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A GROWTH MODEL FOR *ARCTICA ISLANDICA*: THE PERFORMANCE OF TANAKA AND THE TEMPTATION OF VON BERTALANFFY—CAN THE TWO COEXIST?

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ABSTRACT Organisms increase in size over time (age) due to excess assimilation over metabolic (respiration) energy demands. Most organisms reach a maximum size with increasing age as gain and loss balance. The von Bertalanffy length-at-age relationship, which is commonly used in fishery assessment calculations, imposes such a maximum size. However, some fished species, such as ocean quahogs, *Arctica islandica*, are long lived and continue to grow at old age. The Tanaka age-at-length relationship has continued growth at old age, but is rarely used in stock assessment models. A modified form of the von Bertalanffy model is presented, which mimics the continued growth at old age of the Tanaka model by allowing the growth parameter (K) to decline with age. This form is suitable for inclusion in stock assessment models based on von Bertalanffy. The proposed model matches Tanaka curves with precision appropriate for the scatter of data used to fit the curves. The observations of ocean quahog length at age and growth rate from New Jersey and Georges Bank demonstrate the ability of the modified von Bertalanffy relationship to represent continued growth at old age for this fished species. Simulated data generated with continued growth at old age were fit with the Stock Synthesis model (SS3). Results comparing traditional and modified growth relationships showed that the original von Bertalanffy model can reasonably approximate modest nonasymptotic growth as long as the number of observations is sufficient to constrain the parameter values.

KEY WORDS: Arctica islandica, shellfish fisheries, length-at-age, growth model, ocean quahog, Bertalanffy growth

INTRODUCTION

Most organisms increase in size over time in response to excess assimilated energy above metabolic demands, often termed scope for growth (Barillé et al. 1997, Munroe et al. 2013, Sanders et al. 2014). This excess energy is used to increase the body structure of the organism by the addition of somatic or reproductive tissues. For larger organisms, this increase in size is not reversible, should metabolic demands outpace assimilation. This irreversibility depends on how size is determined, however. In bivalves, the size of the shell does not reduce under stress, whereas the tissue wet weight will, leading to the commonly used metric of condition index (Rainer & Mann 1992). In bony fish, the fish length (or other bony structures) do not decline under stress, whereas total wet weight can.

A measure of animal length (total length, shell length, etc.) is normally used to describe the monotonic increase in size with age. This choice leads to a number of mathematical relationships relating animal size (e.g., length) and age. The growth characteristics of the target animal dictate which of the models is most appropriate. One benefit of these mathematical formulas is to average over growth variability due to different environmental effects on individual growth rates, not the least of which is the differential in growth performance within cohorts and populations (Banks & Fitzpatrick 1991, Hofmann et al. 2006, Beukema & Dekker 2015), as well as variability in estimation of length or age from samples (Heery & Berkson 2009, Jacobson et al. 2010). A second benefit is the link between size versus age ($L(A)$) and growth rate versus age ($G(A)$) in which the growth rate is the derivative of the size expression, or

$$G(A) = \frac{d}{dA} L(A). \tag{1}$$

A large number of growth models have been applied to bivalves: these generally fall into two categories. The most common type describes asymptotic growth leading to an estimate of average maximum size. These include Richards, logistic, Gompertz (e.g., McCuaig & Green 1983, Devillers et al. 1998, Millstein & O'Clair 2001, Luquin-Cavarrubias et al. 2016), and the most commonly invoked option, von Bertalanffy (e.g., Kraeuter et al. 2007, Harte & Chute 2009, Selin 2010, Çolakoğlu & Palaz 2014, Peharda et al. 2015, Bottari et al. 2017). The von Bertalanffy model has been the subject of many analyses related to model performance and statistical analysis (e.g., Kimura 1980, Jensen 1997, Wang & Milton 2000, Ohnishi & Akamine 2006, Helidoniotis & Haddon 2013) and is routinely invoked in population dynamics models (e.g., Barry & Tegner 1989, Jensen 1996, Quinn & Collie 2005, Thórarinsdóttir & Jacobson 2005, Hennen et al. 2018).

The von Bertalanffy model (von Bertalanffy 1957) has a fixed largest size, which is appropriate for most marine species with skeletal hardparts, including most fished species. Although the von Bertalanffy model is the common choice in fisheries assessment models, it does not represent the growth behavior of some fished species. In particular, a few species do not have asymptotic growth (Tanaka 1982) and the most famous of these is the ocean quahog, *Arctica islandica* (Pace et al. 2017b, Hemeon et al. 2021). The growth rate of ocean quahogs slows with age, but even the oldest ocean quahogs continue to grow at a rate

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that cannot be described by an asymptotic growth model (Pace et al. 2017b, Hemeon et al. 2021). The Tanaka model (Tanaka 1982, 1988) has been shown to satisfactorily model ocean quahog growth. Unfortunately, this model is not readily available in present-day modeling toolboxes and structurally is foreign to the metrics typically associated with von Bertalanffy growth. Development of a von Bertalanffy style model capable of simulating Tanaka style growth consequently would be useful.

This paper addresses the issue of making a modification to the von Bertalanffy model to have it behave like the Tanaka model for organisms with continuing old age growth. The Tanaka–von Bertalanffy conundrum is addressed using the ocean quahog (*Arctica islandica*) as the paradigmatic species. The ocean quahog is known to live for centuries and is the target of a fishery on the east coast of North America (among other areas) (Kennish & Lutz 1995, Thórarinsdóttir & Jacobson 2005, Hennen 2015). The species is not only characterized by nonasymptotic growth, but also lives sufficiently long that the growth rate at a given age for older animals is lower than for younger animals as the latter have lived later during the time of warming temperatures (Hemeon 2022, Pace et al. 2018, Sower 2022). This further expands the tendency for growth rates at old age to continue to diverge notably from asymptotic behavior. First, the Tanaka growth model is considered. Then, an adaptation of the von Bertalanffy growth model is introduced with the aim of developing an implementation sufficiently similar to the Tanaka model for satisfactory emulation.

TRADITIONAL AGE-LENGTH MODELS

Details of the Tanaka and von Bertalanffy models follow. A suggested modification of the von Bertalanffy model is then presented and compared with the behavior of the Tanaka model. The parameter values initially chosen for the two models are chosen somewhat arbitrarily but have the property that the growth over the first half of the lifetime matches closely. Afterward, the growth models are further compared using growth trajectories obtained from living ocean quahogs obtained from the northwestern Atlantic with birth dates covering the 1800 to 1980 period. In this analysis, length (L) has units of mm and age (A) has units of years.

The development of both of these models proceeds from specification of the growth rate at age relationship, which is then integrated to obtain the length-at-age equation. This explains the simple form of the growth equations and the relatively complicated form of the length equations.

von Bertalanffy Model

The von Bertalanffy model (von Bertalanffy 1957) is represented by Eq. 2, which specifies that the organism length approaches (exponentially) the largest size (L_∞),

$$L(A) = L_\infty\left(1 - e^{-K(A-a_o)}\right), \tag{2}$$

where, a_o is the age of the animal when it recruits and K controls the growth rate.

The growth versus age Eq. 3 is obtained from the derivative of the length Eq. 2 as,

$$G(A) = K L_\infty e^{-K(A-a_o)} = K(L_\infty - L(A)). \tag{3}$$

The growth rate at recruitment ($A = a_o$) is $K L_\infty$, which is the largest growth rate. Clearly, the growth stops as the organism size reaches L_∞.

An illustration of the form of these equations (Fig. 1A,B) is obtained using the following parameters:

$$L_\infty = 100 \text{ mm} \qquad K = .03 \text{ year}^{-1} \qquad a_o = 0 \text{ year}.$$

These parameter choices roughly represent a long-lived mollusc species similar to the ocean quahog.

Tanaka Model

The Tanaka model has been applied to model growth in bivalves (Tanaka 1982, Pace et al. 2017b, Hemeon et al. 2021), sea urchins (Ebert et al. 1999, Lamare & Mladenov 2000, Ebert 2013), and fish (Mercier et al. 2011). The Tanaka model

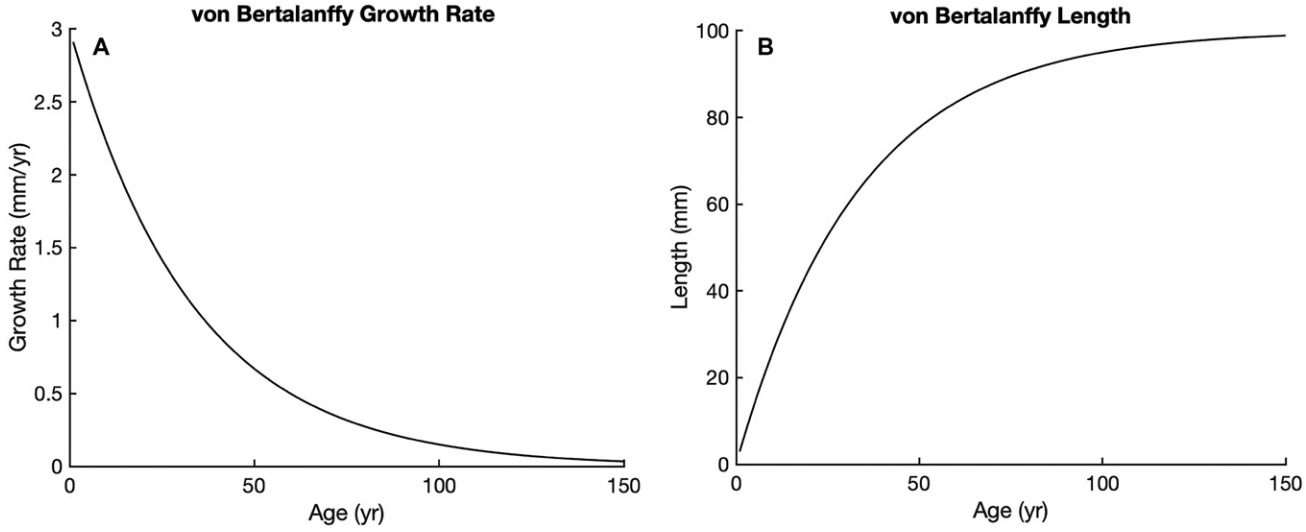

Figure 1. Relationship of von Bertalanffy growth rate (A, left) and length (B, right) versus age. Model parameters are $a_o = 0, L_\infty = 100, K = .03$.

provides for animal growth through all ages, although at a declining rate as age increases. From physiological considerations, most species reach a size where metabolic (respiration), and perhaps reproductive, demands equal the assimilation rate resulting in the animal having no scope for growth and growth effectively ceases. Species represented by the Tanaka model have not reached a size for which metabolism exceeds assimilation. A better explanation is that the animal is able to increase its assimilation as size increases in such a way that scope for growth remains positive at all ages. Although a number of studies have addressed the metabolic energetics of *Arctica islandica* (e.g., Oeschger & Storey 1993, Begum et al. 2009, Begum et al. 2010, Philipp & Abele 2010) and others have considered adaptations permitting survival to extreme old age (Philipp & Abele 2010, Ridgway & Richardson 2011, Ungvari et al. 2012), the metabolic basis for persistent growth at old age is yet to be revealed.

The Tanaka model also represents an organism that grows slowly at a young age, presumably because growth processes of the newly formed organism need time to develop. After this development, the organism grows at a maximum rate after which growth declines with age. A minor S-shape in the growth form early in ontogeny is frequently observed in bivalves and likely originates in the postsettlement development of full gill function (Videla et al. 1998, Beninger & Cannuel 2006, Cannuel & Beninger 2007). The nonlinearity is much more prominent in *Arctica islandica* and its duration likely invokes processes different from postsettlement development of gill morphology, but the basis for it is as yet unknown. Nonetheless, as in the case of nonasymptotic growth, this growth propensity is not adaptable to the von Bertalanffy model formulation.

The Tanaka growth at age relationship is

$$G(A) = \frac{1}{\sqrt{f(A-c)^2 + a}}, \tag{4}$$

which, when integrated from age zero to some age A, gives the length-at-age relationship

$$L(A) = d + \frac{1}{\sqrt{f}} \log\left[2f(A-c) + 2\sqrt{f^2(A-c)^2 + fa}\right], \tag{5}$$

where the parameter d is the integration constant and log is the natural logarithm.

To interpret this formula, example curves are created using the following parameters.

$$a = .1661 \text{ year}^2 \text{ mm}^{-2} \qquad c = 7.0 \text{ year}$$
$$d = 125.2 \text{ mm} \qquad f = .0011 \text{ year}^{-2}.$$

These parameter values are chosen so that the Tanaka length curve (Fig. 2B) has a shape similar to the von Bertalanffy length curve (Fig. 1B). These example curves are used to interpret the influence of the parameter choices.

The easiest interpretation is the effect of parameter c with units of year. From the growth rate relationship in Eq. 4, growth is slower at increasing age because age is in the denominator. Growth rate is largest at the age where the denominator is smallest, which occurs when $A = c$. This effect is clearly seen as the peak in the growth rate curve at age 7 (Fig. 2A).

The maximum growth rate occurs at $A = c$ and is $1/\sqrt{a}$. So, parameter a, with units of year^2 mm^{-2}, gives the reciprocal square of the maximum growth rate, which will occur at age c. For the chosen parameters, the maximum growth rate is 2.45 mm year^{-1}.

The interpretation of the parameter d, with units of mm, can be seen with the following analysis. At age $A = 0$, the length expression reduces to

$$L(0) = d + \frac{1}{\sqrt{f}} \log\left[-2fc + 2\sqrt{f^2c^2 + fa}\right]. \tag{6}$$

The expression inside the log can be factored to give

$$L(0) = d + \frac{1}{\sqrt{f}} \log\left[2fc\left(-1 + \sqrt{1 + fa/(f^2c^2)}\right)\right]. \tag{7}$$

The expression in the log term is clearly positive because all of the model parameters are positive and the term under the square root is greater than 1, making the whole expression

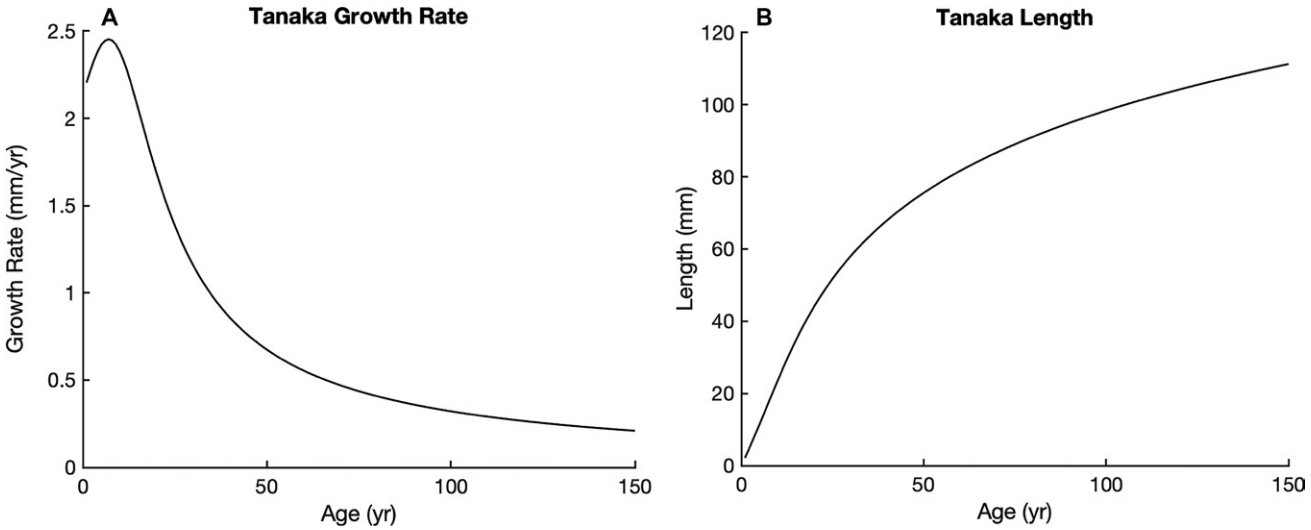

Figure 2. Relationship of Tanaka growth rate (A, left) and length (B, right) versus age. Model parameters are $a = 0.1661, c = 7.0, d = 125.2, f = .0011$.

positive. However, the value of the expression in the log term is likely small (less than e), which will produce a negative logarithm. The parameter d is needed so that L has a positive (or zero) length at zero age. Note that d is not the length at zero age, but is part of a complicated expression involving the other three parameter values giving length at zero age. For the parameters chosen above, the log term has the value -4.153. Choosing $d = 125.2$ creates a zero age length of just above 0 mm.

A more general consideration is that the parameter d shifts the length-age curve by a constant length for all ages. Choosing the value of d sets the length at a specific age. For example, the value of d can be used to set the length at an age of 1 y ($A = 1$), which is typically the age of new recruits to the population.

The final parameter, f with units of year^{-2}, controls the rate at which growth rate declines with age. For ages greater than both c and $\sqrt{a/f}$, the growth rate reduces to $G \sim 1/(\sqrt{f}A)$. For small values of f, such as 0.01, old age growth will decline like $10/A$, meaning that a 10-y-old animal will have a growth rate of 1 per year and a 100-y-old will grow at 0.1 per year. For larger values of f, such as 1.0, the growth rate will decline like $1/A$ so that a 10-y-old animal will have a growth rate of 0.1 per year and a 100-y-old animal will grow at 0.01 per year. This is a relatively slow reduction in growth rate compared with other models, such as von Bertalanffy, that have growth rate declining exponentially with increasing age.

Comparing the Two Age-Length Models

Growth rate curves depicted in Figures 1 and 2 were chosen so that the length-at-age curves for the Tanaka model and the von Bertalanffy model match closely. A more direct comparison is obtained by plotting the curves together (Fig. 3) to see the small differences between the curves. The length curves for the two models (Fig. 3B) compare well until age is above 100 y at which ages the Tanaka curve shows continuing increase in size, whereas the von Bertalanffy curve asymptotes to L_∞. Real growth rate curves measured by Hemeon (2022) and Sower (2022) routinely demonstrate this divergence.

In the case of Figure 3, the first 70 (or so) y for the two length-at-age curves are indistinguishable compared with variability in observations used to determine curve parameters. The growth rate curves for the two models (Fig. 3A) show systematic differences at young and old ages; growth rates from 20 to 50 y match closely. The early slow growth in the Tanaka curve at youngest ages is a feature of the model, which is not expected to match the maximum growth for the von Bertalanffy curve at youngest ages as the von Bertalanffy model cannot emulate an S-shape in growth early in ontogeny. Similarly, the Tanaka growth curve (Fig. 3B) has higher old age growth compared with the von Bertalanffy curve, which again is a design feature of the Tanaka curve, which is not expected from the von Bertalanffy relationship.

In summary, the two models match closely in middle ages and disagree somewhat at both youngest and older ages, with the amount of disagreement at old age rapidly increasing for animals of ever-increasing age.

MODIFIED VON BERTALANFFY MODEL

Given the common use of the von Bertalanffy growth model in population dynamics models, including those used for stock assessment, it would be useful to find a simple modification to that model that allows some growth at old age for long-lived species with nonasymptotic growth. An exploration of this opportunity follows.

The parameter K in the von Bertalanffy model sets the maximum growth rate at age a_o. More correctly, K controls how rapidly the length at any age approaches L_∞. One option to allow continued growth at older ages is to reduce the size of K with increasing age, which will slow the approach of the length-at-age curve to L_∞. Modifying K with age has received considerable study in the context of biphasic growth in which the value of K changes, for example, at maturity (Alós et al. 2010, Armstrong & Brooks 2013, Minte-Vera et al. 2016, Rogers-Bennet & Rogers 2016, Contreras-Reyes et al. 2021), but little attention has favored more flexible approaches to varying

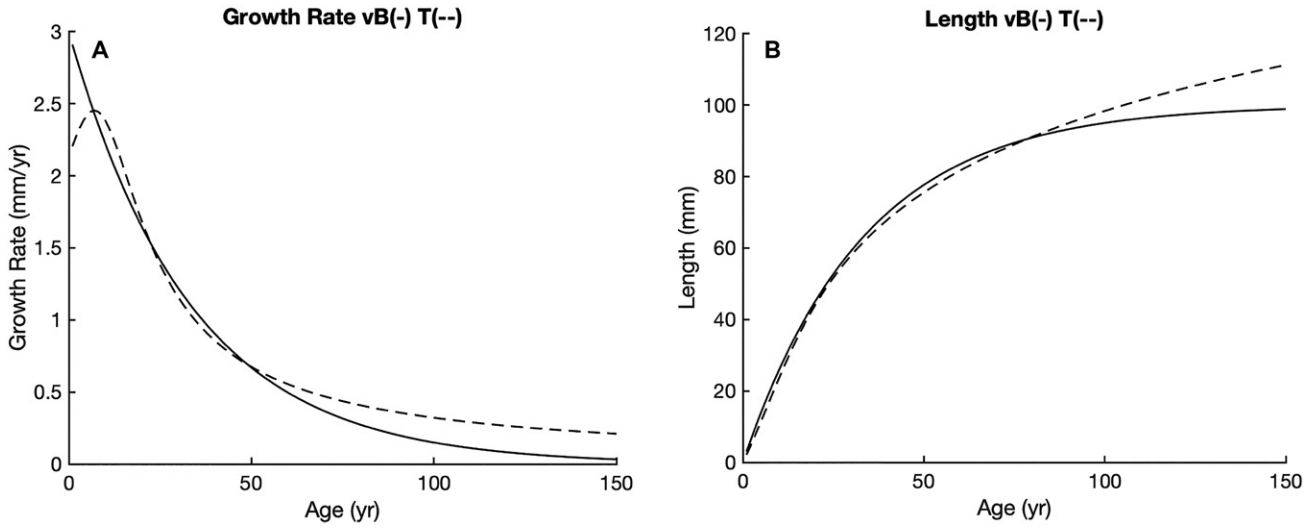

Figure 3. Comparison of von Bertalanffy (solid line) and Tanaka (dashed line) models. (A, left) Growth rate versus age. (B, right) Length versus age. Model parameters are $a_o = 0, L_\infty = 100, K = .03$ and $a = 0.1661, c = 7.0, d = 125.2, f = .0011$.

K with age (Chambers et al. 2017). The simplest mechanism for nonasymptotic growth, explored here, is to define an age-dependent K that becomes smaller with increasing age,

$$K(A) = K_o - K_1 \cdot (A - a_o)^n. \tag{8}$$

Note that a_o is an imposed constant in this analysis and is not a parameter of the age-variable K. To determine whether this extension to the von Bertalanffy model provides a plausible emulation of the Tanaka relationship, a test case is explored to find parameter values of K_o, K_1, and n that fit the modified von Bertalanffy length model to the Tanaka length curve. These parameters are found by fitting the Tanaka length-at-age curve (Fig. 2B), evaluated at every age from 1 to 150 y, to the modified von Bertalanffy curve over the same span of years. The fitting is done with the MATLAB procedure nlinfit. The fitting procedure finds the following parameters:

$$L_\infty = 129.83, K_o = 0.0293, K_1 = 0.0035, n = 0.311$$

A comparison of the two curves is shown in Figure 4B.

The length-at-age curves match very closely. The curves differ less than the scatter of observations used to find parameters for either of these curves. See Hemeon (2022) and Sower (2022) for examples of variability in growth rate among animals from the same location born at similar times. The differences between the curves are amplified by comparing the growth curves. The growth rate formula is obtained by taking the derivative of the modified von Bertalanffy length formula with respect to age. The general form of the equation for length-at-age with age-dependent K is

$$L(A) = L_\infty \left(1 - e^{-K(A)(A-a_o)}\right). \tag{9}$$

Then,

$$G(A) = \frac{d}{dA} L(A) = L_\infty e^{-K(A)(A-a_o)} (K(A) + (A - a_o)\frac{dK(A)}{dA}). \tag{10}$$

A more illuminating formulation is obtained by substituting the exponential term in Eq. 9 to find,

$$G(A) = (K(A) + (A - a_o)\frac{dK(A)}{dA})(L_\infty - L(A)). \tag{11}$$

For the specific choice for the form of $K(A)$ in Eq. 8, this becomes

$$G(A) = (K_o - (n+1)K_1(A - a_o)^n)(L_\infty - L(A)). \tag{12}$$

A comparison of the relationship between growth rate and age for the modified von Bertalanffy and the Tanaka models is shown in Figure 4A. A clear difference in growth rate is observed at early age, where the Tanaka model has slow growth at youngest ages, whereas the von Bertalanffy model has maximum growth at the youngest age. The von Bertalanffy relationship does not permit the tendency toward S-shaped growth early in ontogeny in *Arctica islandica*. The modified von Bertalanffy model overestimates the growth rate over the middle adult years, which corrects for the slightly lower early adult lengths to produce slightly higher late adult lengths (Fig. 4B). Nonetheless, the two growth curves track closely over much of the age range. However, the modified von Bertalanffy growth model still tends (slowly) toward zero growth at old age, whereas the Tanaka curve manifests a slowly declining old age growth rate, emphasizing the fact already made clear by Hemeon et al. (2021) that extrapolation of growth beyond observed old age will often lead to implausible outcomes.

DISCUSSION

A simple ocean quahog-like population model was developed to test the practical consequence of using a traditional versus modified von Bertalanffy growth model in a stock assessment setting under the constraint of a 150-y growth trajectory, which covers the majority of the ocean quahogs presently living in the MidAtlantic region (Pace et al. 2017a). Stock assessment

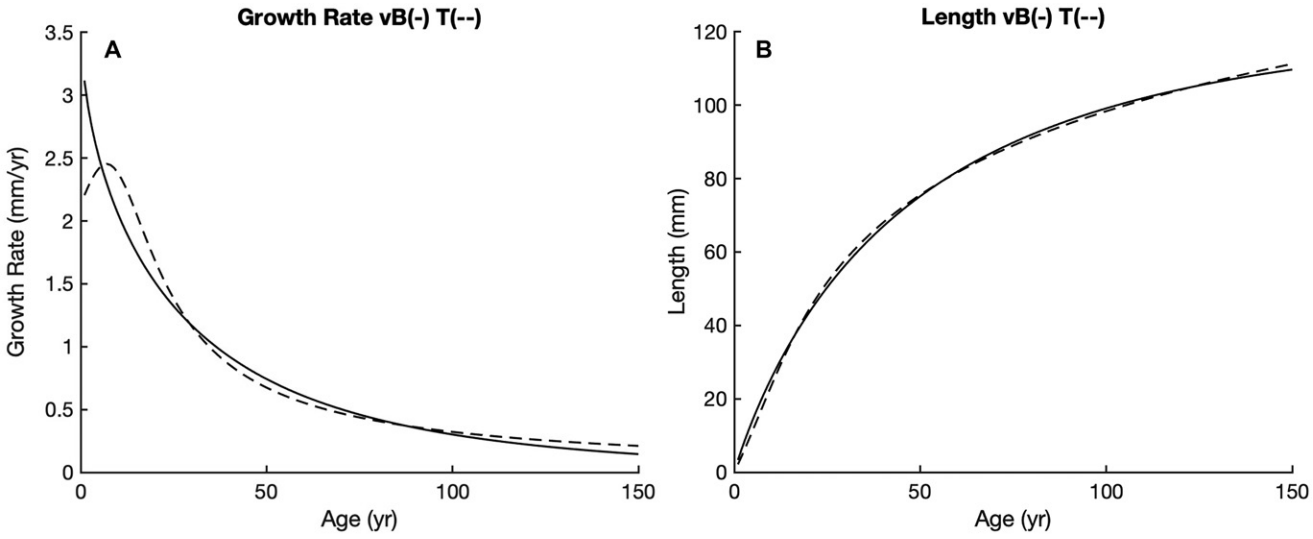

Figure 4. Comparison of the modified von Bertalanffy model (solid line) with the Tanaka model (dashed lines). (A, left) Growth rate comparison. (B, right) Length comparison.

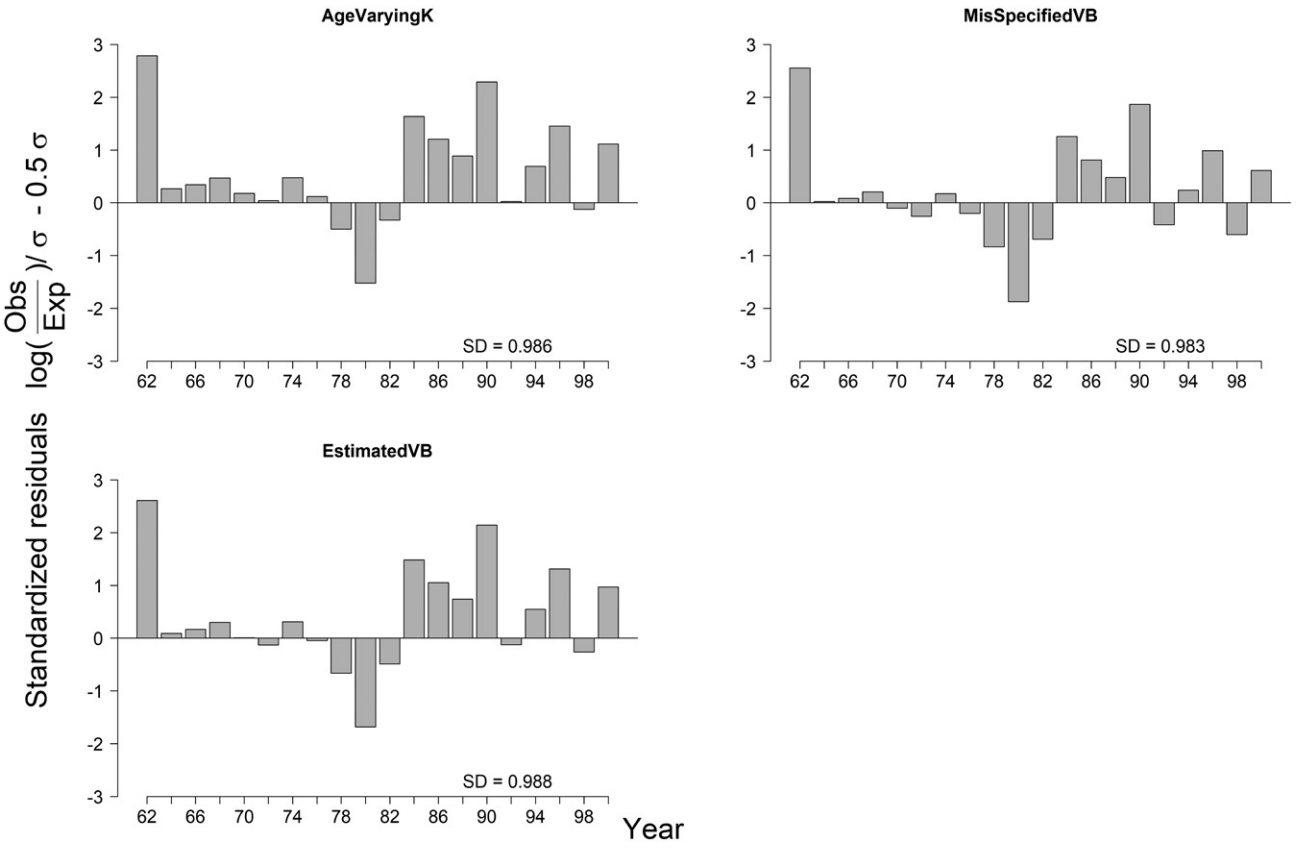

Figure 5. Residuals from the fit to survey indices from three different simple estimation model for simulated *Arctica islandica* data. Upper left, the modified von Bertalanffy formulation; upper right, the original two-parameter von Bertalanffy formulation; lower, the two-parameter von Bertalanffy formulation fit to data obtained from the modified von Bertalanffy formulation.

data were simulated using ss3sim (Anderson et al. 2014), an R package based on the Stock Synthesis model (SS3) (Methot & Wetzel 2013). Life history parameters, fishing behavior, and survey characteristics were designed to be similar to a recent *Arctica islandica* stock assessment [Northeast Fisheries Science Center (NEFSC) 2022]. The operating model simulated ocean quahog growth according to the modified von Bertalanffy model (Fig. 4). Data produced by the operating model were fit using three different estimation models. In the first, growth rate was assumed equal to the growth specified by the modified von Bertalanffy relationship used in the operating model. In the second, growth rate was assumed equal to a traditional von Bertalanffy model in which the K and L_∞ parameters were obtained *a priori* as in Figure 1. In the third case, the traditional two parameters of the von Bertalanffy model (K, L_∞) were estimated from data obtained from the original modified von Bertalanffy model.

Simulation results indicate that modern stock assessment models are able to approximate ocean quahog-like nonasymptotic growth using traditional growth models when enough data are present to estimate growth parameters. The estimation models with age varying K (the modified von Bertalanffy growth model) fixed at the values used in the operating model were nearly indistinguishable from those estimated from the operating model using the traditional two-parameter von Bertalanffy formulation (Figs. 5 and 6). When sufficient information is present in the data to estimate growth, the differences between the modified and traditional two-parameter von Bertalanffy models are minor relative to the uncertainty typical in observed ocean quahog length-at-age data.

The model with fixed but incorrectly specified growth parameters did not fit the data well (Figs. 5 and 6). These results indicate that some risk exists in assuming fixed values for traditional two-parameter von Bertalanffy models when underlying growth is nonasymptotic. The relatively poor fit to the length composition data seen in this case, however, would likely lead analysts to believe that growth and/or selectivity was misspecified.

The motivation for this analysis stems from the fact that the von Bertalanffy length-at-age formulation is commonly used in many population dynamics models, including a range of fisheries stock assessment models, but suffers from the requirement that length asymptotes at old age. Although this is a reasonable approximation for many marine species, *Arctica islandica* diverges dramatically from this norm, as do other species, particularly among the invertebrates. The Tanaka relationship was developed specifically for this eventuality, but suffers from an arcane construction and limited application in standard population dynamics models. The difficulty of constant K and constant L_∞ in describing growth trajectories has been addressed in a number of studies with many focusing on a biphasic K to address changes in growth rate, particularly

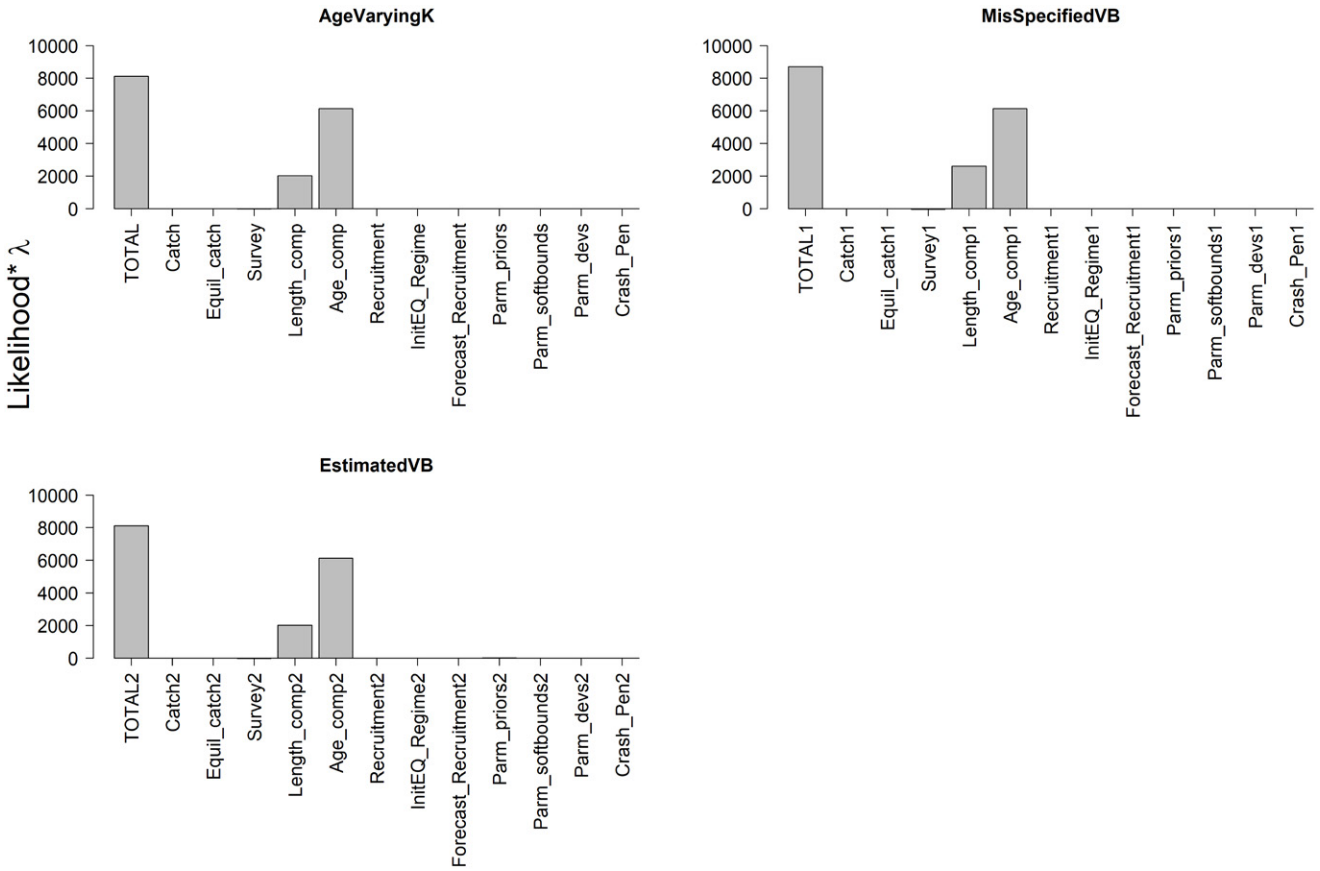

Figure 6. Relative contribution to the likelihood from three different simple estimation models for simulated *Arctica islandica* data. Upper left, the modified von Bertalanffy formulation; upper right, the original two-parameter von Bertalanffy formulation; lower, the two-parameter von Bertalanffy formulation fit to data obtained from the modified von Bertalanffy formulation.

at maturity. The restriction of constant K and L_∞ is further enlarged in the case where asymptotic growth does not occur. This study assumes an easier approach in model parameterization by simply modifying the growth parameter K to allow it to decrease with age.

The modified von Bertalanffy model is shown to produce continued, slower, growth at older ages similar to the Tanaka model. The Tanaka model allows continued growth to very old ages, whereas the modified von Bertalanffy model has declining growth at old age and eventually will approach an asymptotic maximum length of L_∞. Nonetheless, given a proper formulation, the deviation between the two will occur at an age beyond the maximum age that is observed. Thus, despite these differences, the length-at-age curves for the Tanaka and modified von Bertalanffy models are very close (Fig. 4B). Given the scatter in observations to which these curves are fit, the two models are unlikely to be distinguishable from observations. That is, either model will fit the observations within the scatter of the data.

Length and Growth Rate Observations Fit to Models

A set of Tanaka growth relationships were fit to data presented by Hemeon et al. (2021) for Georges Bank and Sower (2022) for northern New Jersey for the decades of 1800, 1860, 1900, 1940, and 1980 (Table 1). The modified von Bertalanffy parameters are estimated from the Tanaka parameters by the following procedure. The Tanaka parameters are used to create lengths at 1 y age intervals up to 150 y. The modified von Bertalanffy curve is then fit to these data points to obtain the parameters given in Table 1. The length (Figs. 7 and 8) and growth (Figs. 9 and 10) curves as a function of age for these two models allow analysis of their behavior.

The length curves (Figs. 7 and 8) have a similar difference pattern to those in Figure 4B. The length curves from both samples underestimate (overestimate) length for the modified von Bertalanffy model at young (old) ages. Although there is a systematic difference between these length curves, scatter in the observations make it unlikely for data to make a clear case for one model over the other. The difference in these curves might be reduced by choosing a different range of ages from the Tanaka fit to determine the modified von Bertalanffy parameters. A better procedure might be to fit directly the modified von Bertalanffy model to the data.

The growth rate curves (Figs. 9 and 10) have a similar difference pattern to those in Figure 4A. Part of this difference is due to the delayed growth behavior in the Tanaka model, which is not a feature of the modified von Bertalanffy model. As explained earlier, this structural difference in the models causes the modified von Bertalanffy model to underestimate (overestimate) growth in the youngest (early adult) ages. The curves basically overlap during middle and older ages. Again, scatter

TABLE 1.

Example growth curve parameters obtained by population subsets of animals born within decades from the northern New Jersey site of Sower (2022) and the Georges Bank site of Hemeon et al. (2021).

		Parameter relationships							
Location	**Birth**	***a***	***c***	***d***	***f***	L_∞	K_o	K_1	***n***
NJ	1800	0.1040	0.0	85.8	0.00198	103.84	0.0635	0.0252	0.1377
NJ	1860	0.0391	0.0	88.1	0.00217	104.27	0.0668	0.0232	0.1605
NJ	1900	0.0158	1.18	89.2	0.00264	105.27	0.0863	0.0326	0.1502
NJ	1940	0.0248	2.62	91.4	0.00282	107.49	0.0887	0.0325	0.1552
NJ	1980	0.0095	3.07	92.3	0.00398	106.89	0.0897	0.0186	0.2515
GB	1800	0.00955	0.0	91.3	0.00299	105.45	0.0959	0.0370	0.1482
GB	1860	0.00555	0.0	94.3	0.00236	108.94	0.0897	0.0353	0.1440
GB	1900	0.00997	1.16	87.1	0.00313	102.76	0.0941	0.0327	0.1652
GB	1940	0.00895	1.59	88.4	0.00345	103.44	0.0858	0.0211	0.2237
GB	1980	0.01571	4.0	111.1	0.00251	124.48	0.0926	0.0313	0.1693

in observations may not allow a definitive preference for one model over the other.

Hemeon (2022) and Sower (2022) have shown that even the Tanaka model cannot provide accurate extrapolations of the growth at old age beyond the range of the data. The same sensitivity will exist for the modified von Bertalanffy model. The obviously limited extrapolative capability likely originates from two processes in *Arctica islandica*. The first is a predefined growth pattern that decrees an ever-increasing size as the animals age, albeit at an ever slower rate as time passes. The second, however, accrues from the extreme sensitivity to temperature embedded in the physiology of the species (Begum et al. 2009, 2010). As these animals live for centuries, many have lived through the entirety of the time since the ending of the Little Ice Age (e.g., Hemeon et al. 2021); these animals, thus, have lived through the entire history of global warming and experienced ever-increasing temperatures over much of that period. As temperatures increase, so too does the rate of growth at a given age. Thus, embedded in the growth curve is a temperature-dependent acceleration in growth that continuously exerts an increase in growth rate relative to what would be anticipated from constant temperature and this adds an additional increment to the continual increase in size at age. As a consequence, with earlier birth dates, the original von Bertalanffy formulation continues to fall farther away from the observations, leading to the necessity of invoking the Tanaka growth function or a modified von Bertalanffy formulation including an ever-changing K with age, as presented here.

However, the physiology of *Arctica islandica* and most other bivalves produces a decline in growth rate at some high temperature. Much of this effect accrues from a parabolic form of the temperature-dependent filtration rate curve (e.g., Hofmann et al. 2006, Munroe et al. 2013). Declining growth at high temperature has been noted in *A. islandica* (LeClaire 2022, Marchitto et al. 2000). Potentially, this would result in a decline in growth rate below that anticipated by the previous rate of growth acceleration with increasing temperature and thus, a reduced fit of either the Tanaka or modified von Bertalanffy models to observed growth. Mortality rates under these conditions are sufficiently high, however, that such occurrences are likely rare (Marchitto et al. 2000), though recent evidence from LeClaire (2022) would suggest that such animals might be observed near the warm-water range boundary during periods of climate change and shifting range.

The mathematical modeling of growth has received wide-ranging attention (e.g., Banks & Fitzpatrick 1991, Devillers et al. 1998, Wang & Milton 2000, Ohnishi & Akamine 2006, Lv & Pitchford 2007, Helidoniotis & Haddon 2013, Rogers-Bennet & Rogers 2016). The present contribution extends this spectrum to species of indeterminate growth in which size fails to asymptote at old age. Such species are not numerous, but species living to very old age, receiving attention for that attribute and its potential to provide a long-term record of environmental conditions otherwise unavailable (e.g., Turekian et al. 1975, Wisshak et al. 2009, Titschock et al. 2010, Bušelić et al. 2015, Luquin-Cavarrubias et al. 2016), should be evaluated to determine the efficacy of an improved growth rate formulation using one of the models proffered here.

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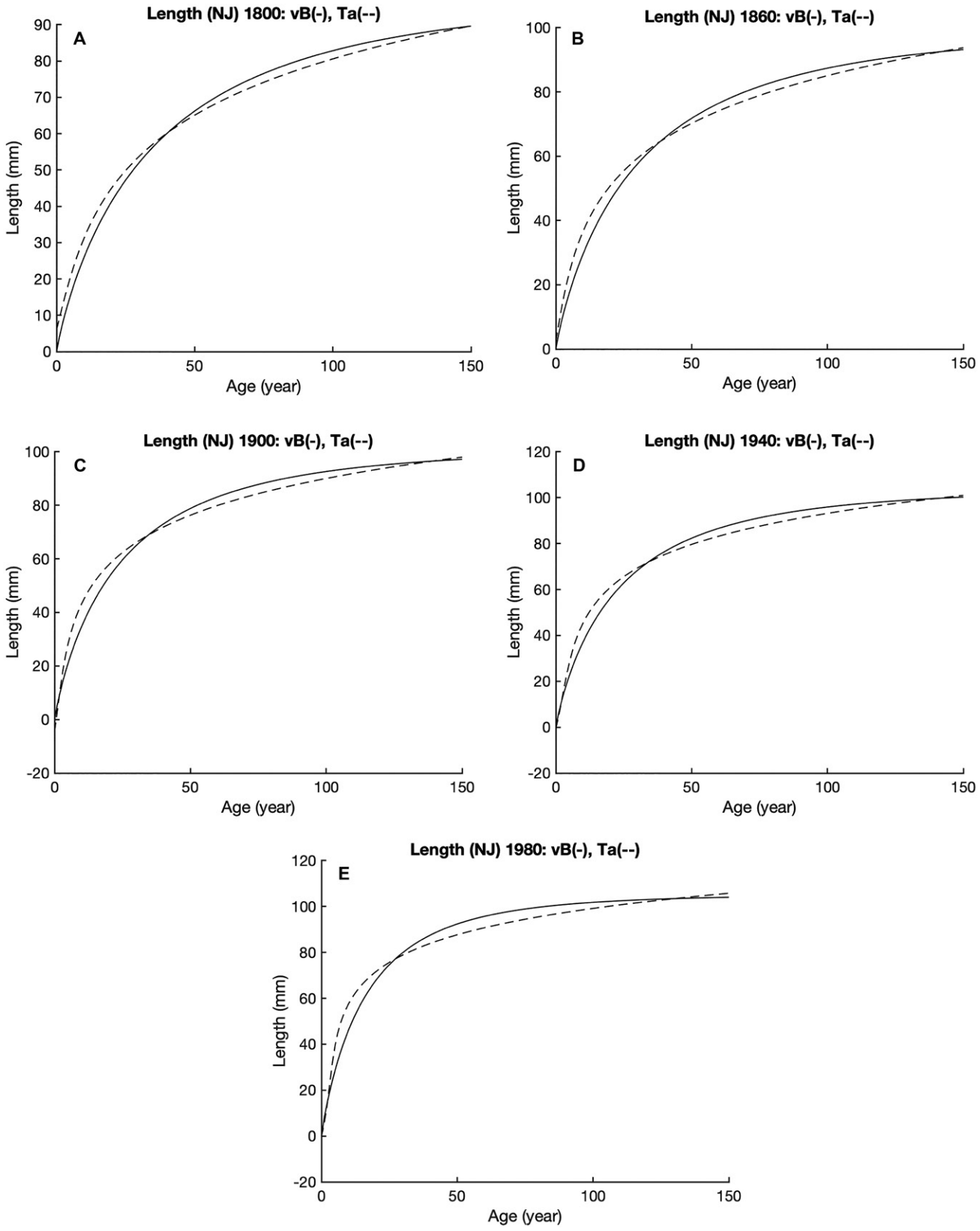

Figure 7. Comparison of length estimated by the modified von Bertalanffy (solid lines) and Tanaka (dashed lines) models. Parameters from fit to New Jersey quahogs with birth years of 1800, 1860, 1900, 1940, and 1980.

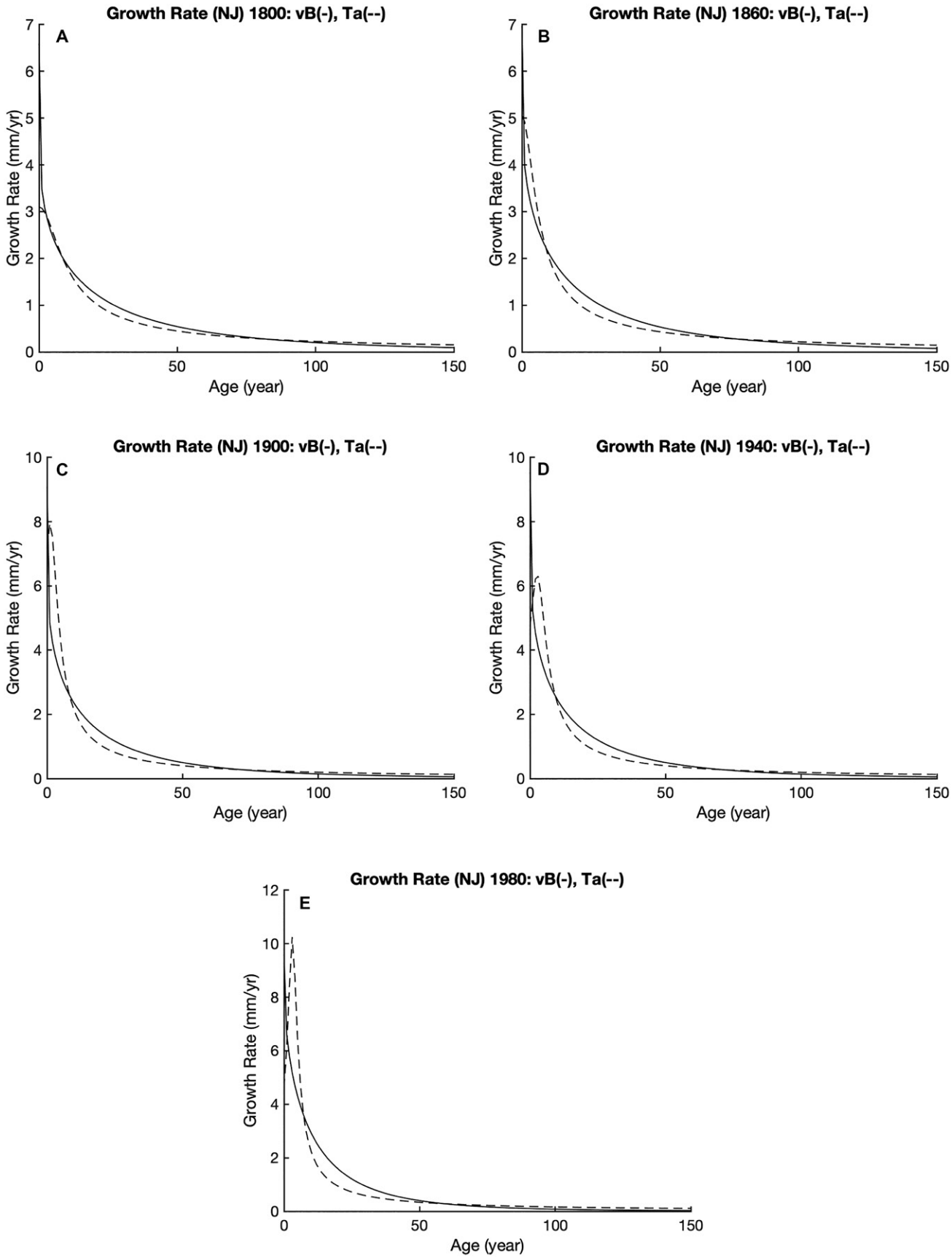

Figure 8. Comparison of length estimated by the modified von Bertalanffy (solid lines) and Tanaka (dashed lines) models. Parameters from fit to Georges Bank quahogs with birth years of 1800, 1860, 1900, 1940, and 1980.

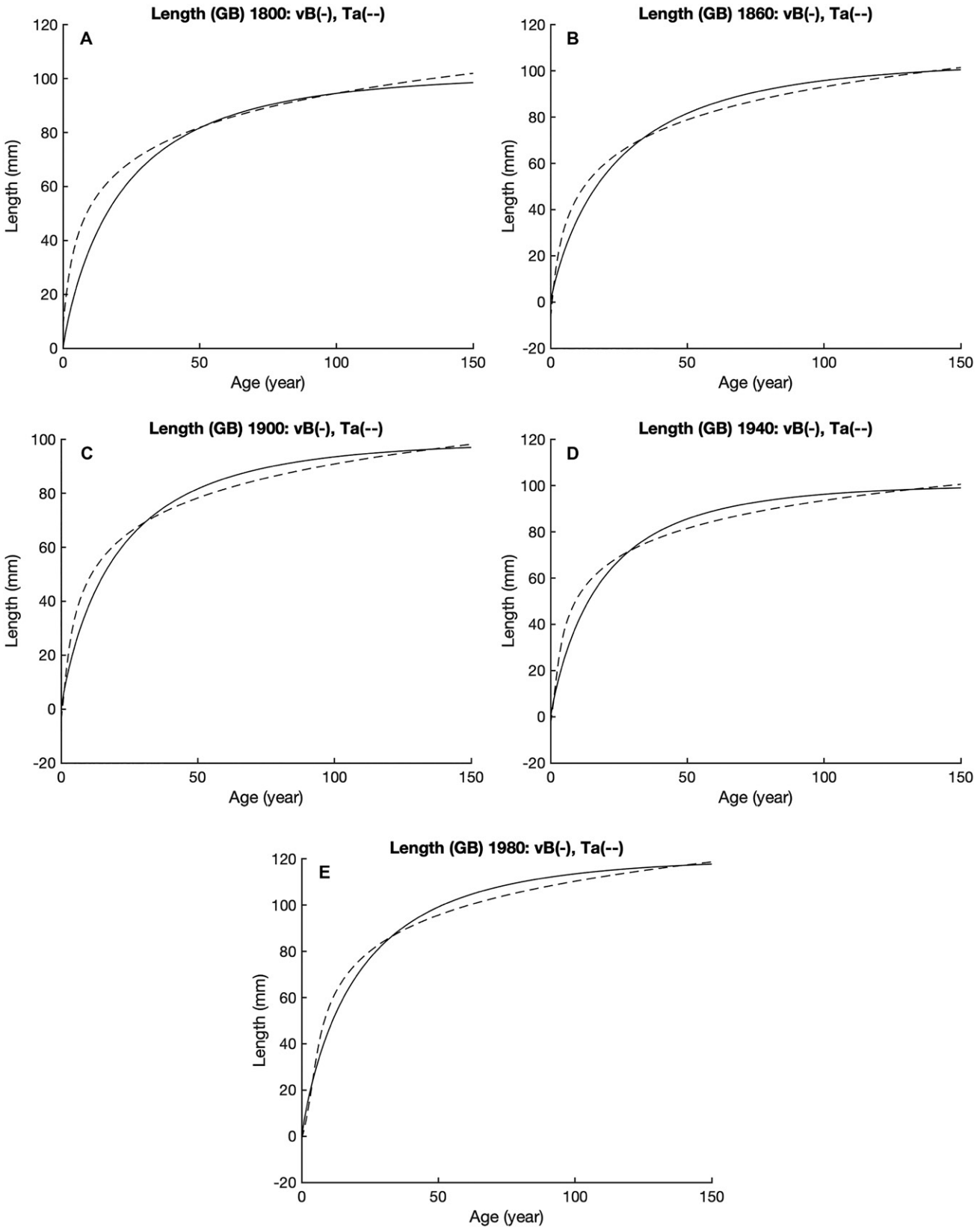

Figure 9. Comparison of growth rate estimated by the modified von Bertalanffy (solid lines) and Tanaka (dashed lines) models. Parameters from fit to New Jersey quahogs with birth years of 1800, 1860, 1900, 1940, and 1980.

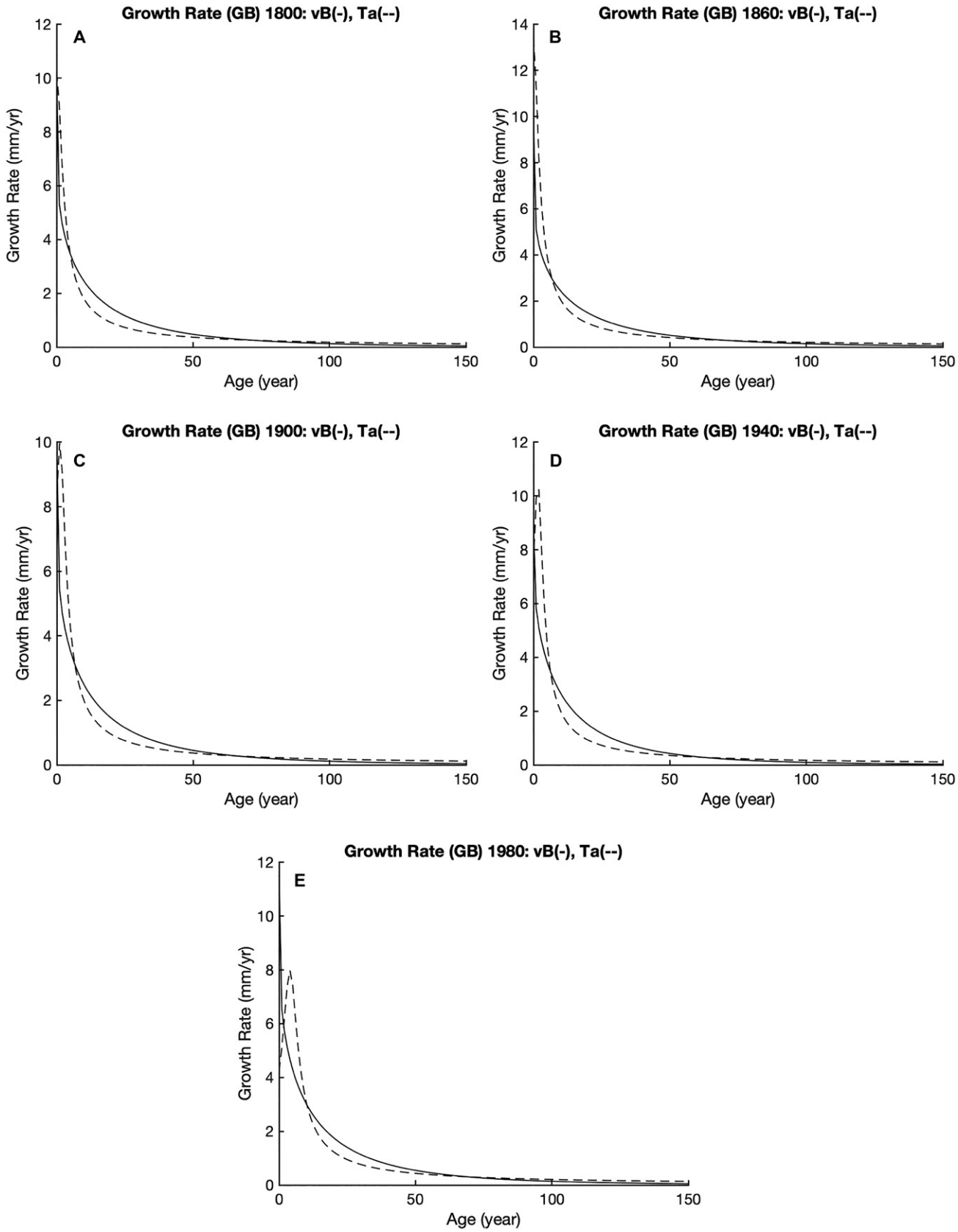

Figure 10. Comparison of growth rate estimated by the modified von Bertalanffy (solid lines) and Tanaka (dashed lines) models. Parameters from fit to Georges Bank quahogs with birth years of 1800, 1860, 1900, 1940, and 1980.

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