa. Energy allocation for elasmobranches varies with habitat and reproductive strategies; this may result in differences in growth.

In this study, growth of the bull shark was best described by the two-parameter VBGM. According to Schmid & Murru (1994), the juvenile bull shark allocates most of its energy to catabolism and waste and little to growth. Conversely, the chain dogfish *Scyliorhinus rotifer*, the growth of which was best described by the Robertson model in this study, allocates most of its energy to growth and reproduction (Duffy, 1999). This suggests that small-size species allocate the most energy to growth and reproduction, while the converse is true for large-size species. The fact that the VBGM or two-parameter VBGM best fit large sharks, while the Robertson and Gompertz models best fit small sharks may therefore be related to their energy allocation.

Cailliet & Goldman (2004) suggested that the Gompertz model better describes changes in body weight over time than changes in length. However, this hypothesis cannot be tested because age-at-weight data are not available in the literature. Most sharks are torpedo-shaped and large, while most skates and rays are flat and small. The best growth model might be related to the ratio of size-at-maturity and maximum observed size. Species for which the VBGM and two-parameter VBGM provide the best fit are mostly sharks that tend to be late-maturing (Table 7), e.g., the pelagic thresher shark, bull shark and blacktip shark. Species best fitted by the Robertson and Gompertz models tend, in contrast, to be early-maturing, such as the common stingray, sharpspine skate, and blue skate (Table 7).

Other growth models

The four-parameter Richards growth model is a general form of the VBGM, Robertson, and Gompertz models and is considered superior to the three-parameter growth models (Quinn & Deriso, 1999). However, in this study, the lack of large specimens and the relatively small sample size for certain species may cause the inconvergence of iterations in parameter estimation by non-linear procedures. Araya & Cubillos (2006) used a two-phase growth model (TPGM) to fit for the porbeagle shark *Lamna nasus* and leopard shark *Triakis semisfaciata*. The TPGM is a five-parameter growth model; the additional parameter is the age at which transition between two phases occurs. Because more detailed age-length data are required for this model, it was not applied in this study.

Estimation of parameters

In this study, L_∞ estimates derived by the VBGM and two-parameter VBGM models were larger than those derived by the Robertson and Gompertz models (Fig. 4). A similar finding has been documented by Katsanevakis & Maravelias (2008). Therefore, it seems that L_∞ is closely related to growth model selection.

In this study, the VBGM provided the best fit for 6 species, with estimated k values of 0.024 - 0.194 year^{-1}. All of these are moderate or slow-growing species (k < 0.2 year^{-1}). The two-parameter VBGM model was the best fit for 16 species, with estimated k values of 0.020 - 0.582 year^{-1}. Most of these are also moderate- or slow-growing species (k < 0.2 year^{-1}), the exceptions being the Atlantic sharpnose shark *Rhizoprionodon terraenovae*, finetooth shark *Carcharhinus isodon*, blacktip shark *C. limbatus*, and common guitarfish *Rhinobatos* (k > 0.2 year^{-1}). The Robertson model provided the best fit for 12 species, with estimated k_r values of 0.131-0.667 year^{-1}. Most of these are fast-growing species (k_r > 0.2 year^{-1}), the exception being the dusky shark (k_r < 0.2 year^{-1}). The Gompertz model was the best fit for 3 species, with estimated k_g values of 0.1138-0.1915 year^{-1}. These included moderate-growing species, the yellownose skate, winter skate, and Kwangtung skate (0.1 < k_g < 0.2 year^{-1}). The VBGM and two-parameter VBGM provided the best fit for slow-to moderate-growing species, while the Gompertz model was the best fit for moderate-growing species, and the Robertson model was the best fit for fast-growing species.

Contingency of fitting models

For the 6 species best fitted by the VBGM, the second-best choice was the Gompertz (100%) (Fig. 5). For the two-parameter VBGM (16 species), the second-best choice was VBGM (81%), while for the Robertson (12 species), the second-best choice was the Gompertz (100%). For the Gompertz model (3 species), the second-best choice was the Robertson (67%). In short, the two-parameter VBGM best fits sharks, while the Gompertz model best fits skates and rays. In their study of elasmobranches, Katsanevakis & Maravelias (2008) proposed four growth models in order of fit, as follows: Logistic-Gompertz-VBGM-Power (where Gompertz is the best choice, and Logistic and VBGM are the second-best choices). They concluded that the VBGM provided the best description of growth among elasmobranches and bony fish. Our study arrived at a similar order of growth models, namely Robertson-Gompertz-VBGM-two-parameter VBGM, although it should be noted that the previous study separated species into sharks, skates, and rays. Mollet et al. (2002) found that the best fit for the growth of the pelagic stingray was the Gompertz model. In this study, the growth of skates/rays is best described by the S-shaped Gompertz or Robertson models.

Comparison with literature results

Of the 37 species analyzed in this study, 12 have been previously fitted with more than one growth model in the literature. Of these, our study found the same best growth model for 10 species. The remaining 25 species have previously been described using VBGM alone, but our study found that 19 of these species are better fit by an alternative model. Thorson & Simpfendorfer (2009) have suggested using AIC, AIC weight, and multi-model inference to obtain the most appropriate model to describe fish growth. In this study, the best growth model for each stock was selected based on similar criteria, AIC_c, $\triangle AIC_c$, and the AIC_c weight, suggesting that the derived results are reasonable.

The relationship between life history traits and best growth model

Based on their life history traits, three groups of sharks have been identified using cluster analysis (Liu et al., 2015) as follows. Group 1: large size, extended life span, slow growth, e.g., the silky shark, sandbar shark, scalloped hammerhead shark, and oceanic whitetip shark. These are similar to the species best described in this study by the two-parameter VBGM. Group 2: small size, short life span, rapid growth, e.g., the smooth dogfish and blacknose shark. These are similar to the species best described in this study by the Robertson model. Group 3: late-maturing, moderate life span, e.g., the pelagic thresher shark, tiger shark, blue shark and night shark. These are similar to the species best described in this study by the VBGM. This study found that the Robertson and Gompertz models provided the best fit for skates and rays. Those best described by the Robertson model are characterized by small size and rapid growth, e.g., the thorny skate, common stingray and little skate. Those best described by Gompertz have the characters of small or large size and moderate growth, e.g., the winter skate,yellownose skate, and Kwangtung skate.

As mentioned above, the Orectolobiformes, Lamniformes and large-sized species of Carcharihidae are best fitted by the VBGM or two-parameter VBGM. Rajiformes and Myliobatiformes are best fitted by the Robertson or Gompertz model, while the Robertson model best describes the growth of small-size species of Carcharihidae.

Most species for which the VBGM or two-parameter VBGM provided the best fit are viviparous, while most species best described by the Robertson or Gompertz models are oviparous (Fig. 6). Species best described by the VBGM or two-parameter VBGM models have lower annual fecundity and mature later (higher L_{mat}/L_{∞}) than those best described by the Robertson or Gompertz models (Table 7).

Although VBGM has been widely used in fitting age and length data, where alternative models have not been tried and evaluated, the derived age structure may be biased and inaccurate (Roff, 1980). This will cause further errors in the estimates of mortality, yield per recruit, and stock assessment. If the Robertson or Gompertz models better describe the growth of certain species, variations in different life stages can be considered, and stock assessment will be improved (Carlson & Baremore, 2005).

CONCLUSION

The best growth model for elasmobranches depends on their size and life history characteristics (Fig. 7). VBGM provides the best fit for large pelagic sharks that are late-maturing and of moderate longevity. These include the pelagic thresher and blue sharks. The two-parameter VBGM best fits large pelagic sharks that are slow-growing and have extended longevity, such as the silky and sandbar sharks. The Robertson model is the best fit for fast-growing small sharks that inhabit deep water. For small sharks in shallow waters, the two-parameter VBGM and the Robertson model provide the best description. The Robertson model is also the best fit for medium and small-size demersal skates and rays, which are fast-growing and of short longevity, such as the smooth dogfish and thorny skate. The Gompertz model best fits large or small, median-growing skates and rays, such as the yellow and Kwangtung skates. For the whale shark, with its huge size, slow growth, extended longevity, late maturity, and prolonged reproductive cycle, the two-parameter VBGM provides the best fit.

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Table 1

Age-length data, reproduction strategy and the information of age determination used in the present study

Sample No.	Scientific name	Sample Size	Data source	Length	R	Precision	Verification	Ageing	References
1	*Amblyraja radiate*	224	a	TL	o	CV	MIR	Ver	Sulikowski et al., 2005*
2	*Carcharhinus acronotus*	67	a	FL	v	IAPE	MIR	Ver	Carlson et al., 1999*
3	*C. brevipinna*	258	a	FL	v	IAPE	MIR	Ver	Carlson & Baremore, 2005
4	*C. falciformis*	289	a	PCL	v	-	MIR	Ver	Oshitani et al., 2003
5	*C. isodon*	240	a	TL	v	-	MIR	Ver	Carlson et al., 2003
6	*C. leucas*	117	a	PCL	v	IAPE	MIR	Ver	Wintner et al., 2002
7	*C. longimanus*	107	a	TL	v	IAPE	MIR	Ver	Lessa et al., 1999
8	*C. plumbeus*	186	a	PCL	v	IAPE	MIR	Ver	Romine et al., 2006
9	*C. porosus*	504	a	TL	v	IAPE	MIR	Ver	Lessa & Santana, 1998
10	*Dasyatis pastinaca*	49	a	TL	ov	IAPE	MIR	Ver	Ismen, 2003
11	*Dipturus chilensis*	400	a	TL	o	IAPE	MIR	Ver	Licandeo et al., 2006*
12	*Etmopterus pusillus*	523	a	TL	ov	IAPE, CV	MIR	Sp	Coelho & Erzini, 2007
13	*Etmopterus spinax*	733	a	TL	ov	IAPE, CV	MIR	Sp	Coelho & Erzini, 2008
14	*Galeocerdo cuvier*	90	a	PCL	v	IAPE	MIR	Ver	Wintner & Dudley, 2000*
15	*Isogomphodon oxyrhynchus*	105	a	TL	ov	IAPE	MIR	Ver	Lessa et al., 2000*
16	*Leucoraja ocellata*	209	a	TL	o	IAPE	MIR	Ver	Sulikowski et al., 2003
17	*Odontaspis taurus*	52	a	TL	v	-	MIR	Ver	Branstetter & Mustck, 1994
18	*Raja texana*	231	a	TL	o	IAPE	MIR	Ver	Sulikowski et al., 2007*
19	*Rhizoprionodon terraenovae*	804	a	PCL	v	IAPE	MIR	Ver	Loefer & Sedberry, 2003
20	*Sphyrna lewini*	307	a	FL	v	IAPE	MIR	Ver	Piercy et al., 2007
21	*Mustelus griseus*	207	a	TL	v	IAPE	MIR	Ver	Wang & Chen, 1982*
22	*Carcharhinus limbatus*	92	a	PCL	v	IAPE	MIR	Ver	Wintner & Cliff, 1996
23	*Rhinobatos rhinobatos*	80	a	TL	o	IAPE	MIR	Ver	Ismen et al., 2007
24	*Galeorhinus galeus*	395	b	TL	ov	IAPE	MIR	Ver	Moulton et al.,1992*
25	*M. antarcticus*	516	b	TL	ov	IAPE	MIR	Ver	Moulton et al.,1992*
26	*Raja batis*	81	b	TL	o	IAPE	MIR	Ver	Du Buit, 1977*
27	*R. naevus*	48	b	TL	o	IAPE	MIR	Ver	Du Buit, 1977
28	*R. erinaceian*	777	b	TL	o	IAPE	MIR	Ver	Waring, 1984*
29	*R. undulata*	182	b	TL	o	-	MIR	Ver	Coelho & Erzini, 2002
30	*Carcharhinus signatus*	317	b	TL	v	IAPE	MIR	Ver	Santana & Lessa, 2004*
31	*Alopias pelagicus*	269	c	PCL	v	-	MIR	Ver	Liu et al., 1999*
32	*D. kwangtungensis*	394	c	TL	o	-	MIR	Ver	Joung et al., 2015*
33	*P. glauca*	431	c	TL	v	IAPE	MIR	Ver	Huang, 2006*
34	*Okamejei acutispina*	329	c	DW	o	-	MIR	Ver	Joung et al., 2011
35	*Chiloscyllium plagiosum*	429	c	TL	o	IAPE, PA	MIR	Ver	Chen et al., 2007
36	*C. obscurus*	387	c	TL	v	-	MIR	Ver	Joung et al., 2015*
37	*Rhincodon typus*	84	c	TL	ov	-	MIR	Ver	Hsu,2009

"a" : sample simulation, "b" : age-length-key, "c" : original data, "Ver" : vertebrae, "Sp" : spines, * : no L_0, "R" : reproduction strategy, "o" : oviparity, "v" : viviparity, "ov" : aplacental viviparity, "CV" : coefficient of variation, "PA" : percent agreement, "IAPE" : index of average percentage error, "MIR" : marginal increment ratio analysis.

Table 2

A list of elasmobranches used in the present study

Order	**Family**	**Scientific name**	**Common name**
Orectolobiformes	Hemiscylliidae	*Chiloscyllium plagiosum*	Whitespotted Bamboo Shark
	Rhincodontidae	*Rhincodon typus*	Whale shark
Lamniformes	Odontaspididae	*Odontaspis taurus*	Sand tiger shark
	Alopiidae	*Alopias pelagicus*	Pelagic thresher shark
Carcharhiniformes	Triakidae	*Galeorhinus galeus*	School shark
		Mustelus antarcticus	Gummy shark
		M. griseus	Smooth dogfish
	Carcharhinidae	*Carcharhinus acronotus*	Blacknose shark
		C. brevipinna	Spinner shark
		C. falciformis	Silky shark
		C. isodon	Finetooth shark
		C. leucas	Bull Shark
		C. limbatus	Blacktip shark
		C. longimanus	Oceanic whitetip shark
		C. obscurus	Dusky shark
		C. plumbeus	Sandbar shark
		C. porosus	Smalltail shark
		C. signatus	Night shark
		Galeocerdo cuvier	Tiger shark
		Isogomphodon oxyrhynchus	Daggernose shark
		Prionace glauca	Blue shark
		Rhizoprionodon terraenovae	Atlantic sharpnose shark
	Sphyrnidae	*Sphyrna lewini*	Scalloped hammerhead shark
Squaliformes	Etmopteridae	*Etmopterus pusillus*	Smooth lantern shark
		E. spinax	Deepwater lantern shark
Rajiformes	Rhinobatidae	*Rhinobatos rhinobatos*	Common guitarfish
	Rajidae	*Amblyraja radiata*	Thorny skate
		Leucoraja ocellata	Winter skate
		Raja batis	Blue skate
		R. erinaceian	Little skate
		D. kwangtungensis	Kwangtung skate
		R. naevus	Cuckoo ray
		R. texana	Roundel skate
		R. undulata	Undulate ray
		Okamejei acutispina	Sharpspine skate
Myliobatiformes	Dasyatidae	*Dasyatis pastinaca*	Common stingray

Table 3

Growth parameters of the species best fitted by VBGM. Parenthese indiccate standard errors.

Scientific name	**Common name**	**L_∞**	**(cm)**	**k**	**(yr^{-1})**	**t_0**	
Galeocerdo cuvier	Tiger shark	364.3	(48.62)	0.1181	(0.0360)	-2.300	(0.6808)
Raja texana	Roundel skate	66.8	(4.84)	0.1944	(0.0449)	-1.071	(0.5341)
Raja batis	Blue skate	47.6	(8.31)	0.0240	(0.0055)	-2.502	(0.3027)
Carcharhinus signatus	Night shark	303.9	(23.12)	0.0746	(0.0132)	-4.947	(0.6565)
Alopias pelagicus	Pelagic thresher shark	189.5	(7.25)	0.1001	(0.0152)	-6.469	(0.9374)
Prionace glauca	Blue shark	355.8	(7.84)	0.1328	(0.0081)	-1.522	(0.1819)

L_∞: asymptotic length, k: growth coefficient, t_0: theoretical age at zero length.

Table 4

Growth parameters of the species best fitted by the two-parameter VBGM. Parenthese indiccate standard errors.

Scientific name	**Common name**	L_∞	**(cm)**	**k**	**(yr^{-1})**	L_0
Carcharhinus falciformis	Silky shark	315.2	(10.16)	0.0732	(0.0035)	56.1
Carcharhinus isodon	Finetooth shark	144.46	(31.25)	0.3015	(0.0221)	64.2
Carcharhinus leucas	Bull shark	255.9	(4.61)	0.1407	(0.0099)	47.0
Carcharhinus longimanus	Oceanic whitetip shark	271.2	(13.80)	0.1114	(0.0124)	82.0
Carcharhinus plumbeus	Sandbar shark	160.2	(4.41)	0.0815	(0.0057)	52.1
Etmopterus pusillus	Smooth lantern shark	53.1	(0.69)	0.1365	(0.0043)	16.3
Odontaspis Taurus	Sand tiger shark	299.5	(9.79)	0.1782	(0.0161)	100.0
Rhizoprionodon terraenovae	Atlantic sharpnose shark	74.9	(4.41)	0.5815	(0.0210)	32.1
Sphyrna lewini	Scalloped hammerhead shark	219.9	(4.11)	0.1198	(0.0063)	41.1
Carcharhinus limbatus	Blacktip shark	193.6	(7.01)	0.2084	(0.0206)	41.0
Rhinobatos rhinobatos	Common guitarfish	153.6	(29.39)	0.2058	(0.0636)	31.0
Mustelus antarcticus	Gummy shark	206.2	(11.22)	0.0715	(0.0070)	63.7
Raja naevus	Cuckoo ray	95.1	(6.02)	0.0996	(0.0112)	14.5
Raja undulata	Undulate ray	110.1	(4.25)	0.1049	(0.0074)	21.6
Chiloscyllium plagiosum	Whitespotted bamboo shark	106.3	(4.57)	0.1721	(0.0131)	15.0
Rhincodon typus	Whale shark	158.0	(30.49)	0.0197	(0.0048)	57.9

L_∞: asymptotic length, k: growth coefficient, L_0: size at birth.

Table **5**

Growth parameters of the species best fitted by the Robertson model. Parenthese indiccate standard errors.

Scientific name	**Common name**	**L_∞**	**(cm)**	**k_r**	**(yr^{-1})**	**c_r**	
Amblyraja radiate	Thorny skate	110.2	(1.96)	0.2664	(0.0113)	1.521	(0.0418)
Carcharhinus acronotus	Blacknose shark	104.8	(4.13)	0.6302	(0.0917)	0.764	(0.0926)
Carcharhinus brevipinna	Spinner shark	188.4	(4.70)	0.2415	(0.0122)	0.735	(0.0607)
Carcharhinus porosus	Smalltail shark	98.9	(1.54)	0.3113	(0.0105)	0.706	(0.0317)
Dasyatis pastinaca	Common stingray	93.4	(3.50)	0.3158	(0.0171)	1.272	(0.0880)
Etmopterus spinax	Deepwater lantern shark	42.3	(0.58)	0.3730	(0.0097)	0.885	(0.0314)
Isogomphodon oxyrhynchus	Daggernose shark	151.2	(5.22)	0.2803	(0.0242)	0.664	(0.0638)
Mustelus griseus	Smooth dogfish	90.4	(2.13)	0.3518	(0.0248)	0.699	(0.0406)
Galeorhinus galeus	School shark	159.8	(3.26)	0.2567	(0.0201)	0.579	(0.0389)
Raja erinaceian	Little skate	49.5	(0.35)	0.6665	(0.0215)	0.930	(0.0211)
Okamejei acutispina	Sharpspine skate	31.7	(1.00)	0.3343	(0.0301)	1.290	(0.0615)
Carcharhinus obscurus	dusky shark	362.9	(8.56)	0.1306	(0.0079)	0.911	(0.0462)

L_∞: asymptotic length, k_r: growth coefficient of Robertson model, c_r: Roberson parameter.

Table **6**

Growth parameters of the species best fitted by the Gompertz model. Parenthese indiccate standard errors.

Scientific name	**Common name**	**L_∞**	**(cm)**	**k_g**	**(yr^{-1})**	**c_g**	
Dipturus chilensis	Yellownose skate	113.9	(2.12)	0.1915	(0.0136)	0.581	(0.0336)
Leucoraja ocellata	Winter skate	102.1	(1.61)	0.1531	(0.0048)	0.592	(0.0162)
Dipturus kwangtungensis	Kwangtung skate	96.7	(16.18)	0.1138	(0.0195)	0.621	(0.1729)

L_∞: asymptotic length, k_g: growth coefficient of Gompertz model, c_g: Gompertz parameter.

Table **7**

The parameters of maturity and reproduction of elasmobranches in each best model

Scientific name	Model	L_{mat}	L_{mat}/L_{∞}	f	R_c	f/R_c	References
Alopias pelagicus	V	287.00	0.78	2.00	1.00	2.00	Liu et al., 1999
C. brevipinna	R	222.50	0.83	8.50	2.00	4.25	Carlson & Baremore, 2005
C. limbatus	V_2	212.37	0.81	8.00	2.00	4.00	Wintner & Cliff, 1996
Dasyatis pastinaca	R	46.00	0.49	5.50	1.00*	5.50	Ismen, 2003
Okamejei acutispina	R	26.23	0.56	9.00	1.00*	9.00	Joung et al., 2011
Raja batis	V	130.75	0.50	40.00	1.00*	40.00	Du Buit, 1977
R. naevus	V_2	47.00	0.62	102.00	1.00	102.00	Du Buit, 1977

V: VBGM, V_2: two-parameter VBGM, R: Robertson model, G: Gompertz model, L_{mat}: size at maturity, L_{mat}/L_{∞}: ratio of size at maturity and asymptotic length, f: fecundity, R_c: reproductive cycle, f/R_c: annual fecundity.*: Reproductive cycle is assumed to be 1 year

Figure legend

Fig 1

The percentage of four growth models being selected as the best model, categorized by sharks, skates and rays.

Fig 2

The percentage of large sharks, small sharks and skates and rays in each best fit growth model.

Fig 3

The percentage of best growth model for each group.

Fig 4

The relationship between asymptotic length estimated from each growth model and averaged asymptotic length.

Fig 5

The second-best choice for each best growth model.

Fig 6

The percentage of reproduction types for each best growth model.

Fig 7

The flow chart of selecting the best growth model for elasmobranches.

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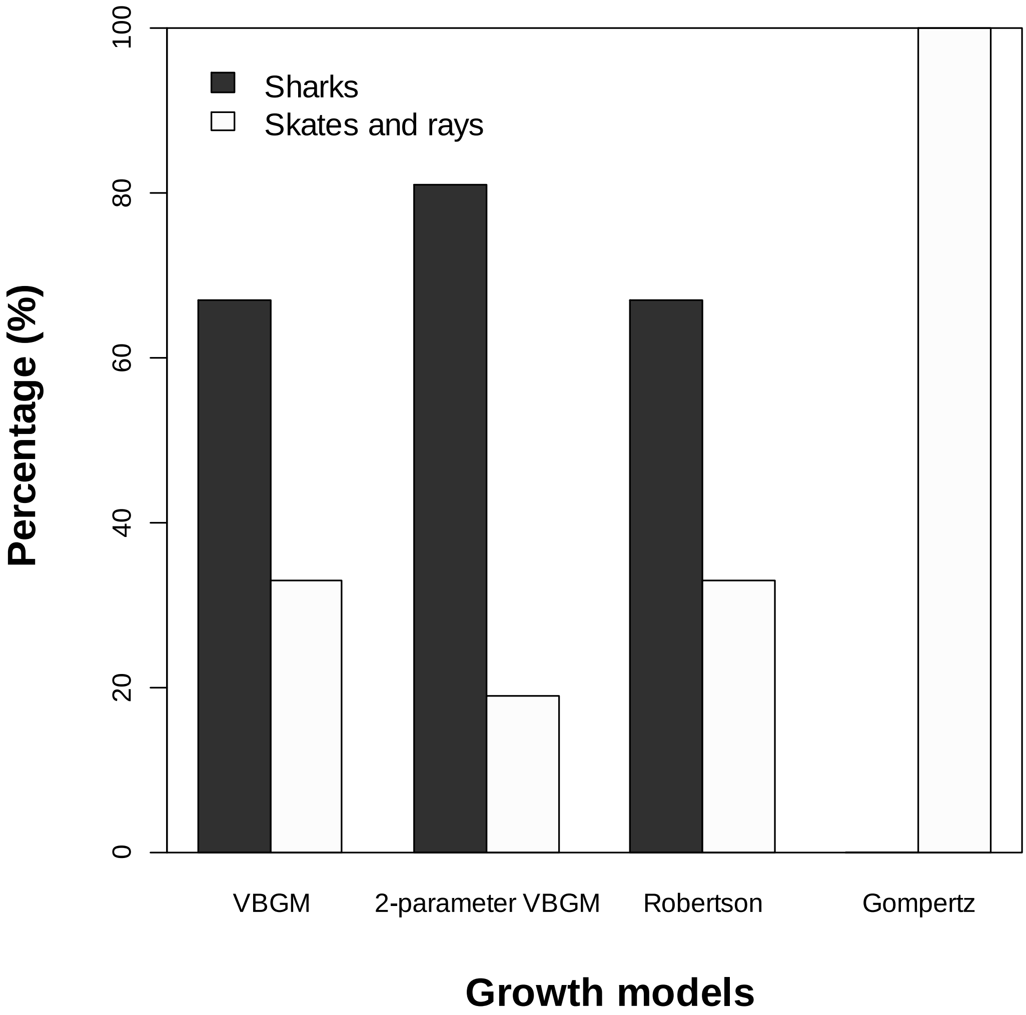


Figure 1 The percentage of four growth models being selected as the best model, categorized by sharks, skates and rays.

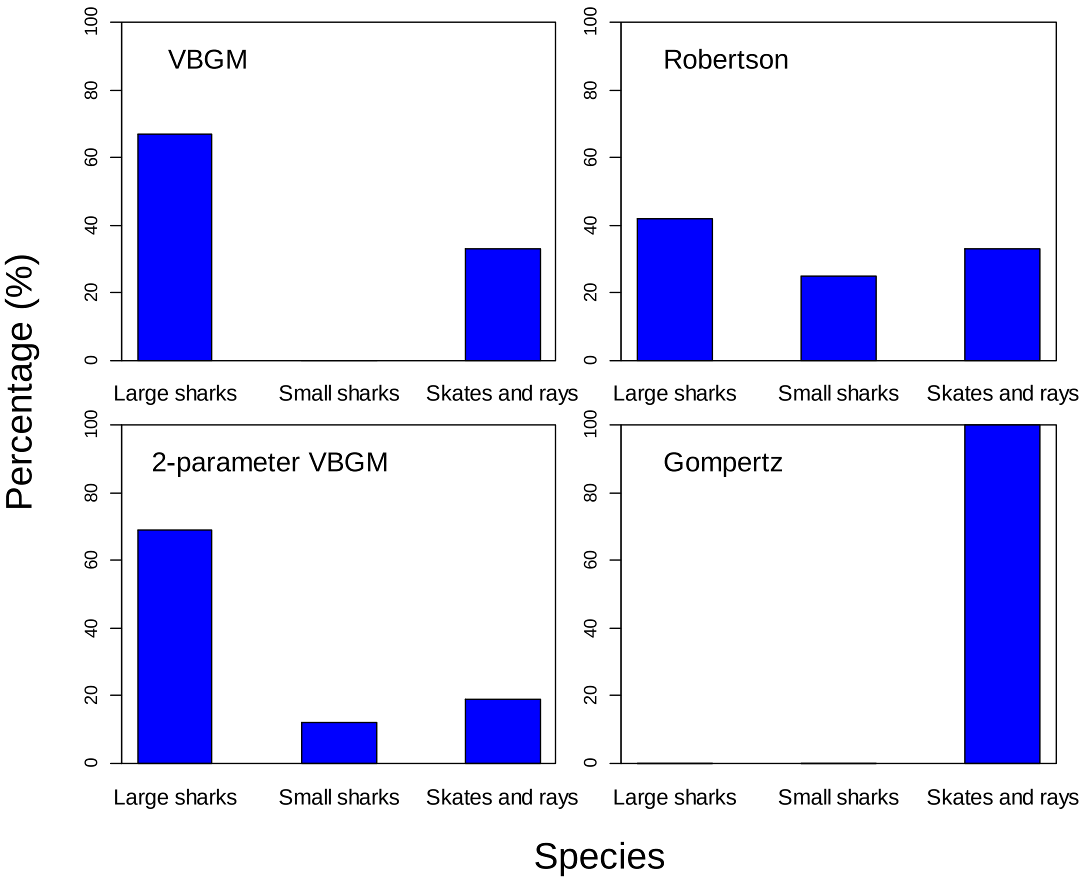


Figure 2 The percentage of large sharks, small sharks and skates and rays in each best fit growth model.

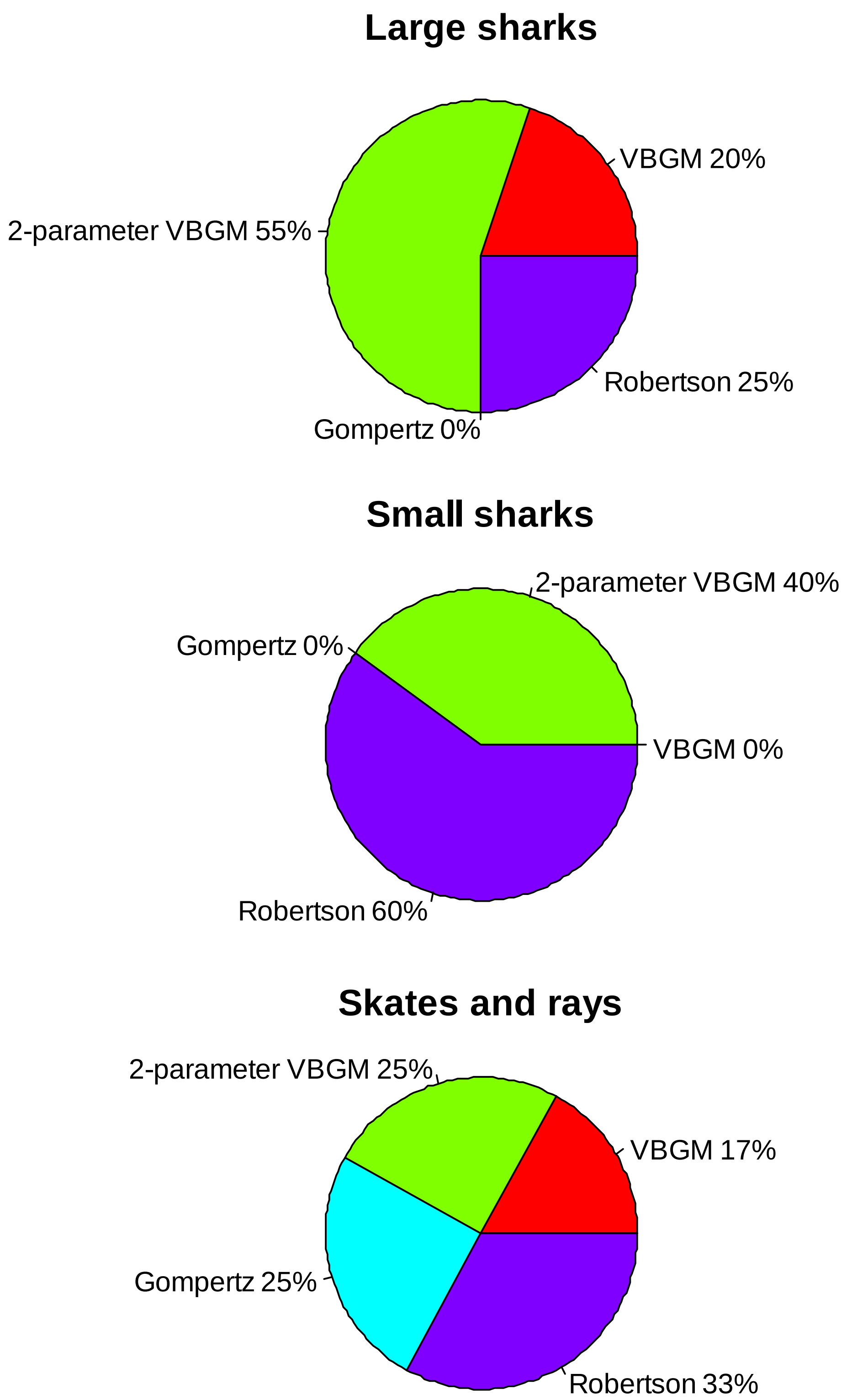


Figure 3 The percentage of best growth model for each group.

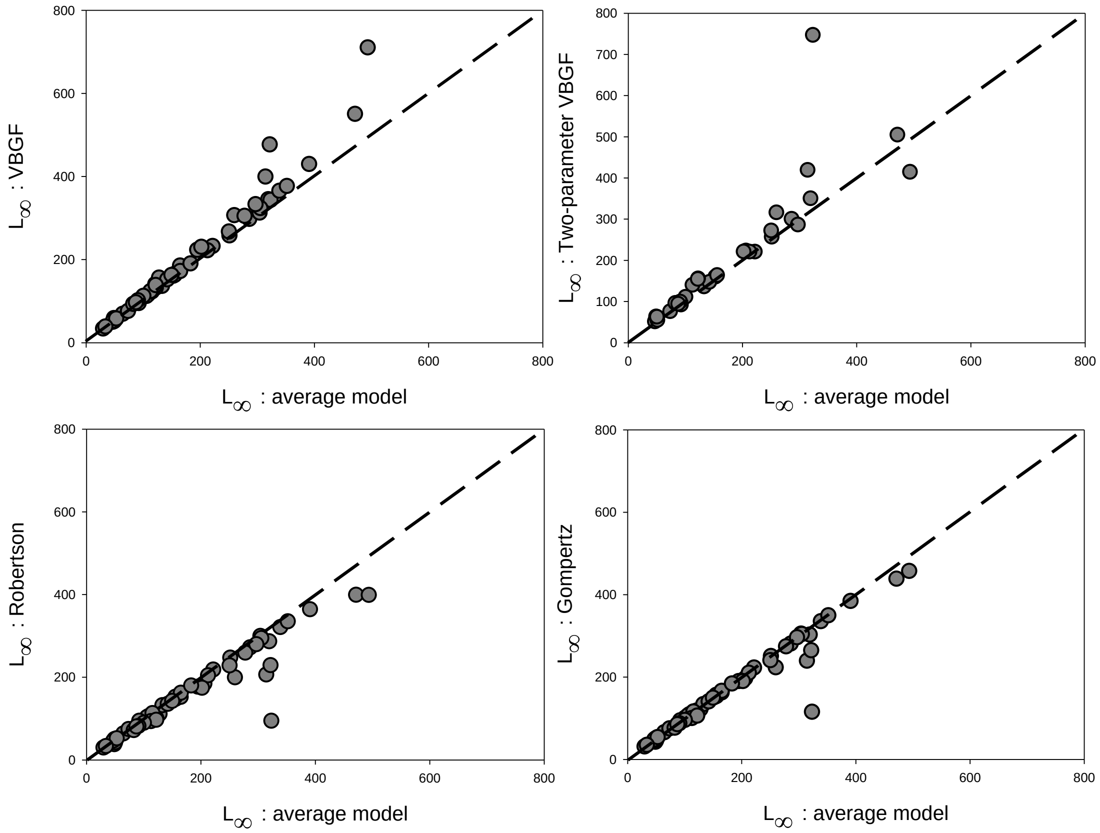


Figure 4 The relationship between asymptotic length estimated from each growth model and averaged asymptotic length.

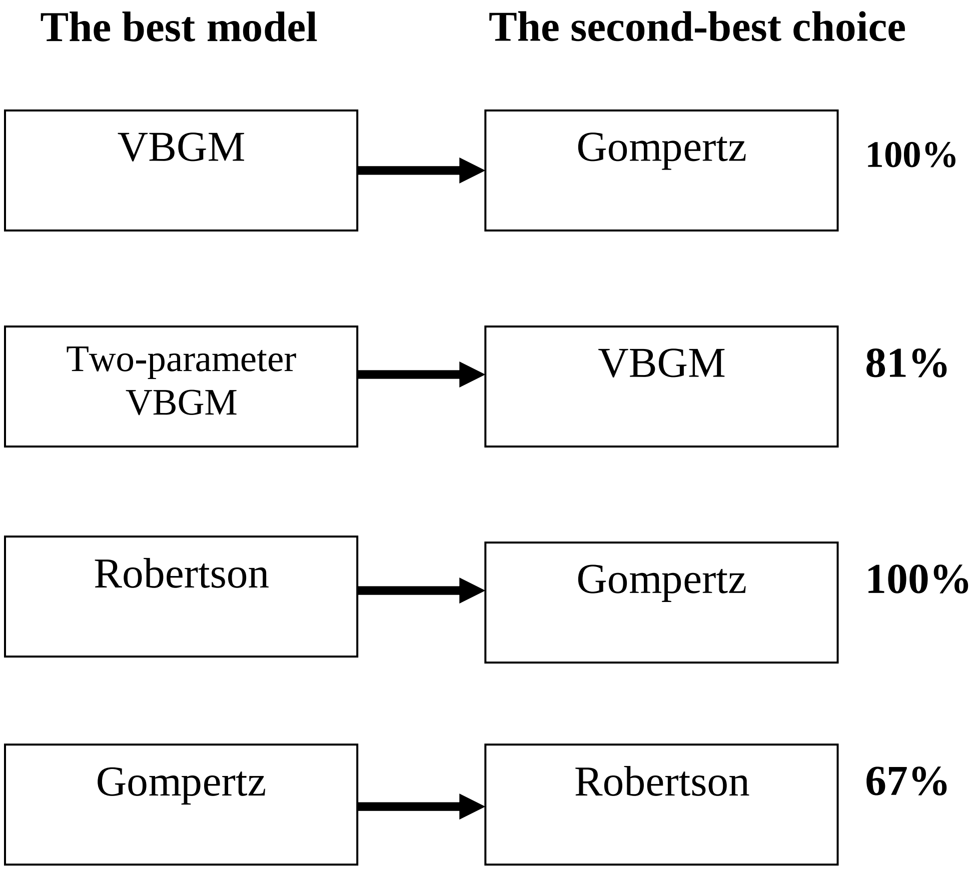
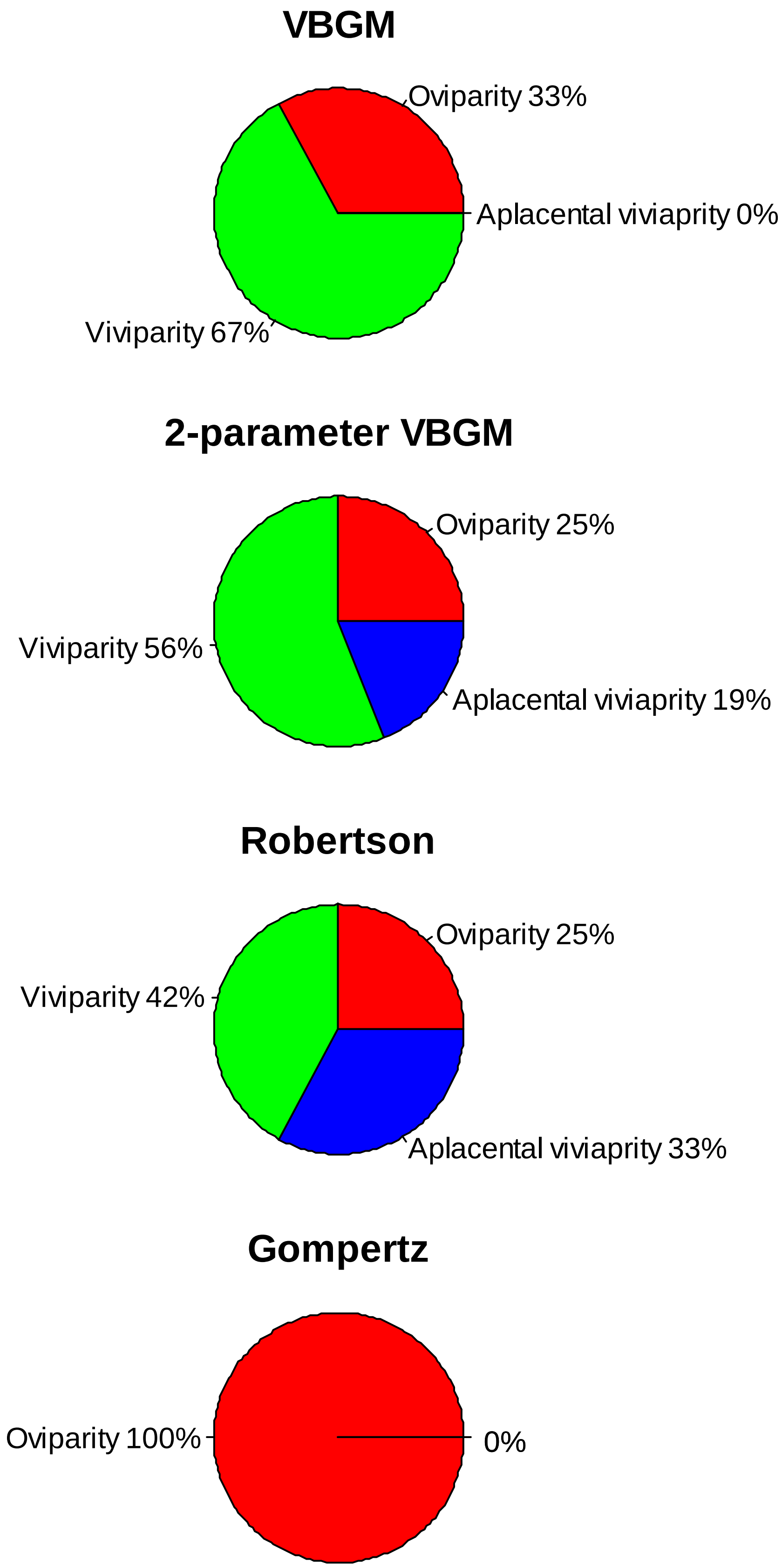


Figure 5 The second-best choice for each best growth model.



870
871 Figure 6 The percentage of reproduction types for each best growth model.

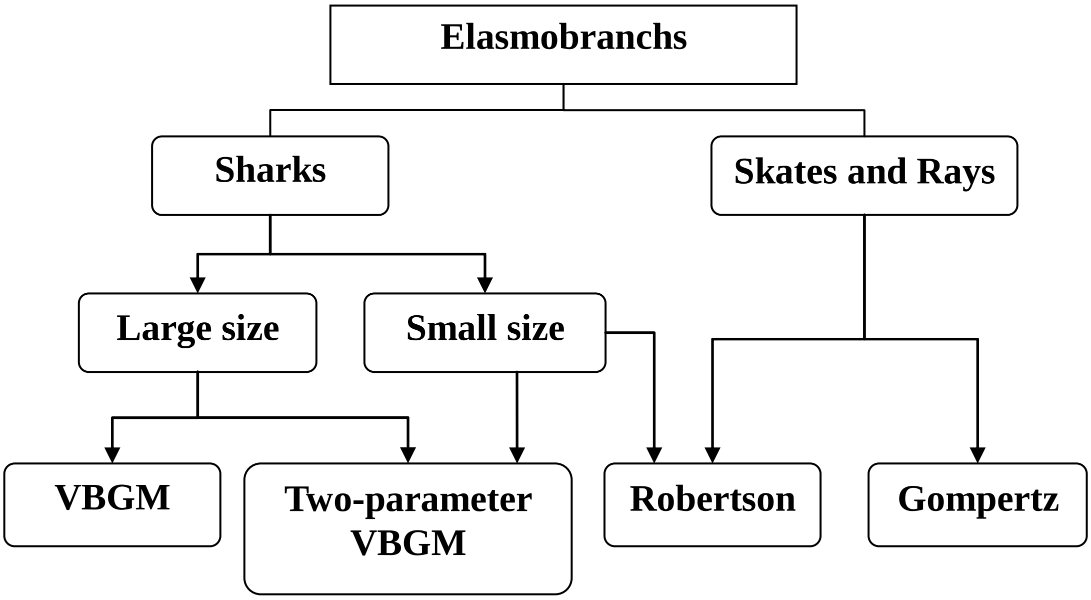


Figure 7 The flow chart of selecting the best growth model for elasmobranches.