Estimating von Bertalanffy growth parameters from growth increment data using a linear mixed-effects model, with an application to the sea scallop *Placopecten magellanicus*

Deborah R. Hart and Antonie S. Chute

We introduce a novel linear mixed-effects method for estimating von Bertalanffy growth parameters from growth increment data that lack explicit age information. The method is simple to implement and can incorporate and estimate variability in both the asymptotic size L_∞ and the Brody growth coefficient K. Simulations indicate that estimates from the method are accurate over a range of conditions. The method is applied to growth data from more than 6000 Atlantic sea scallop (*Placopecten magellanicus*) shells from the Mid-Atlantic Bight and Georges Bank. Sea scallops grow to a larger asymptotic shell height on Georges Bank than on the Mid-Atlantic Bight and in areas closed to fishing on Georges Bank than on the fished portions. Depth and latitude had significant effects on scallop growth in both the Mid-Atlantic and Georges Bank, with smaller asymptotic shell heights in deeper water and at higher latitudes.

Keywords: marine protected areas, mixed-effects model, *Placopecten magellanicus*, scallop, von Bertalanffy growth.

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Introduction

Growth parameters often need to be estimated from growth increment data consisting of a starting length and amount of growth in a period, but where age is not explicitly known. Simple methods for estimating von Bertalanffy growth coefficients from such data, such as Ford–Walford plots or the method of Fabens (1965), give biased estimates when, as usually is the case, the growth parameters vary among individuals (Sainsbury, 1980; Francis, 1988; Maller and deBoer, 1988; Smith *et al.*, 1997). If there can be multiple increments per individual, ignoring individual variability can cause further bias as a result of "Lee's phenomenon" (Ricker, 1969; Vaughan and Burton, 1994), and also induce underestimation of variance by inflating the sample size.

A number of methods has been proposed that account for individual variability in growth by employing non-linear mixed-effects models to fit growth increment data (Hampton, 1991; James, 1991; Palmer *et al.*, 1991; Wang *et al.*, 1995; Wang, 1998, 2004; Laslett *et al.*, 2002). Although these approaches produce unbiased estimates, they can be difficult for non-specialists to implement and compute, and usually they assume individual variability in only one parameter. Here, we introduce a novel linear mixed-effects method for estimating von Bertalanffy growth coefficients from growth increment data that can be considered as a generalization of the Fabens method. Our model can easily be implemented using standard statistical software and can take into account, given sufficient data, variability in both the asymptotic size L_∞ and the Brody growth coefficient K.

We apply this method to an extensive database of growth increments derived from more than 6000 Atlantic sea scallop (*Placopecten magellanicus*) shells. Although sea scallop shell rings are laid down annually (Stevenson and Dickie, 1954; Merrill *et al.*, 1966; Hart and Chute, 2009), the first one or more rings are often obscure or missing, especially on older scallops, making absolute age determination difficult (Claereboudt and Himmelman, 1996). For this reason, we treat the distance between two successive rings on a shell as an annual growth increment, with age unknown. Unlike most tag-recapture growth increment data, multiple growth increments are available for each individual. Our mixed-effects modelling approach naturally accommodates these repeated measures which can cause difficulties for models that do not include random effects because they are typically correlated. The large database allows us not only to make precise estimates of the mean growth coefficients and their variability, but also to explore the effects of covariates such as water depth, latitude, population density, and management status (open or closed to fishing) on sea scallop growth.

Methods
Scallop shell analysis

Sea scallop shells were collected during the 2001–2007 Northeast Fisheries Science Center (NEFSC) sea scallop surveys (Figure 1). The surveyed area was divided into two regions: Georges Bank, including the adjacent areas of the Great South Channel and Nantucket Shoals, and the Mid-Atlantic Bight, from Virginia to Long Island. Growth was analysed separately in these two
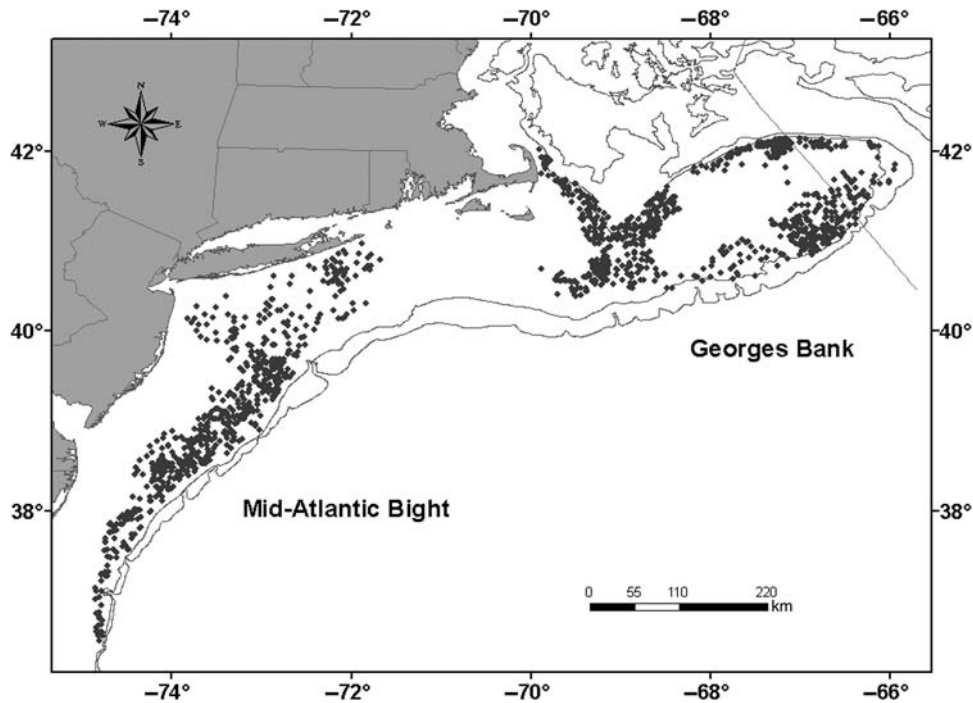
Figure 1. Map of shell sampling locations for sea scallop shells used in this study.

regions. At slightly less than half the random stations in the surveys, scallops were chosen randomly (averaging about six per station) to be used for the growth analysis. The scallops were scrubbed with a wire brush, shucked, and both valves were transported back to shore for later analysis. Rings on the top valve of each shell that represented annuli were marked with a pencil. On some shells, one or more "shock marks" were evident. These were distinguished from true annuli by their irregular nature and because a point of injury was usually evident in the form of a crack or deformation of the shell. After the shells were marked, the distance in millimetres from the umbo to each of the ring marks was measured with calipers. The first one or more annuli are often missing or difficult to discern, but the annuli become clearer with age. For this reason, the annuli on each shell were read starting with the first one that was clearly visible. Additionally, only annuli of more than 40 mm shell height were included in the analysis, both because of questions regarding the reliability of the visual determination of the first year ring and to avoid the early period of growth where the von Bertalanffy equation would be invalid. The shell heights of the annuli on the ith shell will be denoted by $L_{1,i}, L_{2,i}, \ldots$, in the order of increasing shell height. The partial increment from the last ring to the edge of the shell was not used in the analysis because it does not represent a full year's growth.

Growth parameter estimation procedure

The growth increment form of the von Bertalanffy equation is (Fabens, 1965)

$$L_{t+1} = L_t + (L_\infty - L_t)[1 - \exp(-K)]$$
$$= \exp(-K)L_t + L_\infty[1 - \exp(-K)], \quad (1)$$

where L_t is the shell height at time t (or in many applications,

length) and L_∞ and K the von Bertalanffy growth parameters. Equation (1) predicts that a plot of the L_{t+1} vs. L_t will be a straight line with slope $m = \exp(-K)$ and y-intercept $b = L_\infty[1 - \exp(-K)] = L_\infty(1 - m)$. Therefore, one could estimate K and L_∞ from Equation (1) by a linear regression of L_{t+1} vs. L_t (assuming no individual variability in these parameters), with

$$K = -\ln m \quad \text{and} \quad L_\infty = \frac{b}{(1 - m)}. \quad (2)$$

Although this method is biased when applied to the population as a whole if there is variability in the growth parameters among individuals, it can be used to model growth of individual animals. Let K_i and $L_{\infty,i}$ be the growth parameters of the ith individual, and let $m_i = \exp(-K_i)$ and $b_i = L_{\infty,i}(1 - m_i)$. From Equation (1), m_i and b_i represent the expected slope and y-intercept of the L_{t+1} vs. L_t plot for the ith individual. Let K, L_∞, m, and b be the means over the population of the K_i, $L_{\infty,i}$, m_i, and b_i, respectively, and define $\alpha_i = m_i - m$ and $\beta_i = b_i - b$ to be the deviations from the mean slope and intercept for the ith individual. The shell height of the ith individual at time $t + 1$, $L_{t+1,i}$ depends on the random effects (α_i and β_i) as well as the mean slope and intercept:

$$L_{t+1,i} = (m + \alpha_i)L_{t,i} + (b + \beta_i) + \varepsilon, \quad (3)$$

where ε is a random error with expected value zero. Note that the slope and intercept obtained from a simple linear regression of L_{t+1} vs. L_t without random effects is not the same as m and b in Equation (3).

Using this notation, the parameters associated with the ith individual are

$$K_i = -\ln(m_i) = -\ln(m + \alpha_i) \quad (4)$$

and

$$L_{\infty,i} = \frac{b_i}{(1 - m_i)} = \frac{(b + \beta_i)}{(1 - m - \alpha_i)}. \tag{5}$$

Approximating $K_i = -\ln(m + \alpha_i)$ by a second-order Taylor polynomial,

$$K_i = -\ln(m + \alpha_i) \simeq -\left[\ln m + \frac{\alpha_i}{m} - \frac{\alpha_i^2}{2m^2}\right]. \tag{6}$$

Taking expectations in the above equation gives an approximately unbiased estimator for the mean growth parameter K:

$$K = E(K_i) \simeq -\ln m + \frac{\mathrm{Var}(\alpha_i)}{2m^2}. \tag{7}$$

A similar approximately unbiased estimate of $L_\infty = -E([b + \beta_i]/[1 - m - \alpha_i])$ can be obtained as the expected value of a ratio (see e.g. Rice, 1988, p. 147):

$$\begin{aligned}
L_\infty &= E\left(\frac{b + \beta_i}{1 - m - \alpha_i}\right) \\
&\simeq \frac{b}{1 - m} + \frac{1}{(1 - m)^2}\left[\frac{b\mathrm{Var}(\alpha_i)}{1 - m} + \mathrm{Cov}(\alpha_i, \beta_i)\right].
\end{aligned} \tag{8}$$

Approximate formulae for the standard errors of K and L_∞, σ_K and σ_{L_∞}, can be computed from Equations (7) and (8) using propagation of error techniques:

$$\sigma_K \simeq \frac{\sigma_m}{m} \tag{9}$$

and

$$\sigma_{L_\infty}^2 \simeq L_\infty^2\left[\frac{\sigma_b^2}{b^2} + \frac{\sigma_m^2}{(1 - m)^2} + \frac{2\sigma_b\sigma_m\rho}{b(1 - m)}\right], \tag{10}$$

where σ_b and σ_m are the standard errors of the estimated values of b and m, respectively, and ρ the correlation between the estimates of b and m.

It is also of interest to estimate the variability in the growth parameters $L_{\infty,i}$ and K_i in the population. To compute the variance of K_i,

$$\begin{aligned}
K_i^2 &\simeq \left[\ln m + \frac{\alpha_i}{m} - \frac{\alpha_i^2}{2m^2}\right]^2 \\
&\simeq \ln^2 m + \frac{2\alpha_i \ln m}{m} + \frac{\alpha_i^2}{m^2}(1 - \ln m),
\end{aligned} \tag{11}$$

where terms of order α_i^3 and higher have been neglected, as is reasonable because the α_i will be much smaller than 1. Taking expectations gives

$$E(K_i^2) \simeq \ln^2 m + (1 - \ln m)\frac{\mathrm{Var}(\alpha_i)}{m^2}. \tag{12}$$

From Equation (7),

$$E(K_i)^2 \simeq \left[-\ln m + \frac{\mathrm{Var}(\alpha_i)}{2m^2}\right]^2 \simeq \ln^2 m - \frac{\mathrm{Var}(\alpha_i)\ln m}{m^2}, \tag{13}$$

where the higher order term involving $\mathrm{Var}^2(\alpha_i)$ is taken as negligible. Thus,

$$\begin{aligned}
\mathrm{Var}(K_i) &= E(K_i^2) - E(K_i)^2 \\
&\simeq \ln^2 m + (1 - \ln m)\frac{\mathrm{Var}(\alpha_i)}{m^2} - \ln^2 m \\
&\quad + \frac{\mathrm{Var}(\alpha_i)}{m^2} \ln m = \frac{\mathrm{Var}(\alpha_i)}{m^2}.
\end{aligned} \tag{14}$$

The variance of $L_{\infty,i}$ can be computed similarly as

$$\mathrm{Var}(L_{\infty,i}) = \frac{1}{(1 - m)^2}\left[\frac{\mathrm{Var}(\alpha_i)b^2}{(1 - m)^2} + \mathrm{Var}(\beta_i) + \frac{2b}{1 - m}\mathrm{Cov}(\beta_i, \alpha_i)\right]. \tag{15}$$

Including covariates such as depth and latitude can give insights into environmental effects on growth (Kimura, 2008). Such covariates can easily be incorporated in the above model as additional fixed effects. For example, if m and b depend on linear covariates $y_1, y_2, \ldots, y_n$, then

$$m = m_0 + \sum_{i=1}^n m_i y_i \tag{16}$$

and

$$b = b_0 + \sum_{i=1}^n b_i y_i. \tag{17}$$

Equations (16) and (17) can be put into the above formulae [e.g. Equations (7) and (8)] to determine the effects of the covariates on growth coefficients.

All analyses were conducted using the statistical program R (v 2.8.1), using the mixed-effects (Pinheiro and Bates, 2000) package lme4. The increments included in the analysis were from all shells collected at random stations with at least two growth increments. The mixed-effects models were fitted based on maximal likelihood. Although such estimates can be biased for small samples, unlike those based on restricted maximal likelihood (REML), maximal likelihood estimates are statistically consistent, and in particular asymptotically unbiased (Pinheiro and Bates, 2000). Our datasets are quite large, and always the maximal likelihood and REML estimates were identical. We used maximal likelihood because, unlike REML, it can be used to test for significance of fixed-effects (covariate) terms. According to Pinheiro and Bates (2000), simple likelihood ratio tests for testing the significance of covariates can be somewhat "anti-conservative" in that they tend to suggest more parameters are significant than there actually are. For this reason, we used the Bayesian information criterion (BIC; Schwarz, 1978) to determine whether covariates are significant. BIC penalizes extra parameters more severely than the Akaike's information criterion (AIC) and is probably more appropriate for large datasets such as ours, but we report both AIC and BIC values.

Simulations

We conducted simulations to test the effectiveness of the mixed-effects methodology using R and the package MSBVAR. We simulated the growth of 1000 individuals assuming that L_∞ and K vary among the population as random variables with means 140 and 0.4, respectively. Except in the second and fourth sets of simulations, the growth parameters were assumed to be independent and normally distributed. Except the last set of simulations, each simulated individual contributed four shell heights to the analysis, representing their shell heights at ages 2, 3, 4, 5. Measurement error was simulated by perturbing the true simulated shell height L by $N_\sigma (L_\infty - L)$, where N_σ is a random number drawn from a normal distribution with mean 0 and standard deviation σ. This form assumes that measurement error is proportional to the annual growth increment, so that it is greater at smaller shell heights where growth is greater. For each simulation, the mean and standard deviations of the growth parameters K_i and $L_{\infty,i}$ were estimated using the mixed-effects methods discussed above.

The first set of simulations assessed the effect of individual variability in growth by varying the coefficient of variation (CV) of growth for both K and L_∞ between 0 and 0.25, using a measurement error factor of $\sigma = 0.01$. Naive Fabens estimates were also calculated as a comparison. The second set is the same as the first, except that the growth parameters were simulated as independent gamma random variables. Third, we fixed individual variability for K and L_∞ at 0.04 and 14, respectively, corresponding to CVs of 0.1, whereas the measurement error factor σ was varied from 0 to 0.2 to evaluate its effect on the mixed-effects estimates. Next, we simulated K_i and $L_{\infty,i}$ as correlated normals, with the CVs of K and L_∞ fixed at 0.1 and a measurement error factor of 0.01, and the correlation between growth parameters ranging from -1 to 1. Finally, we conducted a simulated tagging experiment, where each individual contributes a single increment, rather than four increments as in all the simulations above. Otherwise, the simulated data were identical to the first set. Because there was only one increment per individual in this set of simulations, we had to assume in the mixed-effects analysis that all the individual variability was in L_∞, although we simulated variability in both growth variables. Assuming that variability occurs in only one growth coefficient is typical in analysis of tagging experiments; these simulations can assess the effects of this simplification.

Results

Simulated data can appear similar to actual data, if there is sufficient variability in t_0 (Figure 2a, cf. Figure 3a; note that neither the value of t_0 nor its variability affects any of the estimates given here). Simulations indicated that our mixed-effects methodology always estimated the mean K and L_∞ to within 2% of their true values, and usually within 1% when individual variability in the growth parameters was varied in the realistic range of 0 to 0.25 CV (Figure 2b). Simulating the parameters as gamma, rather than normal, random variables does not change this result (Figure 2c). In contrast, individual variability caused the naive Fabens model to be biased (Sainsbury, 1980), with the estimates of K biased low and L_∞ high; this bias became severe as the variability was increased. Random measurement error did not appear to affect the estimates of the mean coefficients substantially, which remained within

2% of their true values even with measurement error as high as 20%. Similarly, correlation between the growth parameters K and L_∞ had no effect on the ability of the mixed-effects model to recover the mean growth parameters (Figure 2d). Simulated tagging data, which had only a single growth increment per individual and only estimated variability in L_∞, were still able to recover mean growth parameters well when individual variability in the growth parameters was less than 10% (Figure 2e). At high levels of individual variability, however, the estimates of K tended to be biased low by 2–5%. Additionally, the estimated standard deviation of $L_{\infty,i}$ in this set of simulations was biased slightly high (mean bias <3%), because the random effects in the intercept had to take into account the true simulated variability in both the intercept and the slope (i.e. in both K and L_∞).

Basic von Bertalanffy growth curves for Mid-Atlantic and Georges Bank sea scallops using the mixed-effects model were well estimated with low standard errors (Tables 1 and 2), owing to the large quantity of data (7493 increments from 2494 shells from the Mid-Atlantic, 16 616 increments from 4092 shells from Georges Bank; Figure 3). Mixed-effects estimates of L_∞ were less and estimates of K were greater than those obtained from the Fabens method using Equation (2) that lacks random effects. The estimate of the mean Brody growth coefficient K was greater in the Mid-Atlantic, whereas the mean L_∞ was greater on Georges Bank. These mean growth coefficients imply that growth is similar in the two regions until ∼100 mm shell height, after which sea scallops on Georges Bank grow faster (Figure 3e). Estimated individual growth variability had standard deviations of ∼25% of the estimated mean K and 10% of the estimated mean L_∞. The parameters K and L_∞ were strongly positively correlated (0.6–0.7) among individuals in both regions.

The mean L_∞ decreased significantly and substantially with increasing depth in both regions (Tables 1 and 2, Figure 4). Models that also included depth effects for the mean slope (implying a depth effect on K) only decreased the BIC statistic in the Mid-Atlantic. Similarly, latitude had a significant effect on the intercept (i.e. on L_∞) always, but including a latitude effect on the slope increased BIC except in the closed portion of Georges Bank. The mean L_∞ decreased ∼11 mm from the southernmost to the northernmost latitude in the Mid-Atlantic at fixed depth; the latitude effect on Georges Bank was smaller (Table 2, Figure 5).

Three large portions of Georges Bank and Nantucket Shoals have been closed to scallop and groundfish fishing for most of the time since 1994 (Hart and Rago, 2006). Although some scallop fishing has been permitted in parts of these closed areas during 1999–2001 and since 2004, the overall fishing mortality in the closed areas has been considerably less than that in scallop grounds outside these areas. Therefore, we can examine differences in growth inside and outside the closed areas to determine if fishing induces changes in growth. The asymptotic size L_∞ was greater inside the closed areas by more than 10 mm, but the estimated K was somewhat less than that in the fished areas (Table 1). Combining these effects indicates that growth in closed and open areas is similar until around 80–90 mm shell height, after which sea scallops in the closed areas grow faster (Figure 6a). Inclusion of covariates such as depth, latitude, and density in the analysis does not alter this conclusion.

Scallop density had a significant (negative) effect on growth only in the fished portion of Georges Bank (Figure 6b).
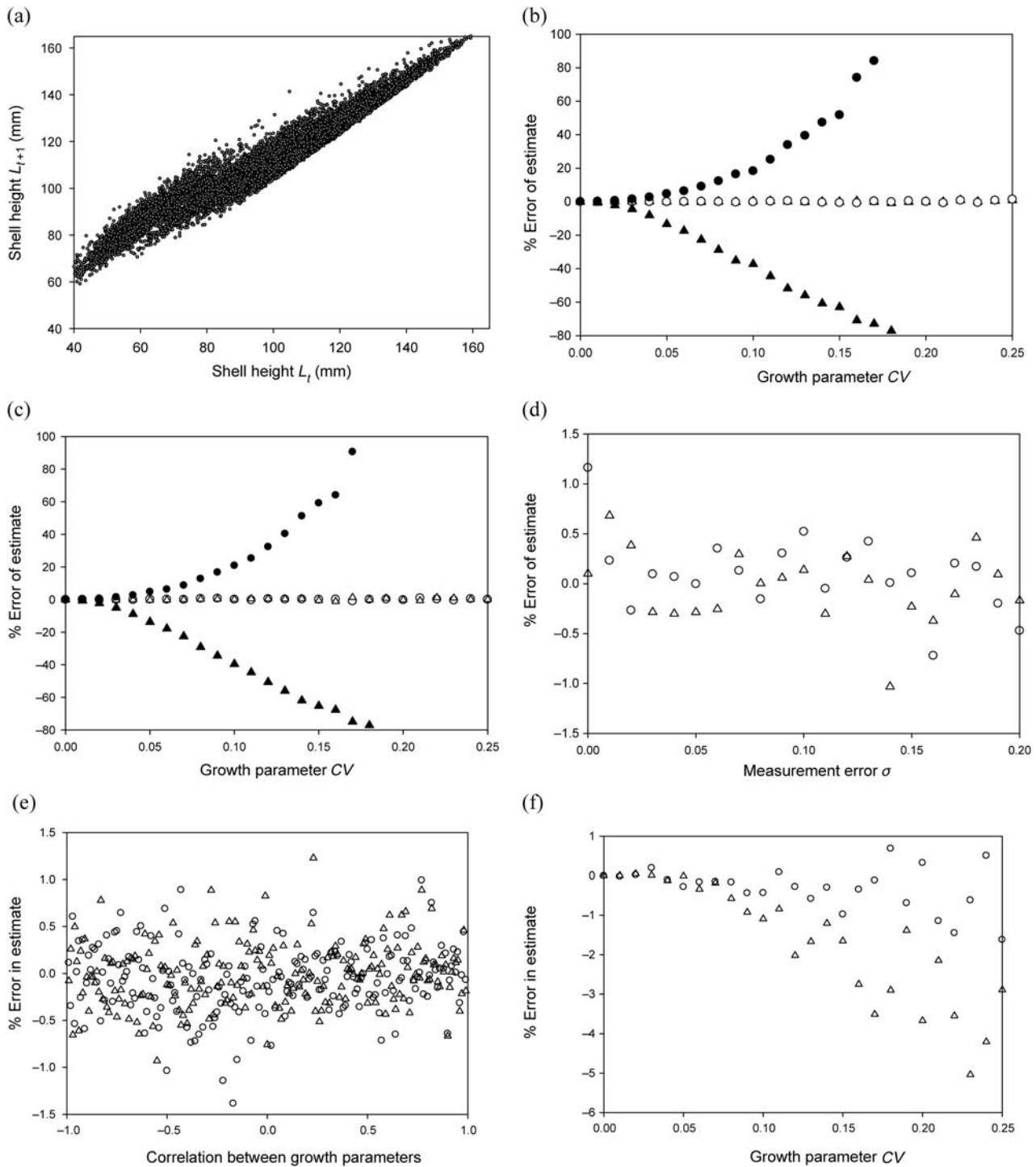
Figure 2. (a) Plot of example simulation, with parameters identical to that estimated in the Mid-Atlantic (cf. Figure 3a), with the variability in t_0 set at 0.2. (b) Percentage errors in the mean estimates of K (triangles) and L_∞ (circles) at various coefficient of variations (CVs) of individual variability of the growth parameters using the naive Fabens model (closed) and mixed-effects model (open). Errors in the Fabens model for CVs greater that 0.18 are extreme and not shown. (c) As in (b), but K and L_∞ are simulated as gamma random variables, rather than normal. (d) Effects of measurement error on the percentage errors in the mean estimates of K (triangles) and L_∞ (circles) for the mixed-effects model. (e) Effects of correlation between growth parameters on the percentage errors in the mean estimates of K (triangles) and L_∞ (circles) for the mixed-effects model. (f) As in (b) (mixed-effect estimates only), but using simulated tagging data, with only one growth increment per individual, and estimating individual variability in L_∞ only.

The density effect for Mid-Atlantic was also negative, but borderline non-significant in that inclusion of density as a covariate decreased the AIC statistic but increased the BIC. In the closed portion of Georges Bank as well as Georges Bank as a whole, including a density effect increased both AIC and BIC, so density was not included as a covariate.
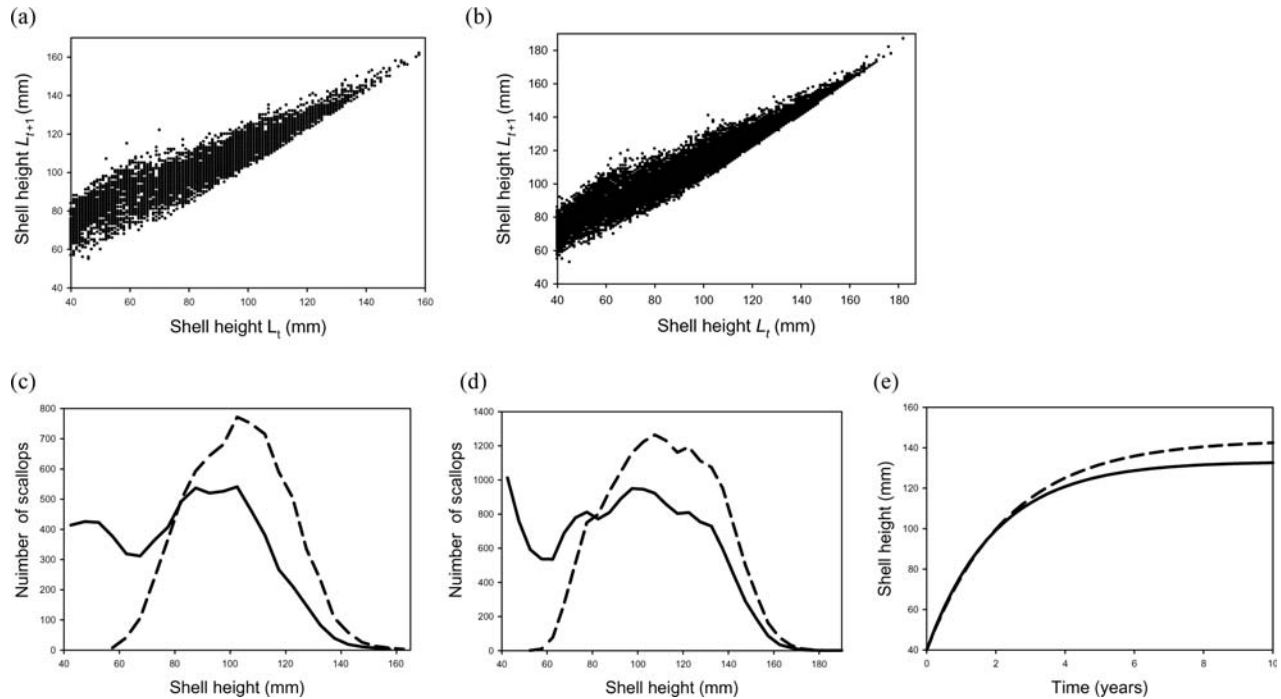
Figure 3. Plots of shell heights L_t vs. L_{t+1} for sea scallops in (a) the Mid-Atlantic Bight and (b) Georges Bank. Plots of L_t (solid line) and L_{t+1} (dashed line) for the Mid-Atlantic (c) and Georges Bank (d). (e) Plot of the growth of a 40-mm scallop with the mean growth parameters in the Mid-Atlantic (solid line) and Georges Bank (dashed line).

Table 1. Estimates of von Bertalanffy growth parameters without covariates for sea scallops in the Mid-Atlantic Bight (MA), Georges Bank (GB), and the open (fished) and closed portions of GB using the mixed-effects model.

Area	K	L_∞	σ_K	σ_{L_∞}	s.d. K_i	s.d. $L_{\infty,i}$	# incr.	# shells
MA	0.508	133.3	0.004	0.4	0.13	13.4	7 293	2 294
GB	0.427	143.9	0.002	0.3	0.11	14.8	16 616	4 092
MA naive	0.416	138.6	–	–	–	–	7 493	2 494
GB naive	0.339	152.4	–	–	–	–	16 616	4 092
GB open	0.457	136.3	0.004	0.5	0.12	15.1	5 428	1 463
GB closed	0.413	147.8	0.003	0.3	0.10	13.2	11 188	2 629

Basic estimates without covariates. Naive estimates for MA and GB using the Fabens (1965) model without random effects are also given for comparison. The columns represent, respectively, mean K, mean L_∞, the standard errors of those estimates (σ_K and σ_{L_∞}), estimated standard deviations of the individual variability in K and L_∞ in the populations (s.d. K and s.d. L_∞), and the number of increments and shells used for each area.

Discussion

The linear mixed-effects approach introduced here gives a simple method for accommodating individual growth variability into the von Bertalanffy growth models. It can be applied using any standard statistical software that can include random factors in linear models. Because it only requires estimates of the variance of the individual variability of the growth parameters, this method makes no assumption regarding the distribution of individual variability other than the existence of the second moment and that the approximations by the second-order Taylor polynomials are good. Both of these assumptions are likely to be valid in most practical applications. The Taylor polynomials will be good approximations if $\mathrm{Var}(\alpha_i)$ and $\mathrm{Cov}(\alpha_i, \beta_i)$ are well below 1. This will almost certainly be true because the individual slopes $m + \alpha_i$ are bounded between 0 and 1, and the random component α_i is typically much smaller than the population mean slope m.

The simulations indicated that the model is robust to the level of individual variability, measurement error, and correlation between the growth parameters. The mixed-effects package we employed (R with lme4), like nearly all such software, is based on the assumption that the random effects are normally distributed. This could cause difficulties if, under this assumption, there was a non-negligible probability of an individual having a slope greater than 1 or less than zero (implying a negative or non-existent value of K). In our applications, however, the population mean slopes were all more than 4 s.d. from zero and 1, indicating that normality of this variable is a reasonable approximation. This was confirmed by the simulations where the growth parameters were assumed to follow gamma distributions, but the mixed-effects model was still able to recover the simulated mean growth parameters nearly precisely, although the assumption of normality was not exactly satisfied. Techniques have recently been developed for the estimation of linear mixed-effects models that allow for non-normal distributions (Chen et al., 2002), which could be employed when the normality assumption is seriously violated.

Our data are unusual in that there are multiple growth increments for each individual. This allowed us to assume and

Table 2. Estimates of von Bertalanffy growth parameters including the covariates of depth (m), latitude (lat, degrees), and density (den, numbers per tow).

| Region	Covariates	K	L_∞	AIC	BIC
MA	None	0.508	133.3	42 466	42 507
MA	Depth (L_∞ only)	0.506	187.8 − 0.922 depth	41 202	41 250
MA	Depth (L_∞ and K)	0.574 − 0.00134 depth	177.4 − 0.882 depth	41 192	41 247
MA	Depth (L_∞ and K) + lat (L_∞ only)	0.574 − 0.0012 depth	309.0 − 0.947 depth − 3.1 lat	41 102	41 164
GB all	None	0.427	143.9	93 373	93 420
GB all	Depth (L_∞ only)	0.424	174.1 − 0.420 depth	92 724	92 778
GB all	Depth + lat (L_∞ only)	0.424	244.3 − 0.414 depth − 1.71 lat	92 714	92 776
GB open	None	0.457	136.3	30 151	30 190
GB open	Depth (L_∞ only)	0.453	169.6 − 0.447 depth	29 838	29 884
GB open	Depth + lat (L_∞ only)	0.453	71.4 − 0.446 depth + 2.38 lat	29 830	29 883
GB open	Depth + lat + den (L_∞ only)	0.451	7.661 − 0.434 depth + 4.03 lat − 0.003 den	29 785	29 851
GB closed	None	0.413	147.8	62 795	62 839
GB closed	Depth (L_∞ only)	0.411	172.0 − 0.343 depth	62 519	62 570
GB closed	Depth + lat (L_∞ only)	0.411	266.9 − 0.332 depth − 2.32 lat	62 507	62 566
GB closed	Depth (L_∞ only) + lat (L_∞ and K)	1.41 − 0.0243 lat	193.4 − 0.339 depth − 0.53 lat	62 492	62 558

The Akaike's information criterion statistic (AIC) as well as the Bayesian information statistic (BIC) are also shown. Only covariates which reduced the BIC when included in the model are shown.
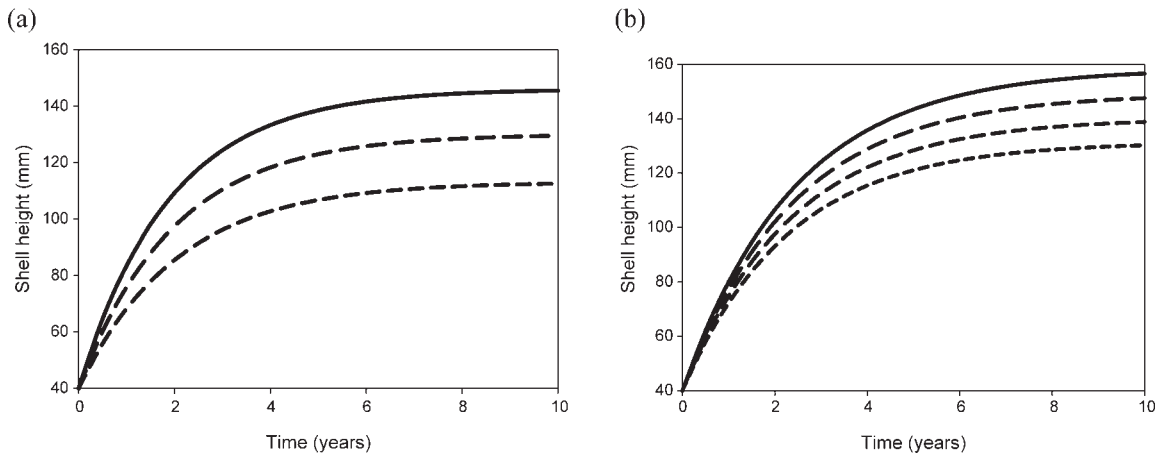
Figure 4. (a) Effects of depth on the growth of a 40-mm sea scallop with the mean growth parameters at 40 m (solid line), 60 m (long dashed line), and 80 m (short dashed line) in the Mid-Atlantic. (b) Effects of depth on growth of a 40-mm sea scallop on Georges Bank with the mean growth parameters at 40 m (solid line), 60 m (long dashed line), 80 m (medium dashed line), and 100 m (short dashed line).
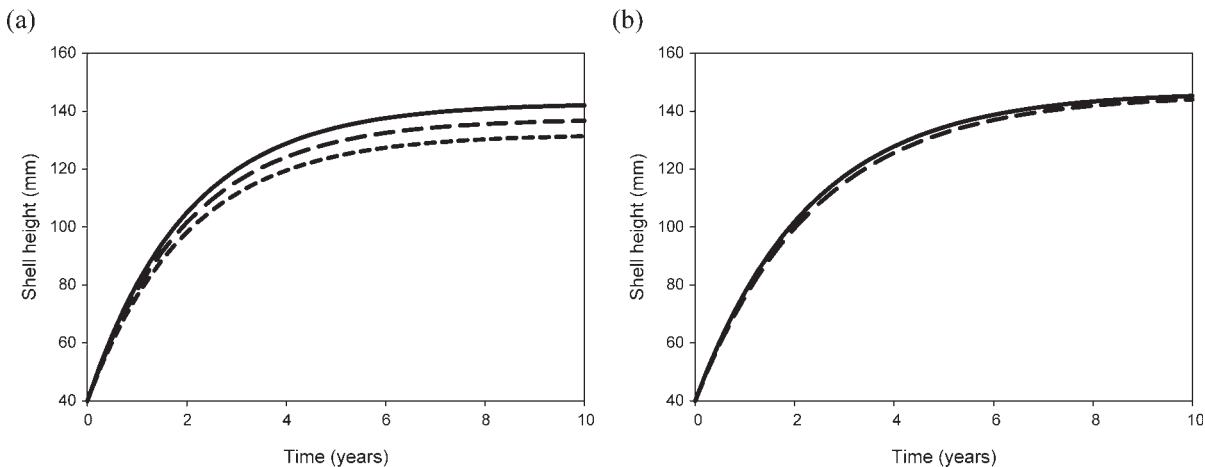
Figure 5. Effects of latitude on the growth of a sea scallop starting at 40 mm with the mean growth parameters at (a) 37°N (solid line), 39°N (long dashed line), and 41°N (short dashed line) in the Mid-Atlantic and (b) 40.5°N (solid line) and 42°N (dashed line) on Georges Bank.

(a)

(b)
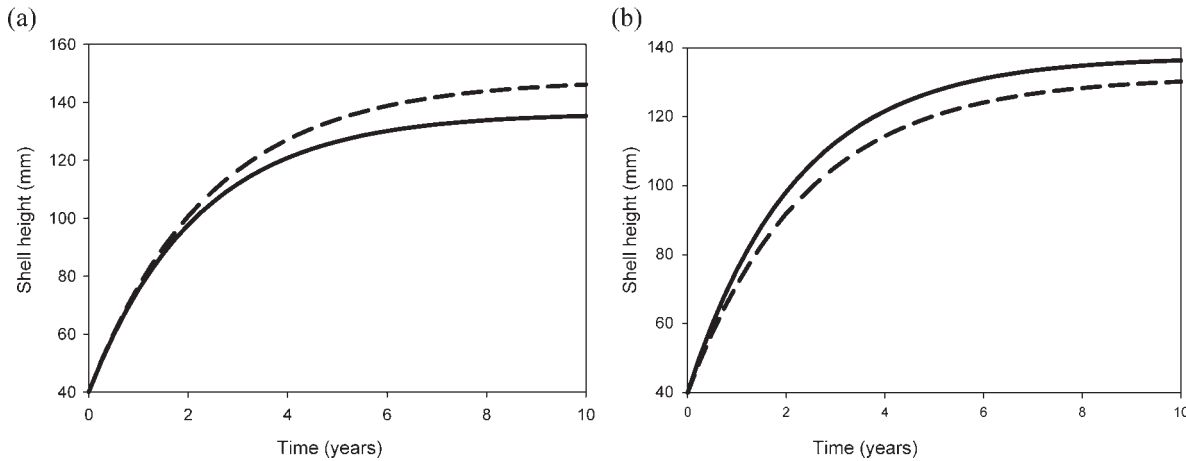
Figure 6. (a) Growth of a sea scallop starting at 40 mm with mean growth parameters in the fished (solid line) and closed (dashed line) portions of Georges Bank. (b) Growth of a sea scallop starting at 40 mm with mean growth parameters at low density ($<$300 tow^{-1}, solid line) and high density (3000 tow^{-1}, dashed line) in the fished portion of Georges Bank at 70-m depth and 41°N latitude.

estimate variability in both growth parameters and to estimate their correlation. In the more common case where only one growth increment exists for most or all individuals, as is typical for most tag-recapture data, it would be difficult to estimate individual variability in both K and L_∞. However, it appears that estimating individual variability in L_∞ alone is sufficient to produce approximately unbiased estimates of the mean growth parameters, even in the case where this assumption is not correct, i.e. even when K varies among individuals, except at very high levels of individual variability.

Fabens' method can be alternatively expressed in terms of relating the growth increment ΔL during a time Δt to starting length (or shell height) L:

$$\Delta L = (L_\infty - L)[1 - \exp(-K\Delta t)]. \tag{18}$$

This leads to an alternative formulation of the mixed-effects model as

$$\Delta L_i = (\mu + \mu_i)L + (c + c_i) + \varepsilon, \tag{19}$$

where $\mu + \mu_i = -[1 - \exp(K_i\Delta t)]$, $c + c_i = L_{\infty,i}[1 - \exp(K_i\Delta t)]$, and $E(\mu_i) = E(c_i) = 0$. Estimates for the mean von Bertalanffy parameters can then be derived in a similar manner to that in the methods section:

$$K \simeq -\ln(1 + \mu) + \frac{\text{Var}(\mu_i)}{2(1 + \mu)^2} \tag{20}$$

$$L_\infty \simeq -\frac{c}{\mu} - \frac{1}{\mu^2}\left[\frac{c}{\mu}\text{Var}(\mu_i) - \text{Cov}(c_i, \mu_i)\right]. \tag{21}$$

We preferred the formulation described in the methods section because the left-hand side of Equation (19) is a derived quantity, rather than the directly measured quantity in Equation (3). Additionally, simulations indicated that using this alternative formulation gave slightly less precision than our preferred method.

Most previous studies of scallop growth (e.g. Merrill *et al.*, 1966; Thouzeau *et al.*, 1991; Smith *et al.*, 2001) were based on shell height-at-age data. Obtaining absolute ages of scallops is difficult because of the lack of distinct early rings (Claereboudt and Himmelman, 1996). The approach used here avoids this issue by using growth increment data that do not require knowledge of absolute age, and it may be a more reliable method of estimating sea scallop growth. Our large dataset allowed us to obtain precise estimates of both growth parameters as well as their variances among the population. In cases where the data for each population are more limiting, Bayesian hierarchical models may be useful (Helser and Lai, 2004; Helser *et al.*, 2007).

Our estimate of L_∞ on Georges Bank is similar to that estimated by a number of other studies, but our estimate of K is somewhat higher than most others (Table 3). Some of these other estimates were based on data from only a few sites (e.g. Harris and Stokesbury, 2006) or only a portion of Georges Bank (Thouzeau *et al.*, 1991). The estimate most comparable with ours is that of Serchuk *et al.* (1979), who estimated a slightly larger L_∞ and smaller K than our estimate. The difference between our estimate

Table 3. Comparison of (mean) growth parameter estimates for sea scallops from selected studies on Georges Bank and the Mid-Atlantic.

Source	K	σ_K	L_∞	σ_{L_∞}
Georges Bank				
This study	0.427	0.002	143.9	0.11
Harris and Stokesbury (2006)[a]	0.51	0.04	140.0	2.1
Harris and Stokesbury (2006)[a]	0.36	0.04	148.6	4.0
Harris and Stokesbury (2006)[a]	0.27	0.09	121.1	6.2
Thouzeau *et al.* (1991)	0.281	–	144.9	–
Serchuk *et al.* (1979)	0.337	–	152.5	–
Posgay (1979a)	0.37	–	143.6	–
Merrill *et al.* (1966)	0.232	–	143.3	–
Merrill *et al.* (1966)	0.226	–	145.1	–
Mid-Atlantic				
This study	0.508	0.004	133.3	0.13
Serchuk *et al.* (1979)	0.300	–	151.8	–

When available, estimates of the standard errors of the estimates are also given.
[a]The first two estimates from Harris and Stokesbury (2006) were from one site, using two different estimation techniques, and the third estimate was from a second site. All their estimates may be biased because they did not include random effects nor seasonal variability of growth in the analysis of their tagging data.

and that of Serchuk *et al.* (1979) was much greater in the Mid-Atlantic region. This area was a much smaller component of the sea scallop fishery before 1979 than more recently (Hart and Rago, 2006), and the shell samples from the Mid-Atlantic were much more limited. Additionally, many of the shell samples used by Serchuk *et al.* (1979) were collected from commercial fishers, who likely fish the nearshore and relatively shallow portions of the Mid-Atlantic harder than those in deeper water, and thus may have biased that estimate towards greater asymptotic shell height.

The asymptotic size of sea scallops on Georges Bank was estimated here to be greater than that in the Mid-Atlantic, whereas K was larger in the Mid-Atlantic. Independent evidence that L_∞ is greater on Georges Bank can be seen from the shell heights from the annual NEFSC sea scallop survey (Figure 7). Both populations exhibited truncated size distributions before the late-1990s as a result of overfishing (Hart and Rago, 2006). As the populations recovered, the number of scallops between 100 and 140 mm shell height increased dramatically in both regions, and scallops >140 mm became common on Georges Bank but remained rare in the Mid-Atlantic. The negative relationship between K and L_∞ between these two populations of sea scallops is similar to that noted in other studies (e.g. Helser and Lai, 2004; Helser *et al.*, 2007).

The growth parameters K and L_∞ were positively correlated within each population for sea scallops, contrary to the usual idea that these parameters are negatively correlated. Negative correlations are often caused by an estimation artefact: a given pair of parameters K and L_∞ produces a similar growth curve to one with slightly smaller K and slightly larger L_∞. This phenomenon is distinct from the true correlation of these parameters among individuals within the population that was estimated here. The positive relationship we found for sea scallops differs from the only other study that estimated this correlation: Pilling *et al.* (2002) found a negative correlation for the tropical emperor fish *Lethrinus mahsena* using back-calculated length-at-age from scales. This suggests that the sign of the correlation between growth coefficients may be species-dependent. Alternatively, errors in the back-calculated lengths may have created an artificial negative correlation.

The decreased asymptotic shell height of sea scallops that we observed with depth has been noted before (Posgay, 1979b; MacDonald and Thompson, 1985, 1988; Schick *et al.*, 1988; Smith *et al.*, 2001) and is likely the result of reduced concentrations of phytoplankton at greater depths (Broom and Mason, 1978; MacDonald and Thompson, 1985; Hart and Chute, 2004). Scallop meat weights at shell height also tend to decline with depth (Smith *et al.*, 2001; Lai and Helser, 2004; Hart and Rago, 2006). Bottom currents $<10 \text{ cm s}^{-1}$ can cause reduced feeding rates, resulting in reduced growth (Wildish *et al.*, 1987; Fréchette and Daigle, 2002; MacDonald *et al.*, 2006). Bottom currents are $<10 \text{ cm s}^{-1}$ in the Mid-Atlantic but generally greater than this number on Georges Bank (Moody *et al.*, 1984) which may explain the differential asymptotic sizes in the two regions. Bottom current speed also tends to decline with depth. This would not affect growth on Georges Bank, where currents stay well above the 10 cm s^{-1} threshold, but may cause further reduction in growth in the Mid-Atlantic. This may be why growth declines faster with depth in the Mid-Atlantic than on Georges Bank. The warmer mean temperatures in the Mid-Atlantic suggest that metabolic rates are generally faster there, leading to a higher K, whereas the lower L_∞ may be the result of lower bottom current speeds in this region.

Perhaps our most surprising result is that growth is substantially greater in areas closed to fishing. We can envision three putative explanations: (1) sublethal incidental damage caused by discarding and/or contact with fishing gear causes slower growth; (2) the result is an artefact caused by false annuli created by sublethal incidental damage; (3) faster-growing scallops are removed in fished areas at a greater rate than slow-growing ones. Sublethal damage by gear would be expected most often with smaller scallops that are more likely to be discarded or pass through the dredge bag rings. However, growth in fished and closed areas appear similar until around 90 mm, the shell height at which the scallops are recruited to the fishery. Therefore, the evidence is inconsistent with hypothesis (1), which would predict reduction in growth in prerecruit scallops. This argument can also be applied to hypothesis (2). Additionally, the primary effect of false annuli would be to induce an underestimation in K, whereas it is L_∞ rather than K that is decreased in the fished
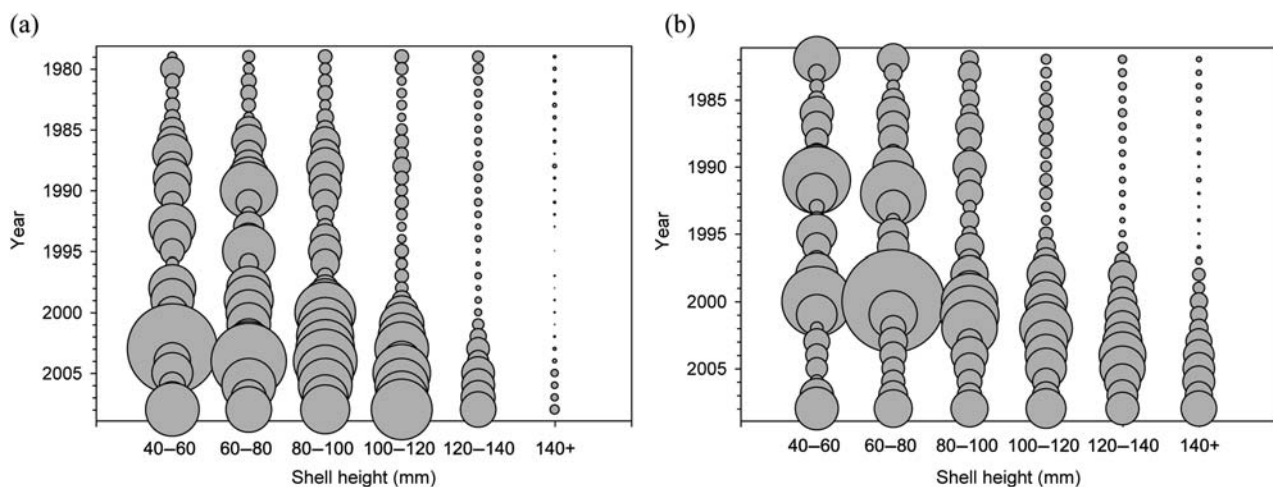
Figure 7. Relative mean stratified numbers-at-shell height of sea scallops in (a) the Mid-Atlantic and (b) Georges Bank, from the annual NEFSC sea scallop survey. The areas of the bubbles are proportional to the numbers-at-shell height.

areas. On the other hand, hypothesis (3) is consistent with the results. In particular, removal of fast-growing scallops by the fishery would only affect the growth of larger recruited scallops, as observed. Kaiser *et al.* (2007) similarly found that the gonad and adductor muscle weights of the great scallop *Pecten maximus* were greater in areas closed to scallop fishing.

In most fisheries, the selective removal of faster-growing individuals is usually caused by the fact that faster-growing fish will recruit sooner to the fishery (Lee's phenomenon). However, it is unlikely that this effect can be the full cause of the difference, because the differential growth is most apparent for fully recruited scallops >90 mm. Additionally, fishing mortality in the fished areas has been greatly reduced in recent years (Hart and Rago, 2006), so that only a small fraction of the fast-growing individuals would be removed during the fairly short time (~1 year) that they are recruited to the fishery, but the slower-growing individuals of the same age are not. Because they are sedentary, sea scallop growth is affected by their microenvironment and, in particular, by their phytoplankton food supply. It appears from this and other studies that food supply strongly affects L_∞. Areas of rapid growth will be attractive to fishers because the scallops will tend to be larger there than in other areas. Therefore, the faster-growing individuals are likely subject to greater fishing mortality, so that the apparent mean growth of the remaining scallops in the fished areas will be less (and in particular would have a smaller L_∞ than that observed in closed areas).

Scallop density appears to have little effect on growth. The maximum observed density was 11 732 scallops tow^{-1}. A survey tow sweeps ~4500 m^2, with an efficiency of ~0.35 (NEFSC, 2007), giving a maximum observed density over a tow of ~7.4 scallops m^{-2}. Sea scallops filter around 10 l h^{-1} (Pilditch *et al.*, 2001), so that 7.4 scallops would filter around 1776 l d^{-1}. This compares with a total water column volume of 50 000 l m^{-2} at a typical depth of 50 m, so that even at the highest densities, the scallops would clear <4% of the water volume per day. Density-dependent growth resulting from food limitation has been observed in sea scallops only at much higher densities, e.g. in cultured environments (Côté *et al.*, 1993, 1994). Because density-dependence in growth was only observed in fished portion of Georges Bank, it cannot be the result of food depletion. Fishing mortality in sea scallops increases with their local density (Hart, 2001), so selective removal of fast-growing scallops may become more severe at higher densities and fishing mortalities, thus leading to a reduction in observed growth with density in fished areas only.

Acknowledgements

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