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Estimating growth from tagging data: an application to north-east Atlantic tope shark *Galeorhinus galeus*

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This study addresses the inherent uncertainty when estimating growth from limited mark–recapture information. A selection procedure was developed utilizing 18 competing growth estimation methods. The optimal method for a given data set was identified by simulating the length at capture and recapture under different scenarios of measurement error and growth variability while considering the structure of observed data. This selection procedure was applied to mark–recapture data for 37 female and 16 male tope sharks *Galeorhinus galeus* obtained from tagging studies in the north-east Atlantic Ocean. Parameter estimates differed strongly among methods, showing the need for careful method selection. The selection approach suggested that best estimates for males and females were given by James' weighted least-squares approach with a fixed asymptote. Given an average total length (L_T) at birth of 28 cm, the von Bertalanffy growth function of north-east Atlantic *G. galeus* would be $L_T = 200{\cdot}85 - (200{\cdot}85 - 28)e^{-0{\cdot}076t}$ for females and $L_T = 177{\cdot}30 - (177{\cdot}30 - 28)e^{-0{\cdot}081t}$ for males. The resulting age estimates were up to 11 years lower when compared with previous estimates derived from highly uncertain vertebrae readings. More generally, this procedure can help identify optimal estimation methods for a given data set and therefore aid in estimating more reliable growth parameters from mark–recapture information.

Key words: age; growth; mark–recapture; method; von Bertalanffy.

INTRODUCTION

Growth of individuals is a key aspect in fisheries science as it determines the gain of biomass for a particular stock. In 1938, von Bertalanffy published a model that allows predicting the length of an organism from its age, which has become the most commonly used approach to estimate growth of both bony and chondrichthyan fishes (Cailliet & Goldman, 2004). In sharks, most growth studies use length-at-age data obtained from growth-band deposition in vertebrae that assumes periodic ring formation (Cailliet & Goldman, 2004). Although the periodicity of ring formation is often not tested, many sharks are believed to have annual band deposition (Cailliet & Goldman, 2004; Cailliet, 2015). For some shark species, however, age obtained from vertebrae band readings can be misleading due to irregular formation or decay of annual growth bands (Natanson & Cailliet, 1990; Kalish & Johnston, 2001; Campana *et al.*, 2002; Ardizzone *et al.*, 2006; Francis *et al.*, 2007; Andrews *et al.*, 2011; Hamady *et al.*, 2014; Natanson *et al.*, 2014). Tope shark *Galeorhinus galeus* (L. 1758) is considered to be

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*Author to whom correspondence should be addressed: Tel.: +1 902 494 2478; email: Manuel.Dureuil@Dal.Ca such a species (Kalish & Johnston, 2001), requiring alternative approaches to estimate growth.

Although tagging studies primarily focus their research on distribution and movement, these studies can also provide information on a variety of biological aspects, including growth (Kohler & Turner, 2001). Approaches for estimating growth based on mark–recapture tagging data use differential length measurements (Gulland & Holt, 1959; Fabens, 1965; Francis, 1988*a*) and have been applied to several shark species (Simpfendorfer, 2000; Skomal & Natanson, 2003; Meyer *et al.*, 2014). These methods, however, can produce different results for the same data set and can give biased results if growth is variable, time at liberty is short, or the sample size is small, outlier contaminated or not representative of all age classes (Sainsbury, 1980; Francis, 1988*b*; Maller & deBoer, 1988; Kimura *et al.*, 1993; Wang & Thomas, 1995; Simpfendorfer, 2000; Natanson *et al.*, 2002, 2006; Skomal & Natanson, 2003; McAuley *et al.*, 2006; Eveson *et al.*, 2007). Currently, it remains unclear which method performs best for a given data set, in particular when only limited data is available.

Here, a procedure to help select the best performing growth estimation method for a given mark–recapture data set was developed. A simulation analysis with known input parameters for growth was used, which considered sample size, length and time at liberty distributions, *i.e.* the structure of the data, as well as individual growth variability (GV) and measurement error (ME). From this, the best performing method was identified and applied to a small data set containing tagging information for *G. galeus* in the north-east Atlantic Ocean.

The north-east Atlantic stock of *G. galeus* ranges from the North Sea to north-west Africa and the Mediterranean Sea (ICES, 2009). In this region, this species is classified as data deficient on the IUCN Red List (Walker *et al.*, 2006) and an analytical assessment is missing (ICES, 2014). Despite reliable catch data, information about life history of *G. galeus* is also lacking. Growth studies have been undertaken for *G. galeus* stocks elsewhere (Grant *et al.*, 1979; Ferreira & Vooren, 1991; Moulton *et al.*, 1992; Francis & Mulligan, 1998; McCord, 2005), but to date, only one study has examined age structure of this stock based on vertebral samples of four males (Henderson *et al.*, 2003). Therefore, the aim of this study was to determine growth parameters of *G. galeus* in the north-east Atlantic Ocean. This can aid in future assessment and may help to better understand this species' resilience to exploitation.

MATERIALS AND METHODS

GROWTH ESTIMATION METHODS

All growth curves were fitted using the von Bertalanffy growth function (von Bertalanffy, 1938):

$$L_t = L_\infty - \left(L_\infty - L_0\right) e^{-kt} \tag{1}$$

where L_t is the total length (L_T; cm) at age t (years), L_∞ is the asymptotic L_T, L_0 is the L_T at birth and k is a curve parameter describing how fast L_∞ is approached. Capapé *et al.* (2005) found L_0 for *G. galeus* to range between 24 and 32 cm with a mean ± s.d. of 28·05 ± 2·68 cm, thus L_0 was set to 28 cm. In total, 18 different variants of the von Bertalanffy growth function were considered, based on seven broader growth estimation methods for mark–recapture data (Table I).

TABLE I. Summary of the different methods considered to estimate growth of *Galeorhinus galeus* from tagging data. In total, 18 different approaches were investigated, based on seven broader growth estimation methods. The equations of the latter are provided. For the methods that did not consider growth variability, it was investigated if variants with a fixed value of the asymptotic length L_∞ (*fix*) can reduce bias in parameter, in addition to the basic methods. The value used as fixed asymptotic length was obtained from its relationship to the species' maximum length $L_{\max}$. For the methods that did not consider heteroscedasticity, it was investigated if variants utilizing a natural logarithm (ln−ln) transformed error structure (*e*) can produce better parameter estimates, in addition to the basic methods. Note that the delta-*t* method with a fixed asymptote (*dtfix*) requires the lengths at capture and recapture to be smaller than, the ln−ln transformed Fabens and Gulland and Holt methods with a fixed asymptote (*fabfixe*, *GHfixe*) require the length at capture to be smaller than L_∞

Symbol	Name	Equations*	Variants	Fixed parameters	Estimated parameters	Reference
GH	Gulland and Holt method	$\frac{\delta L}{\delta t} = a + bL_{\text{mean}}$	*GHe*		L_∞, k	Sparre & Venema (1999)
		$L_{\text{mean}} = (L_{\text{r}} + L_{\text{c}})2^{-1}$	*GHfix*	$L\infty$	k	
		$k = -b, L_\infty = -ab^{-1}$	*GHfixe*	$L\infty$	k	
fab	Fabens method	$\delta L = (L_\infty - L_{\text{c}})(1 - e^{(-k\delta t)})$	*fabe*		L_∞, k	Fabens (1965)
			fabfix	$L\infty$	k	
			fabfixe	$L\infty$	k	
wfab	Weighted Fabens method	$\sum\{[L_{\text{r}} - L_{\text{c}} - (L_\infty - L_{\text{c}})(1 - e^{(-k\delta t)})]^2(1 + e^{(-2k\delta t)})^{-1}\}$	*wfabfix*	$L\infty$	k	James (1991)
δt	Delta-*t* method	$\delta t = -k^{-1}\ln[(L_\infty - L_{\text{r}})(L_\infty - L_{\text{c}})^{-1}]$	*dte*		L_∞, k	This study
			dtfix	$L\infty$	k	
			dtfixe	$L\infty$	k	
jam	James method	$\sum\left[L_{\text{r}} - L_{\text{c}} - \left(L_\infty - L_{\text{c}}\right)\left(1 - e^{(-k\delta t)}\right)\right] = 0,$ $\sum\delta t\left[L_{\text{r}} - L_{\text{c}} - \left(L_\infty - L_{\text{c}}\right)\left(1 - e^{(-k\delta t)}\right)\right] = 0$			L_∞, k	James (1991)
wan	Wang method	$\delta L = \left[L_\infty + \beta\left(L_{\text{c}} - \overline{L}_{\text{c}}\right) - L_{\text{c}}\right]\left(1 - e^{(-k\delta t)}\right)$	*wane*		L_∞, k	Wang (1998)
fra	Francis method	$\delta L = \left[\left(L_2 g_{L_1} - L_1 g_{L_2}\right)\left(g_{L_1} - g_{L_2}\right)^{-1} - L_c\right]$ $\left\{1 - \left[1 + \left(g_{L_1} - g_{L_2}\right)\left(L_1 - L_2\right)^{-1}\right]^{\delta t}\right\}$ $k = -\ln\left[1 + \left(g_{L_1} - g_{L_2}\right)\left(L_1 - L_2\right)^{-1}\right]$ $L_\infty = \left(L_2 g_{L_1} - L_1 g_{L_2}\right)\left(g_{L_1} - g_{L_2}\right)^{-1}$			L_∞, k	Francis (1988*a*)

*Descriptions: all length L are total length (L_{T} cm). The variable δL is the growth increment, δt is the time at liberty (years), b is the slope, a the intercept, L_{C} is the length at capture, L_{r} is the length at recapture, k is the von LBertalanffy growth constant, L_∞ is the asymptotic length, the parameter β allows L_∞ to vary, L_{c}^{-} is the mean length at capture, and g_{L1} and g_{L2} are estimated mean growth rates at two user selected reference lengths L_1 and L_2.

The Gulland and Holt (1959) method uses the graphical interpretation of annual growth increments and mean length to estimate von Bertalanffy growth parameters (VBGP). This method was applied as described by Sparre & Venema (1999). The Fabens method (Fabens, 1965) uses a least-squares method to estimate growth parameters k and L_∞. James (1991) proposed to use a weighted least-squares approach of the Fabens method, instead of ordinary least squares. The weighting factor of the weighted Fabens method is the inverse variance. In addition to the Fabens method, which solves for length increments, a transformed version was tested, the delta-t method. This method minimizes the residual sum of squares between the observed and predicted time at liberty. The James method is another estimator suggested by James (1991) to obtain unbiased parameters by solving two equations simultaneously instead of using a least-squares approach. A joint solution for both equations was obtained by the Newton–Raphson method of the *rootSolve* package (Soetaert, 2009) in the statistical software R (R Core Team, 2013). The Wang method (Wang, 1998) considers GV by letting the asymptotic length vary. Therefore, an additional parameter to Fabens' equation is introduced. The Francis method (Francis, 1988*a*) is an extension to the Fabens method using a maximum likelihood approach. This function includes two estimated mean growth rates g_{L_1} and g_{L_2} at two user-selected reference lengths L_1 and L_2. These reference lengths should lie within the length-at-capture range. In this study, the mean of the three smallest and largest values of length at capture was used for the smaller and larger reference lengths, respectively. The Francis method also allows the estimation of GV, the mean and S.D. of MEs (m and s), the probability of outlier contamination (p) and the seasonality of growth. The latter was not considered here. Overall, up to six parameters were estimated by this method (model 1: g_{L_1}, g_{L_2} and s; model 2: g_{L_1}, g_{L_2}, s and GV; model 3: g_{L_1}, g_{L_2}, s, GV and m; model 4: g_{L_1}, g_{L_2}, s, GV, m and p). The simplest model (model 1) was investigated first, and parameters were added successively up to model 4. The AIC was used to investigate an improvement of the model by adding parameters. In this study, time at liberty for Francis method was added to an arbitrary time at capture, because the exact date was lacking for three individuals. The analysis of Francis method was performed in R software (www.r-project.org) using a modified *grotag* function of the *fishmethods* package (Nelson, 2013). In addition to these seven broader growth estimation methods, it was investigated if a fixed value of the asymptotic length L_∞ can reduce bias in parameter estimates for methods that did not consider GV. For the methods that did not consider heteroscedasticity, it was investigated whether a multiplicative error structure (ln–ln transformation) can produce better parameter estimates. The value used as fixed asymptotic length for *G. galeus* was obtained from the species' maximum length L_{max}, determined by the average L_T of the three largest (or heaviest) specimens caught in the north-east Atlantic Ocean. If only total body mass (M_T; g) was given, L_T was estimated *via* the inverted length and mass relationship of *G. galeus* for the north-east Atlantic Ocean for females

$$L_\text{T} = \left[M_\text{T}\left(0{\cdot}0029^{-1}\right)\right]^{3{\cdot}1^{-1}} \tag{2}$$

and males

$$L_\text{T} = \left[M_\text{T}\left(0{\cdot}0042^{-1}\right)\right]^{3{\cdot}01^{-1}}, \tag{3}$$

respectively (Dureuil, 2013). Asymptotic length was estimated from its relationship to maximum length (Froese & Binohlan, 2000):

$$L_\infty = 10^{\left(0{\cdot}044+0{\cdot}9841\log_{10}L_{\text{max}}\right)}. \tag{4}$$

The 95% C.L. of L_∞ were based on S.E. estimates given by the authors.

DATA

Information on north-east Atlantic *G. galeus* sex, date of release and recapture and length or mass at capture and recapture was extracted from the literature (Holden & Horrod, 1979; Stevens, 1990) and provided by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) tagging database, the U.K. Shark Tagging Programme and the Scottish Sea Angling

Table II. Simulation runs executed in this study of growth in *Galeorhinus galeus*. Small errors were simulated with an s.d. of 0·01 and large errors with an s.d. of 0·05. Here, the s.d. was multiplied with the length to simulated size-dependent errors. Growth variability was simulated with an s.d. of 1 or 5 for small or large variability, respectively

Simulation	Error (*E*)	Variability (*V*)	Name
Run 1	small	small	Run *ev*
Run 2	large	large	Run *EV*
Run 3	large	small	Run *Ev*
Run 4	small	large	Run *eV*

Conservation Networks (SSCAN) shark tagging programme. Duplicate records were deleted. Values for length obtained from mass by Stevens (1990) were backcalculated to mass by the formula he applied. Equations (2) and (3) were then used to calculate L_T whenever mass was given instead of length or when length values were erroneous. Data on growth rates from tagging data can be subject to significant MEs (Holden & Horrod, 1979; Stevens, 1990) because of the inherent variability in body mass or imprecise measurements. Therefore, negative growth rates and biologically questionable data points were excluded. The latter was identified by the assumption of a linear decrease when plotting growth per year against the mean length (Gulland & Holt, 1959). This method is believed to be strong in detecting data points that deviate from the von Bertalanffy growth model (Sparre & Venema, 1999). Outliers were identified using the *influence plot* function of the *car* package in R (Fox & Weisberg, 2011), which combines Studentized residuals, hat-values and Cook's distance. Values showing a large Cook's distances and deviating more than three times the average hat value and ± two times the Studentized residuals were discarded. In total, four female and three male data points were considered as outliers and removed from the analysis, giving a final sample size of 37 female and 16 male individuals. Details on outlier removal are provided in Appendices S1–S3 (Supporting Information).

METHOD SELECTION

The best performing method for the given data was identified *via* a simulation analysis with known growth parameters, executed in R. From the basic growth relationship, 1000 random bootstrapped data sets were generated with either small or large GV, and small or large ME. In total, four simulation runs were executed (Table II). The complete simulation analysis was run twice, for males and females independently. If not stated otherwise above, the optimizer command was used for fixed L_∞ approaches, and the optim command was used for all other approaches. A commented R script for the simulation analysis is provided in Appendices S1–S3 (Supporting Information). The method selection procedure *via* the simulation analysis involves the following steps.

Define true VBGPs

The true value of the asymptotic length $L_{\infty\text{true}}$ was set equal to the asymptotic length obtained from the maximum size, as described above. The true value of the growth constant k_{true} was set at 0·092 year^{-1} for males and 0·075 year^{-1} for females, obtained from growth studies of *G. galeus* in southern Brazil (Ferreira & Vooren, 1991).

Consider the sample size

The number of individuals was set equal to the observed number of individuals in the *G. galeus* tagging database to account for the sample size of the given data.

Calculate a true age at capture

The user-selected true VBGP were used to calculate the true age at capture for each individual t_{ci} from the observed length-at-capture L_{ci}, to reflect the length distribution of the sampled data: $t_{\text{ci}} = k_{\text{true}}^{-1} \ln[(L_{\infty\,\text{true}} - L_0)(L_{\infty\,\text{true}} - L_{\text{ci}})^{-1}]$, where L_0 was assumed to be 28 cm.

Introduce GV in the length at capture

Individual GV was introduced by letting the asymptotic length of each individual $L_{\infty\mathrm{i}}$ vary. The effect of small and large GV was considered by sampling from a normal distribution with zero mean μ and an S.D. σ of 1 and 5, respectively:

$$L_{\infty\mathrm{i}} = L_{\infty\mathrm{true}} + \mathcal{N}\ (\mu = 0, \sigma = 1\ or\ 5) \tag{5}$$

A new length at capture was then simulated to account for individual GV: $L_{t_{\mathrm{ci}}} = L_{\infty\mathrm{i}} - \left(L_{\infty\mathrm{i}} - L_0\right)\left(e^{\left(-k_{\mathrm{true}}t_{\mathrm{ci}}\right)}\right)$.

Introduce MEs in the length at capture

Random MEs in the individual length at capture were introduced by sampling from a normal distribution with zero μ and a σ of 0·01 and 0·05 for small and large ME, respectively. The S.D. σ was multiplied by length, to account for the possibility that ME increases with size, *e.g.* because large sharks might be more difficult to straighten out. The individual length at capture accounting for GV and ME l_{ci} was then calculated:

$$l_{t_{\mathrm{ci}}} = L_{t_{\mathrm{ci}}} + \mathcal{N}\ \left(\mu = 0, \sigma = 0{\cdot}01 L_{t_{\mathrm{ci}}}\ or\ \ 0{\cdot}05 L_{t_{\mathrm{ci}}}\right) \tag{6}$$

Calculate the true age at recapture

The true age at recapture t_{ri} was obtained by adding the observed time at liberty δt to the true age at capture t_{ci}: $t_{\mathrm{ri}} = t_{\mathrm{ci}} + \delta t$, to reflect the time at liberty structure of the sampled data.

Introduce GV and MEs in the length at recapture

The length-at-recapture for each individual with GV accounted for was simulated after $L_{t_{\mathrm{ri}}} = L_{\infty\mathrm{i}} - \left(L_{\infty\mathrm{i}} - L_0\right)\left(e^{\left(-k_{\mathrm{true}}t_{\mathrm{ri}}\right)}\right)$ and the ME was introduced by:

$$l_{t_{\mathrm{ri}}} = L_{t_{\mathrm{ri}}} + \mathcal{N}\ \left(\mu = 0, \sigma = 0{\cdot}01 L_{t_{\mathrm{ri}}} or\ \ 0{\cdot}05 L_{t_{\mathrm{ri}}}\right) \tag{7}$$

To avoid biological unreasonable negative growth increments, $l_{t_{\mathrm{ri}}}$ was forced to be larger $l_{t_{\mathrm{ci}}}$, by calculating the absolute values of the simulated individual growth increments: $\delta l_{\mathrm{i}} = \left| l_{t_{\mathrm{ri}}} - l_{t_{\mathrm{ci}}} \right|$ and recalculating the length at recapture: $l_{t_{\mathrm{ri}}} = \delta l_{\mathrm{i}} + l_{t_{\mathrm{ci}}}$.

Evaluate method performance

To evaluate the performance of each method, the simulated length at capture $l_{t_{\mathrm{ci}}}$ and length at recapture $l_{t_{\mathrm{ri}}}$ were used as input data for the different growth estimation methods, and the results were investigated *via* bias–precision–accuracy plots. The definitions by Walther & Moore (2005) and their recommendation to use scaled measures, which allow comparison between males and females or other studies, were followed. Accordingly, average bias over all four simulation runs was defined as relative bias (B_{R}): $B_{\mathrm{R}} = (An)^{-1}\sum_{i=1}^{n}\left(\theta_{\mathrm{i}} - A\right)$, where A is the known growth parameter ($L_{\infty\mathrm{true}}$, k_{ture}) and θ_{i} is the single bootstrap value that was computed $n = 1000$ times for each simulation run. Average precision over all four simulation runs was defined as the C.V. (y) $y = 100\left[\sqrt{n^{-1}\sum_{i=1}^{n}\left(\theta_{\mathrm{i}} - \overline{\theta}\right)^2}\right]\overline{\theta}^{-1}$, where $\overline{\theta}$ is the mean of the bootstrap values. Average accuracy over all four simulation runs was defined as scaled mean squared error (SMSE; Z): $Z = \left(A^2 n\right)^{-1}\sum_{i=1}^{n}\left(\theta_{\mathrm{i}} - A\right)^2$. Means were calculated as trimmed means with 1% of the largest and smallest values removed, to decrease the influence of extreme values which may arise from numerical instabilities during the simulation analysis. Smaller values for relative bias, C.V. and SMSE indicated better performance, and the best performing method was selected as the method with the lowest SMSE value, as this measure incorporates bias and precision. The best performing method was subsequently utilized to estimate VBGP from tagging data of north-east Atlantic *G. galeus*. Confidence limits of the obtained parameters were estimated as the 2·5 and 97·5 percentiles of a bootstrapped data set. Therefore, 1000 replicates were generated by random selection with replacement from the original *G. galeus* data set, each with the original sample size of males or females, respectively.

GROWTH COMPARISON AMONG *G. GALEUS* POPULATIONS

Estimated VBGP of *G. galeus* from the north-east Atlantic Ocean were compared with other regions *via* an auximetric grid. In an auximetric grid, $\log_{10} k$ values are plotted against $\log_{10} L_\infty$ values, to investigate the growth performance of different populations across geographical areas. Different populations typically cluster in $\log_{10}$–$\log_{10}$ space (Pauly *et al.*, 1996).

AGE AT MATURITY AND LONGEVITY

The age at maturity was estimated from length at 50% maturity by the rearranged form of equation (1) solving for age instead of length. Longevity $t_{\max}$ was estimated as the time span required to attain 99% of the asymptotic length following Skomal & Natanson (2003) and Manning & Francis (2005):

$$t_{\max} = k^{-1} \ln \left\{ \left(L_\infty - L_0\right) \left[(1 - 0{\cdot}99)\, L_\infty\right]^{-1} \right\} \tag{8}$$

as well as Fabens (1965), who defined the time required to attain >99% of the asymptotic length as:

$$t_{\max} = 5 \ln (2)\, k^{-1}. \tag{9}$$

RESULTS

DATA

In males, three observations were considered biologically questionable. These included two individuals with annual growth rates of over 20 cm and one individual with L_T at recapture of 184 cm. In females, four observations were considered outliers. This included three individuals with annual growth rates >17 cm and one individual with an annual growth rate of only 7 cm at a mean size of 45·5 cm. The influence plots are provided in Appendices S1–S3 (Supporting Information). The final data set contained capture–recapture information of 16 male and 37 female sharks. The annual growth ranged from 0·15 to 14 cm in females, with a mean of 5 cm, and from 0·6 to 11 cm in males, with a mean of 4 cm. L_T ranged from 84 to 175 cm in females and 126 to 168 cm in males. The time at liberty of females ranged from 64·0 days to 6·7 years, with a mean of 2·2 years. In males, the shortest time at liberty was 70 days and the highest 10·9 years, with a mean of 2·7 years.

ASYMPTOTIC LENGTH

The largest or heaviest female *G. galeus* caught in the north-east Atlantic Ocean were 200·00 cm (Capapé & Mellinger, 1988), 37·4 kg (EFSA, 2013) and 36·7 kg

(SSTP, 2010). These masses correspond to an L_T of 196·69 and 195·53 cm. The largest or heaviest male *G. galeus* caught in the north-east Atlantic Ocean were 177·80 cm, 22·7 and 22·3 kg (Stevens, 1990). These masses correspond to an L_T of 172·45 and 171·49 cm. Therefore, the asymptotic length obtained from the average maximum size using equation (4) was 200·85 cm (with 95% C.L. of 171·72 and 229·98 cm) for females and 177·30 cm (151·58 and 203·01 cm) for males. These values were subsequently used for the fixed asymptotic length and as true values in the simulation runs.

METHOD SELECTION

The overall performance of each method was evaluated *via* bias–precision–accuracy plots derived from the simulation analysis considering all four scenarios of GV and ME. For both female and male data, the overall best performing method in estimating the growth constant was the weighted Fabens method with a fixed asymptote (Figs 1 and 2), whereas the Fabens method performed best in estimating the asymptote (Figs 3 and 4). The detailed results for each of the four simulation runs are provided in Appendices S1–S3 (Supporting Information). Performance in estimating the asymptote was generally better than performance in estimating the growth constant, but none of the methods performed best for both parameters. Accordingly, the error associated with estimating the growth constant was larger. In addition, the estimated fixed asymptotic lengths using equation (4) were not significantly different to the methods that performed best in estimating the asymptote (Tables III and IV). Therefore, von Bertalanffy growth estimates from the weighted Fabens method with a fixed asymptote were selected as growth parameters for male and female *G. galeus* in the north-east Atlantic Ocean. The fit of the mark–recapture information to the selected VBGP is shown in Fig. 5.

GROWTH COMPARISON AMONG *G. GALEUS* POPULATIONS

The VBGP of *G. galeus* for the north-east Atlantic Ocean were compared with estimates for populations of other geographical areas *via* an auximetric grid (Fig. 6). Growth performance was more closely related to New Zealand and southern Brazil stocks, than to Australian and South African stocks. The slope of all growth estimates combined was −2·05 and therefore close to the expected value of −2 (Pauly *et al.*, 1996).

AGE AT MATURITY AND LONGEVITY

The length at which 50% of the individuals are mature was summarized by Dureuil (2013) from the literature as 155 cm in females and 121 cm in males. From this, it follows that age at maturity is 17 years in females and 12 years in males. Longevity estimates ranged from 46 to 59 years in females and from 43 to 55 years in males using equations (9) and (8), respectively.

DISCUSSION

This study presented a structured selection procedure that helped identify the best performing method to estimate growth for a small mark–recapture sample of *G. galeus*.

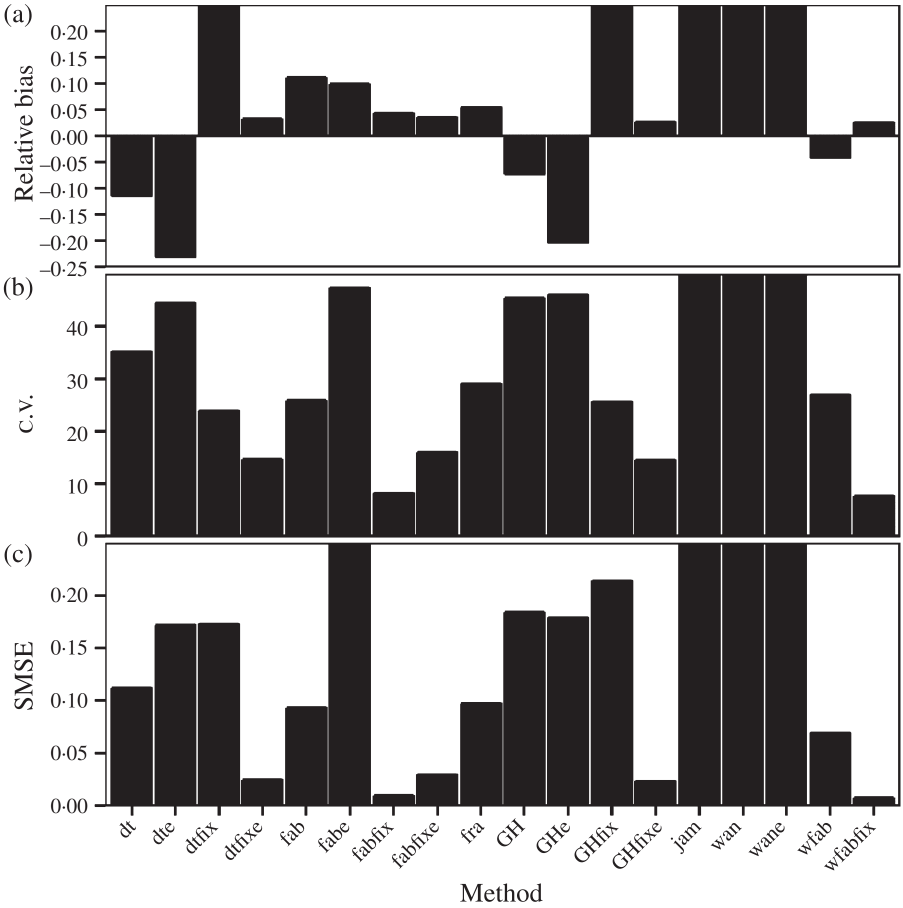

FIG. 1. Simulation results for the growth constant *k* (female data). The (a) relative bias, (b) precision (C.V.) and (c) accuracy (scaled mean squared error, SMSE) of mean estimates are contrasted for 18 different methods (see Table I). Simulations considered the structure of *Galeorhinus galeus* data and different magnitudes of growth variability and measurement error. Lower values indicate better performance.

Parameter estimates differed strongly among methods, showing the need for careful method selection. In this study, the majority of tagged and recaptured individuals were mid-sized sharks. Maximum and mean time at liberty was larger for males, but the sample size was smaller for males than for females. In males, some capture and recapture information was present for larger individuals, but lacking for small individuals. In females, the length distribution was more representative, although data for small and very large individuals were also scarce (Fig. 5). In order to find the best method for estimating growth parameters from this limited tagging information, the performance of the three commonly utilized methods from Gulland & Holt (1959); Fabens (1965) and Francis (1988*a*) was tested, as well as 15 attempts to improve these models. Therefore, small and large GV and MEs were simulated while considering the structure of the data (*i.e.* sample size, observed length distribution and time at liberty).

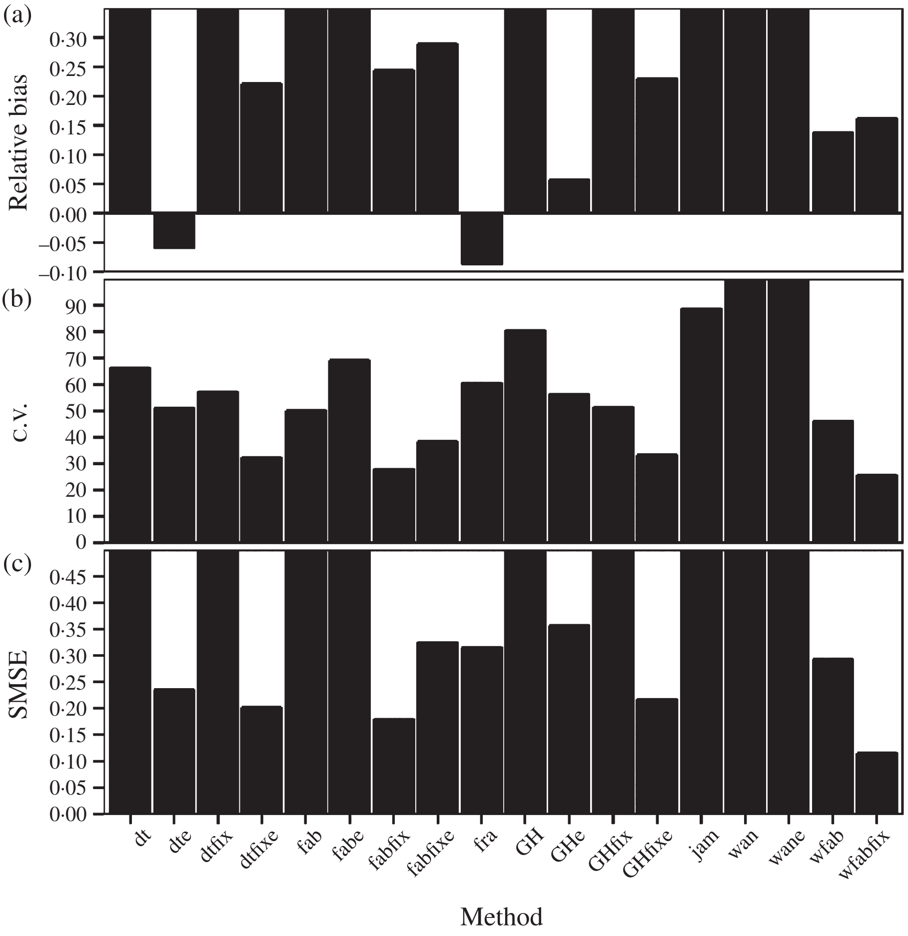

FIG. 2. Simulation results for the growth constant *k* (male data). The (a) relative bias, (b) precision (C.V.) and (c) accuracy (scaled mean squared error, SMSE) of mean estimates is contrasted for 18 different methods (see Table I). Simulations considered the structure of *Galeorhinus galeus* data and different magnitudes of growth variability and measurement error. Lower values indicate better performance.

In agreement to the findings in this study, previous studies have shown bias in the commonly utilized methods. From validated age data for sandbar sharks *Carcharhinus plumbeus* (Nardo 1827), it was shown that large differences can occur when comparing growth parameters obtained by direct ageing methods with those obtained from the Francis method, with the latter likely to overestimate the VBGP *k* and to underestimate the asymptote (McAuley *et al.*, 2006). McAuley *et al.* (2006) suggested that the bias was due to variability in growth, especially when time at liberty was short and the sample size was small and outlier contaminated. Other studies found that if old porbeagle *Lamna nasus* (Bonnaterre 1788) were absent in the sample, the Francis method can produce higher *k* and lower asymptote values (Natanson *et al.*, 2002) or higher values in both parameters (Skomal & Natanson, 2003). The Gulland and Holt and the Fabens methods may fail if time at liberty is short and GV is high (Simpfendorfer, 2000). It

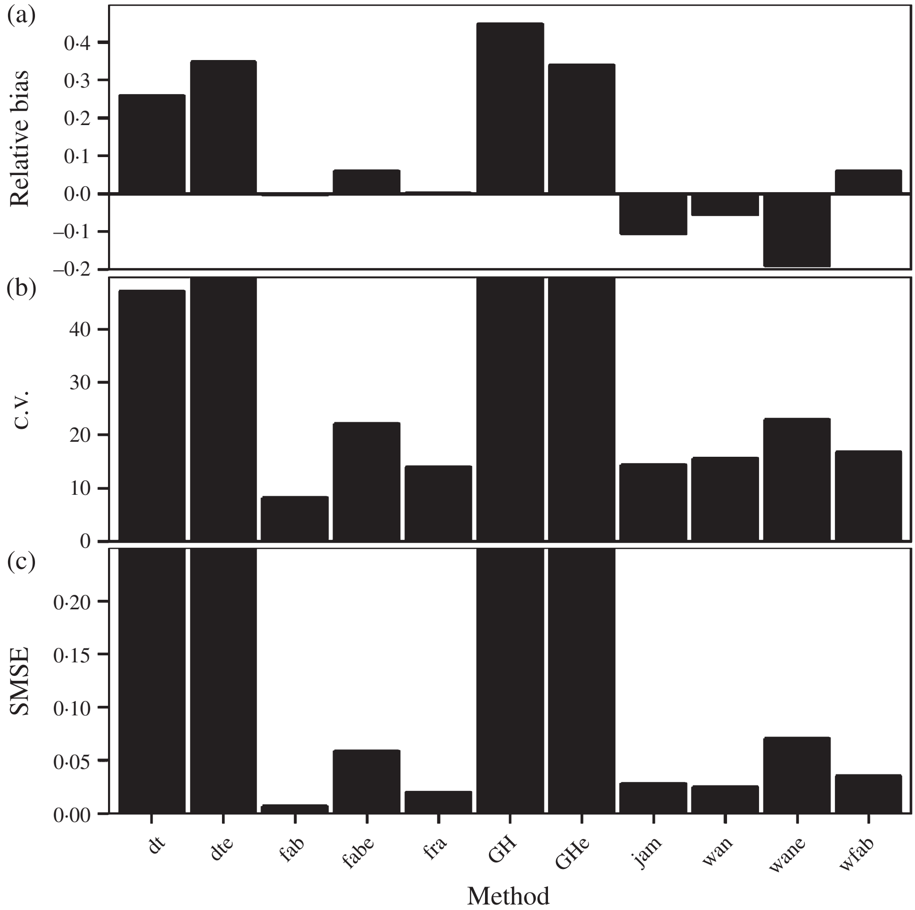

FIG. 3. Simulation results for the asymptotic length constant L_∞ (female data). The (a) relative bias, (b) precision (C.V.) and (c) accuracy (scaled mean squared error, SMSE) of mean estimates is contrasted for 18 different methods (see Table I). Simulations considered the structure of the *Galeorhinus galeus* data and different magnitudes of growth variability and measurement error. Lower values indicate better performance.

is well described that the Fabens method can produce bias estimates when individual growth is variable (Sainsbury, 1980; Francis, 1988*b*; Maller & deBoer, 1988; Kimura *et al.*, 1993; Wang & Thomas, 1995; Eveson *et al.*, 2007) or MEs are high (Eveson *et al.*, 2007), which can lead to an overestimation of mean length at age (Sainsbury, 1980). The present findings indicate that the Francis method tends to be the least biased out of the commonly utilized methods, in particular when the sample is larger and both smaller and larger individuals are present. The Fabens method showed higher bias and was particularly sensitive to MEs, and the Gulland and Holt method was biased even when ME and GV were small (Appendices S1–S3, Supporting Information). The best performing method for both sexes was the weighted Fabens method with a fixed asymptotic length.

The lack of small individuals in the data, as well as a small sample size, may positively bias the results and lead to a higher uncertainty and larger errors in the parameter

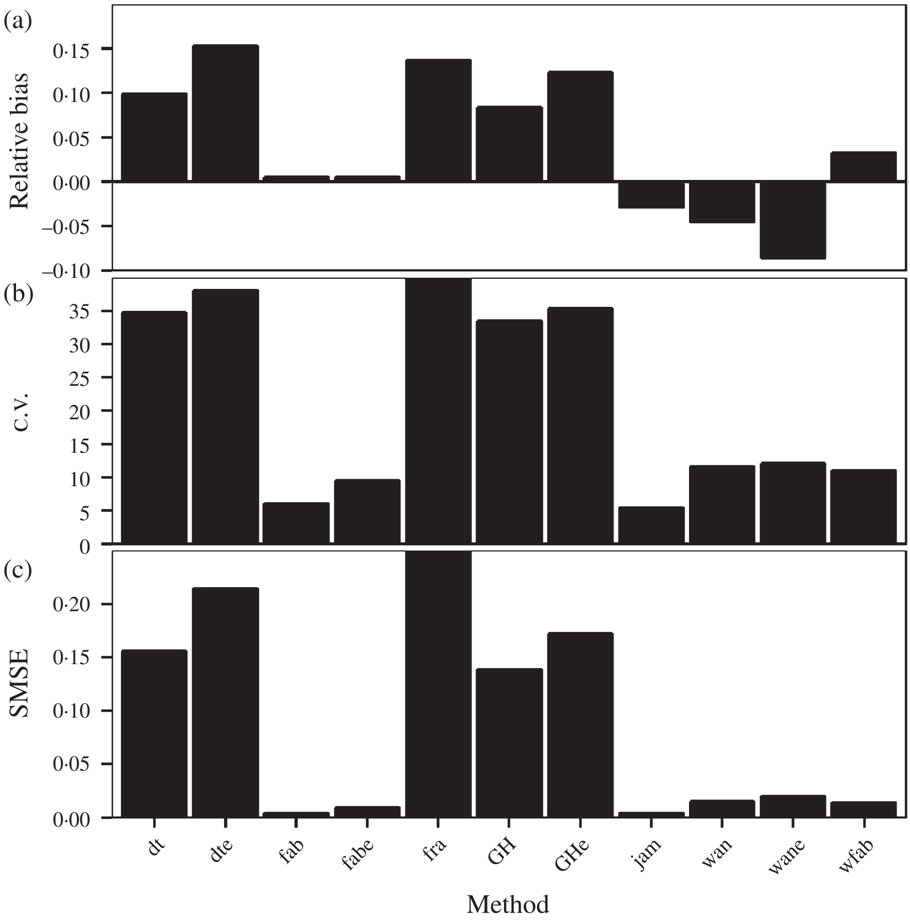

FIG. 4. Simulation results for the asymptotic length constant L_∞ (male data). The (a) relative bias, (b) precision (C.V.) and (c) accuracy (scaled mean squared error, SMSE) of mean estimates is contrasted for 18 different methods (see Table I). Simulations considered the structure of the *Galeorhinus galeus* data and different magnitudes of growth variability and measurement error. Lower values indicate better performance.

estimates in general. Overall, MEs had the largest effects on the performance of all methods, which is indicated by the larger errors in run *Ev* than in run *eV* (Appendices S1–S3, Supporting Information). The simulated GV had a mean of zero and ranged from about ±3 to ±15 cm for small and large variability, respectively, and the simulated MEs had a mean of zero and ranged from about ±5 to ±25 cm for small and large errors, respectively (Appendices S1–S3, Supporting Information). Thus, the S.D. estimates utilized in equations (5)–(7) for GV and MEs were considered to be reasonable for a shark species with a maximum size of 200 cm. Factors leading to ME can include the accuracy of the measurement (especially for larger sharks being measured alive), the method (measuring board or tape measure) and the type of measurement, *e.g.* L_T or fork length (Francis, 2006). Therefore, it should be recommended that measurements are done as accurately as possible. In addition, length measurements should be preferred over measurements in mass, as the latter might be more variable. Finally, it

TABLE III. von Bertalanffy growth estimates for the asymptotic length L_∞ and the growth constant k from 37 mark–recapture data points of female *Galeorhinus galeus* for all methods (see Table I) with lower (LCL) and upper (UCL) 95% C.L. In bold is the method from which the parameters were chosen. This method performed best for the given data according to the simulation analysis. The ln–ln transformed method of Wang (1998) did not converge

Method	L_∞	LCL L_∞	UCL L_∞	k	LCL k	UCL k
fra	200·27	166	280	0·071	0·028	0·140
wan	196·89	144	333	0·081	0·026	0·385
wane	NA	NA	NA	NA	NA	NA
jam	220·05	−449	914	0·058	−35·926	0·215
GH	246·78	177	900	0·043	0·007	0·097
GHe	209·58	157	1060	0·049	0·004	0·133
GHfix	200·85	172	230	0·069	0·057	0·082
GHfixe	200·85	172	230	0·055	0·041	0·071
fab	182·25	162	234	0·106	0·051	0·161
fabe	183·09	154	371	0·072	0·017	0·179
fabfix	200·85	172	230	0·078	0·061	0·091
fabfixe	200·85	172	230	0·054	0·040	0·070
wfab	191·87	163	307	0·088	0·028	0·147
wfabfix	**200·85**	**172**	**230**	**0·076**	**0·059**	**0·089**
dt	243·15	179	662	0·057	0·013	0·123
dte	216·69	168	1181	0·045	0·004	0·092
dtfix	200·85	172	230	0·100	0·074	0·132
dtfixe	200·85	172	230	0·055	0·041	0·072

should be explicitly stated which type of length measurement was utilized. Individual GV may become a more important issue if the capture–recapture data are seasonally biased (Simpfendorfer, 2000). Therefore, it can be necessary to include seasonal effects to account for the fact that growth might slow down at certain times of the year (Pauly *et al.*, 1992). In this study, the division of the total days individuals spent at liberty during spring and summer by the total days individuals spent at liberty in autumn and winter was 1·01 for females and 0·99 for males. Therefore, no effect of seasonality was expected. If this is not the case, growth models allowing for seasonality may be applied (Pauly & Gaschütz, 1979; Francis, 1988*a*; Somer, 1988; Wang, 1999) or the sample might be adjusted to become equally distributed among seasons.

The natural logarithm (ln–ln) transformation had no consistent positive effect on method performance, whereas fixing the asymptote generally increased the performance of the methods. It has been shown previously that the weighted Fabens method produces only unbiased results when observational errors occurred, whereas variability in the asymptote produced biased results (Kimura *et al.*, 1993). The findings of this study suggest that fixing the asymptote can help overcome this problem.

When applying the 18 different methods to the observed data, significant difference in VBGP was found (Tables III and IV), which in turn resulted in considerably different growth curves among the methods for females and males (Fig. 7). This demonstrates that it is important to select the method that performs best for a given data structure. Although the simulation analysis revealed that for the given data none of the methods performed best in estimating both parameters, accuracy in estimating the growth

TABLE IV. von Bertalanffy growth estimates for the asymptotic length L_∞ and the growth constant k from 16 mark–recapture data points of male *Galeorhinus galeus* for all methods (see Table I) with lower (LCL) and upper (UCL) 95% C.L. In bold is the method from which the parameters were chosen. This method performed best for the given data according to the simulation analysis

Method	L_∞	LCL L_∞	UCL L_∞	k	LCL k	UCL k
fra	176·38	−295	830	0·085	−0·027	0·133
wan	152·86	144	177	0·444	0·083	3·200
wane	148·51	143	160	1·122	0·200	4·851
jam	166·78	150	174	0·157	0·084	0·646
GH	179·56	162	400	0·117	0·014	0·255
GHe	177·47	165	312	0·100	0·017	0·216
GHfix	177·30	152	203	0·124	0·086	0·171
GHfixe	177·30	152	203	0·100	0·071	0·142
fab	174·33	161	223	0·096	0·030	0·209
fabe	170·90	160	211	0·134	0·046	0·280
fabfix	177·30	152	203	0·085	0·066	0·116
fabfixe	177·30	152	203	0·105	0·073	0·152
wfab	177·41	163	281	0·081	0·019	0·172
wfabfix	**177·30**	**152**	**203**	**0·081**	**0·065**	**0·110**
dt	171·83	164	305	0·142	0·021	0·279
dte	178·39	165	323	0·097	0·017	0·196
dtfix	177·30	152	203	0·097	0·078	0·157
dtfixe	177·30	152	203	0·101	0·072	0·143

constant was lower and the associated error higher. In addition, the values for the fixed asymptotic length were similar to the results of the methods performing best in estimating the asymptote. Therefore, methods were selected according to their performance in estimating the growth constant.

The results of the selected method should also be discussed in terms of biological reasonability. Hence, estimated growth parameters from this study were compared with those from *G. galeus* populations in other regions. The comparison of the growth performance of different populations revealed that growth parameters of the north-east Atlantic stock were more similar to those from New Zealand and southern Brazil stocks, than to Australian and South African stocks. The female asymptotic length of 201 cm is larger than the 162 cm reported from south-eastern Australia (Grant *et al.*, 1979), the 179 cm reported from New Zealand (Francis & Mulligan, 1998) and the 163 cm from southern Brazil (Ferreira & Vooren, 1991). Likewise, male asymptotic length of 177 cm was found to be larger than the 143 cm reported from New Zealand (Francis & Mulligan, 1998), 154 cm from South Africa (McCord, 2005), 152 cm from southern Brazil (Ferreira & Vooren, 1991) and 158 cm from south-eastern Australia (Grant *et al.*, 1979). This comparison suggests that the asymptotic length tend to increase with latitude for the same species, a pattern that has been described before (Kimura, 2008). The VBGP k found in this study of 0·076 year^{-1} for females and 0·081 year^{-1} for males was close to the southern Brazil stock, where k was estimated at 0·075 year^{-1} for females and 0·092 year^{-1} for males (Ferreira & Vooren, 1991). In females, k was most different from the south-east Australia stock, where

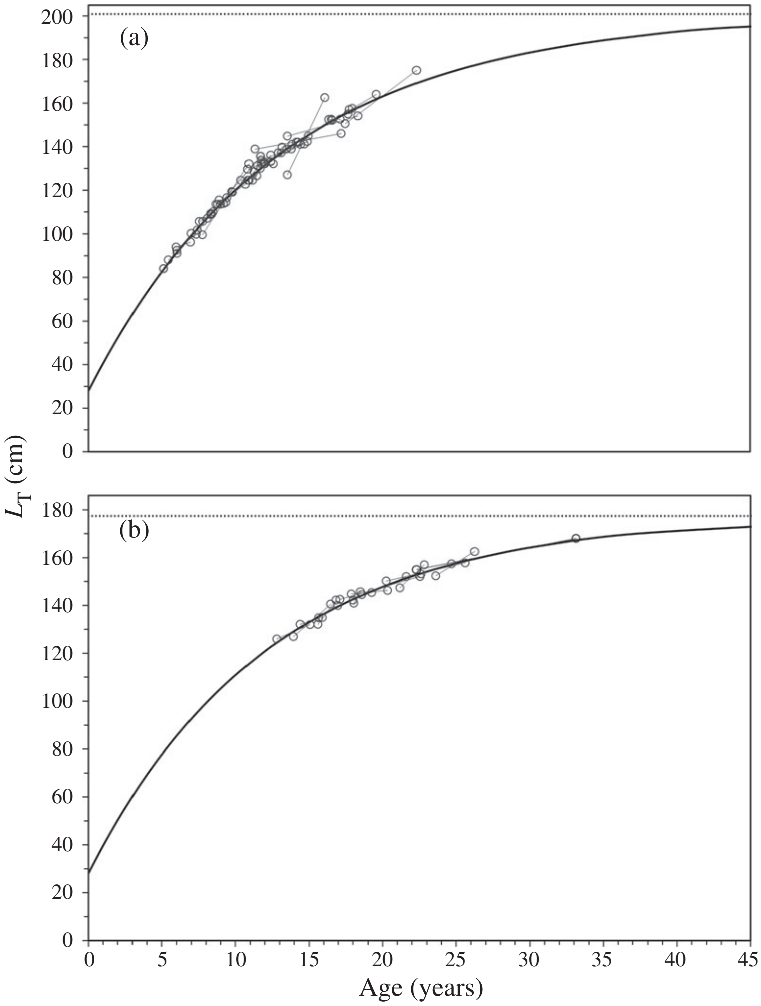

FIG. 5. Growth curves of total length (L_T). Shown are the von Bertalanffy growth curve of (a) female *Galeorhinus galeus* and (b) male *G. galeus* obtained from the method that performed best in the simulation analysis, the weighted Fabens method introduced by James (1991) with a fixed asymptote. ○, the capture and recapture data, where the data of each individual are connected (——). ………, the asymptotic length, L_∞.

it was estimated at 0·16 year^{-1} (Grant *et al.*, 1979). In males, the South African stock showed least agreement, where *k* is believed to be 0·21 year^{-1} (McCord, 2005). The high growth constant found for *G. galeus* in South Africa might be an artefact of vertebral readings, the high growth constant for *G. galeus* from Australia might be an artefact of the method chosen to estimate growth from tagging information. Grant *et al.* (1979) used the Fabens method, which in this study produced large bias, particularly for the growth constant. Overall, the comparisons of the VBGP are in agreement with the general pattern, that organisms grow faster towards a lower asymptote in an environment with higher temperature (von Bertalanffy, 1960), because the asymptote and *k* are negatively correlated (Kimura, 1980). From the VBGP, age at maturity for the north-east

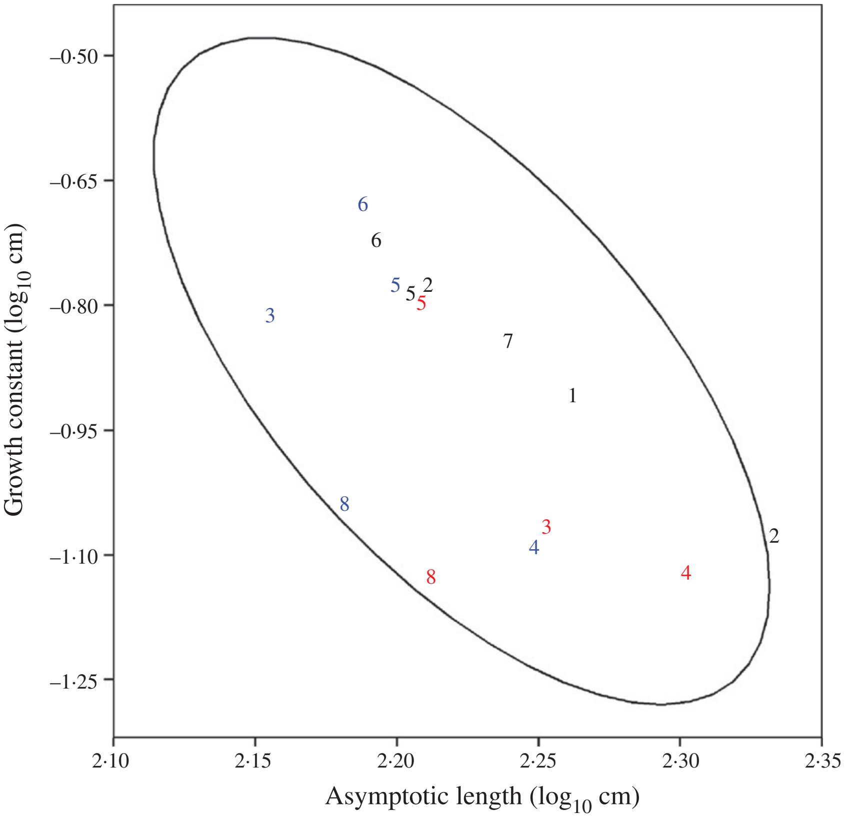

FIG. 6. Growth in total length of *Galeorhinus galeus* in various regions (○, females; ○, males; ○, combined sexes). The ellipse represents the 95% confidence limit. The numbers refer to the regions: 1, Australia (Moulton *et al.*, 1992); 2, Bass Strait, Australia (Moulton *et al.*, 1992); 3, New Zealand (Francis & Mulligan, 1998); 4, north-east Atlantic Ocean (this study); 5, south-eastern Australia (Grant *et al.*, 1979); 6, South Africa (McCord, 2005); 7, southern Australia, (Moulton *et al.*, 1992); 8, southern Brazil (Ferreira & Vooren, 1991).

Atlantic stock was estimated at 17 and 12 years for female and male *G. galeus*, respectively. In other stocks, female age at maturity was reported to be 10 years in Australia (Olsen, 1954), 16 years in southern Brazil (Peres & Vooren, 1991) and 13–15 years in New Zealand (Francis & Mulligan, 1998). For males, age at maturity was reported to be 11 years in southern Brazil (Peres & Vooren, 1991), 12–17 years in New Zealand (Francis & Mulligan, 1998), 6 years in South Africa (McCord, 2005) and 8 years in Australia (Olsen, 1954). Like growth performance, age at maturity in the north-east Atlantic Ocean is most similar to the southern Brazil stock. These findings are in agreement with the general finding that slower growth result in later maturation (Roff, 1984; Jensen, 1996). Longevity estimates ranged from 46 to 59 years in females and from 43 to 55 years in males using equations (9) and (8), respectively. These values include the suggested maximum age of 53 years for females (Olsen, 1984) and 45 years of males, the latter estimated based on tag returns (Moulton *et al.*, 1989). In summary, the comparison of the growth performance, the age at maturity and longevity estimated in this

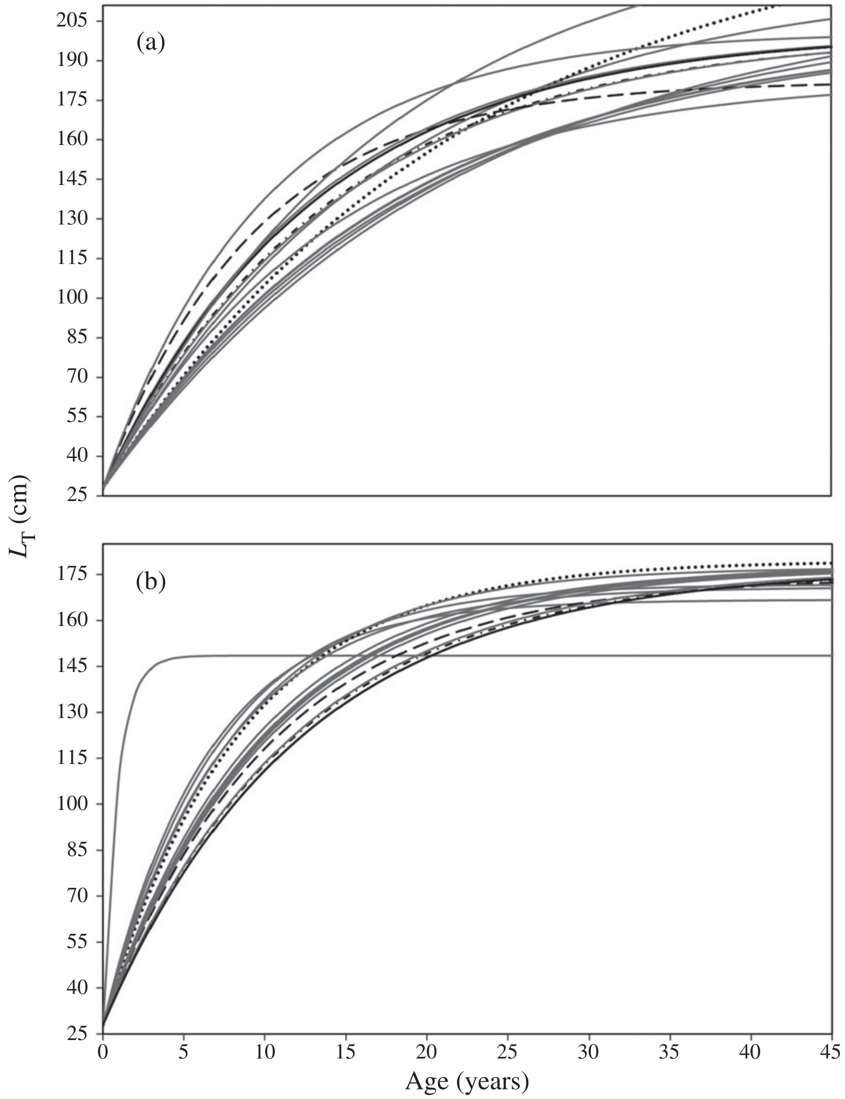

FIG. 7. Growth in total length (L_T) curve comparison. von Bertalanffy growth functions for (a) female and (b) male *Galeorhinus galeus* with the parameters derived from each of the 18 methods (see Table I) are shown, but not all identified. The best method is the weighted Fabens method (James, 1991) with a fixed asymptote (——). The other commonly used methods are: the Gulland & Holt (1959) method (………), the Fabens (1965) method (- - - -) and the Francis (1988*a*) method (–·–·–). The ln−ln transformed method of Wang (1998) did not reach convergence for female data and therefore could not be shown.

study to other regions suggests that the results are reasonable, despite being based on a small sample size. Hence, the productivity of north-east Atlantic *G. galeus* is low, increasing the species risk of extinction (Musick, 1999).

To conclude, this is, as far as is known, the first comparative study of methods to estimate growth from tagging information in a shark species and the first applying the weighted Fabens approach from James (1991) for this group of animals. Results reinforce the need to apply different approaches on a given data set and to verify the method used to estimate growth. Obtaining growth estimates from mark–recapture data can be particularly important for species such as *G. galeus*, where vertebral readings may not represent an adequate procedure to estimate age (Kalish & Johnston, 2001). The results of this study were compared with the only available age data of *G. galeus* in the north-east Atlantic Ocean, obtained from vertebrae (Henderson *et al.*, 2003). Their preliminary age estimates of four male specimens with a L_T of 141, 148, 149 and 152 cm were 10, 12, 10 and 11 years, respectively. The estimates would suggest ages of 17, 20, 21 and 22 years for the same L_T. Hence, the estimated ages from the growth parameters obtained in this study were up to 50% higher than to those reported by Henderson *et al.* (2003), which would support previous concerns that vertebral readings can underestimate age in this species (Officer *et al.*, 1996; Kalish & Johnston, 2001). The presented method selection procedure can aid in obtaining less biased growth parameters from mark–recapture tagging data by finding the best performing method for a given data set, especially if the sample size is small. More accurate growth parameters will in turn improve stock assessments. The results of the selection procedure, however, are limited to the chosen methods. Hence, it is important to test a variety of different growth estimation methods. Future studies should ideally include new growth estimation methods in the selection procedure, such as Bayesian methods, to make the method selection more reliable. In particular, a Bayesian version of the Francis method could be promising, as this method was designed to account for MEs, GV and the proportion of outliers within the data. In addition, future studies should include both age and length-based approaches to gauge the robustness of either.

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Supporting Information

Supporting Information may be found in the online version of this paper:
Appendix S1. Outlier identification for the observed *Galeorhinus galeus* data.
Appendix S2. Detailed simulation results of the selection procedure.
Appendix S3. R code used in the simulation analysis (selection procedure).

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