



# Ocean quahog (*Arctica islandica*) growth rate analyses of four populations from the Mid-Atlantic Bight and Georges Bank

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## ABSTRACT

Growth rates from 1480 *Arctica islandica* from New Jersey, collected in 2019 from north and south of the Hudson Canyon, were analyzed and compared to animals obtained from Long Island and Georges Bank. New Jersey represents the southern portion of the *A. islandica* stock in the Mid-Atlantic Bight, and animals here may experience warmer temperatures compared to their northern counterparts. *Arctica islandica* from New Jersey have slower maximum growth rates compared to northern *A. islandica*, particularly from Georges Bank; however, *A. islandica* from south of the Hudson Canyon have higher growth rates at older ages compared to the other three sites. Growth rates have been increasing over the past three centuries, potentially due to increasing bottom water temperatures, with time to maturity and time to commercial size drastically decreasing, leading to fewer years for reproduction prior to recruiting into the fishery. Three growth models, von Bertalanffy, Tanaka, and modified Tanaka were examined for goodness of fit to growth data. The von Bertalanffy, commonly used in fisheries management, had the worst fit for all populations, males and females, and at all 20-year cohort groups, and should not be used in the management of this species. The Tanaka and modified Tanaka models are recommended in its place, as these models best fit *A. islandica* growth at young (Tanaka) and older (>160 years, modified Tanaka) ages.

## 1. Introduction

The ocean quahog (*Arctica islandica*) is an extremely long-lived species, often reaching at least 200 years in age, with the oldest-recorded individual aged at 507 years (Butler et al., 2013). This species also supports one of the largest shellfish fisheries in the U.S. (Hennen, 2015; NEFSC, 2017). Growth rates of extremely long-lived animals such as *A. islandica* can provide proxies of environmental patterns of the past, as growth rates can fluctuate over time with changes in temperature or food availability and quality (Ballesta-Artero et al., 2017; Mette et al., 2016; Schöne et al., 2005; Wanamaker et al., 2009). This species deposits distinct annual growth lines in their valves, termed annuli (Jones, 1980; Ropes et al., 1984b; Thompson et al., 1980), which can be counted to determine age. Variations in annulus thickness can be used to describe past environmental fluctuations (Marali and Schöne, 2015; Murawski et al., 1982; Wanamaker et al., 2019).

Bivalves tend to grow faster at higher temperatures within their

thermal tolerance (Pace et al., 2018; Schöne et al., 2005). Mann (1982) observed an ideal thermal range of 6–10 °C for *A. islandica*, and Milano et al. (2017) reported diminished growth rates at 15 °C. Thus, increasing temperatures in recent decades due to climate change may have influenced *A. islandica* growth. The metabolism of *A. islandica* is particularly sensitive to temperature in comparison to most bivalves (Begum et al., 2009), themselves distinctly sensitive (Munroe et al., 2013; van der Veer et al., 2006). New Jersey represents the southern portion of the range of *A. islandica* in the western Atlantic. Pace et al. (2018) found that New Jersey *A. islandica* from southern areas have faster growth rates than those of their northern counterparts from Georges Bank and Southern New England, with animals being significantly younger at 60 mm shell length (SL) compared to more northern sites due to the higher bottom water temperatures experienced off New Jersey. To build upon the study by Pace et al. (2018), the growth rates from larger sample sizes of *A. islandica* from two New Jersey sites north and south of the Hudson Canyon were measured and compared to those from Long Island and

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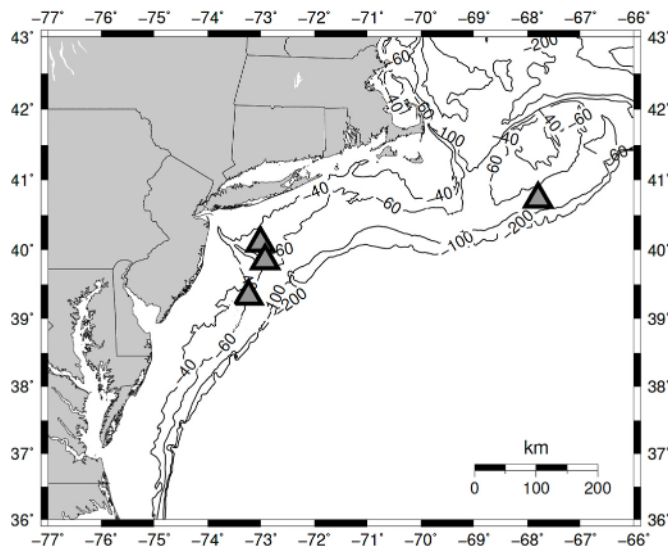


Fig. 1. Map of sample locations. From north to south, sites are Georges Bank (GB), Long Island (LI), New Jersey north (NJ1), and New Jersey south (NJ2).

Georges Bank (Hemeon et al., 2023) to determine how growth rates may change by location. Three growth models were then tested to determine which fit *A. islandica* growth best: von Bertalanffy, which is a commonly used growth model applicable to many marine species (Brey and Gage, 1997; Helidoniotis and Haddon, 2013; Tanaka (1982, 1988), which was designed for animals with continuous growth into old age; and a modified Tanaka that includes an extra parameter to improve model fit at older ages (Hemeon et al., 2023).

Pace et al. (2018) considered the influence of warming temperatures since the end of the Little Ice Age (~1400–1850 CE) as an important effector generating long-term trends in increasing growth rates and suggested that one reason for the wide range of ages with small size classes (e.g., 5 mm SL) might be the rate of growth in the first several decades of life leading to larger sizes at age for more recent birth years. To examine the potential of warming temperatures interacting with birth years in determining *A. islandica* demographics, time to milestone sizes important to the fishery were analyzed over time to determine whether growth rates have remained similar over recent centuries, or whether they have fluctuated as a result of changing environmental factors.

## 2. Materials and methods

### 2.1. Sample collection

In August of 2019, *Arctica islandica* were sampled from north and south of the Hudson Canyon off New Jersey (Fig. 1). The northern New Jersey sample (herein referred to as NJ1) was collected at 39.84056 N, 72.82167 W, while the southern New Jersey sample (NJ2) was collected at 39.33 N, 73.12278 W. The sex of each animal was determined using gonadal smear slide, and shells were processed to expose the hinge plate and annuli for ageing. For more information on shell processing techniques, see Pace et al. (2017a, 2017b) and Hemeon et al. (2021a). Once processed, each shell was photographed using a combination microscope and camera, and said photographs were uploaded into the open-source software ImageJ with the ObjectJ plugin. This software was used to annotate the darkest portion of each individual annulus to determine age. Distances between markers, originally specified in pixels, were then converted to millimeters using a proportion of the animal's overall shell length to determine annual growth. Animals used for comparison in this study from Long Island and Georges Bank were collected in 2017 and analyzed by Hemeon et al., 2023.

### 2.2. Growth models: population, males, females

Growth increments were cumulatively summed for each individual animal per site. The von Bertalanffy (Eq (1)), Tanaka (Eq (2)), and modified Tanaka (Eq (3)) models were applied to the cumulative growth increments for the population, male, and female groups for both NJ1 and NJ2. The von Bertalanffy model is widely used in fisheries management and is currently used in *A. islandica* management (NEFSC, 2017; von Bertalanffy, 1938). The formulation includes an assumed maximum size that the growth trajectory asymptotes to a specified length,  $L_{\infty}$ , at old age. The Tanaka model was chosen as it fits species with continuous growth into old age (Pace et al., 2017b; Tanaka, 1982), as is observed in *A. islandica*. This formulation does not assume an asymptotic size at old age. The modified Tanaka is an updated version of the Tanaka that contains an additional parameter that better fits *A. islandica* growth at older age classes (Powell & Klinck, pers comm).

$$L_t = L_{\infty} (1 - e^{-k(t-t_0)}), \quad \text{Eq (1)}$$

$$L_t = d + \frac{1}{\sqrt{f}} \log \left( 2f(t-c) + 2\sqrt{f^2(t-c)^2 + fa} \right), \quad \text{Eq (2)}$$

$$L_t = d + \frac{1}{\sqrt{f}} \log \left( 2f(t-c) + 2\sqrt{f^2(t-c)^2 + fa} \right) + gt^{2.5} \quad \text{Eq (3)}$$

where  $t$  is age in years and  $L$  is length in mm.

The variables used in the Tanaka model can be described as follows. Parameter  $c$  (years) denotes the age at maximum growth rate. At the age of maximum growth,  $c$ , the growth rate is  $1/\sqrt{a}$ . So, parameter  $a$  ( $\text{yr}^2 \text{mm}^{-2}$ ) describes the maximum growth rate which will occur at age  $c$ . Parameter  $f$  ( $\text{yr}^{-2}$ ) controls the rate at which growth declines with increasing age. For older animals, growth rate reduces to  $1/(t\sqrt{f})$ . Parameters  $d$  (mm) and  $g$  ( $\text{mm yr}^{-2.5}$ ) are scalars of size, with  $g$  influencing the rate of growth rate decline with increasing age determined by parameter  $f$ . All model parameters except  $d$ , were forced to be  $\geq 0$  during model convergence to prevent the estimation of negative square roots and logarithms.

These models were first applied to the overall populations to determine whether differences in growth exist. These models were then applied to the male and female components of each population to ascertain if growth rates differ between sexes, as has been hypothesized by Steingrímsson and Thorarindóttir (1995) and Hemeon et al. (2021b).

### 2.3. Growth models: age-specific cohorts

Growth rates are expected to vary over time as environmental conditions change, such as temperature and food availability which are the primary determinants of scope for growth in bivalves including *A. islandica* (Canu et al., 2010; Harding et al., 2008; Munroe et al., 2013; Schöne et al., 2005). As *A. islandica* commonly live to 200+ years, variations in growth are expected across generations based on the environmental conditions in their birth and subsequent years. The whole population, males, and females were divided into twenty-year cohorts based on birth year as described in Hemeon et al., 2023. The three growth models were then applied to determine the degree to which growth rates have changed over time in New Jersey *A. islandica*.

### 2.4. Growth rates

Three milestone sizes were used to analyzed growth rates important to the fishery and population maintenance as suggested by Hemeon et al., 2023. Two of these sizes, corresponding to lengths at maturity and recruitment to the fishery, and the time required to reach said sizes, are important in *A. islandica* population dynamics, and, as the species is commercially harvested, fisheries management. Most bivalves reach

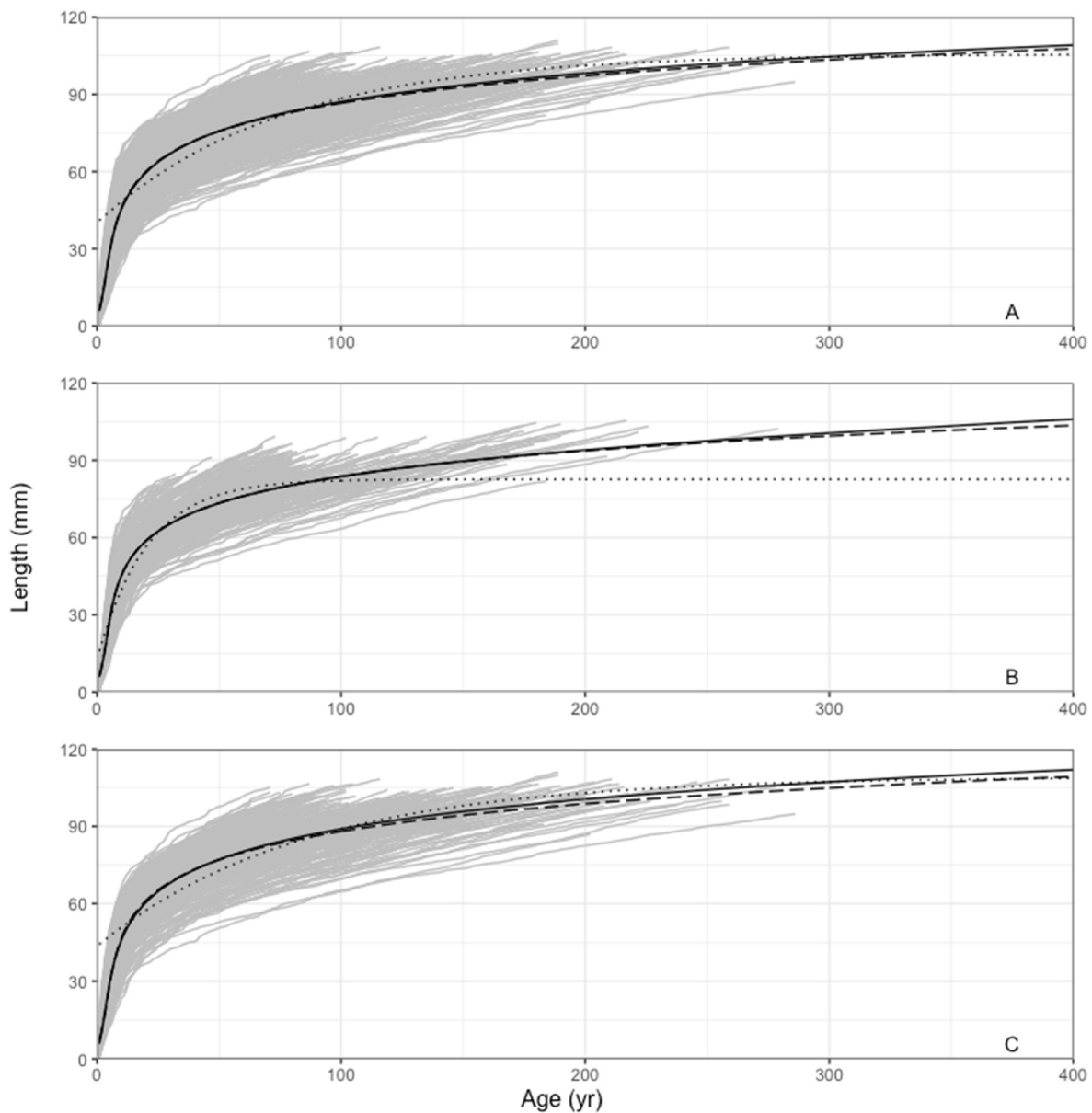


Fig. 2. Growth models for NJ1 population (A), male (B), and female (C). Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

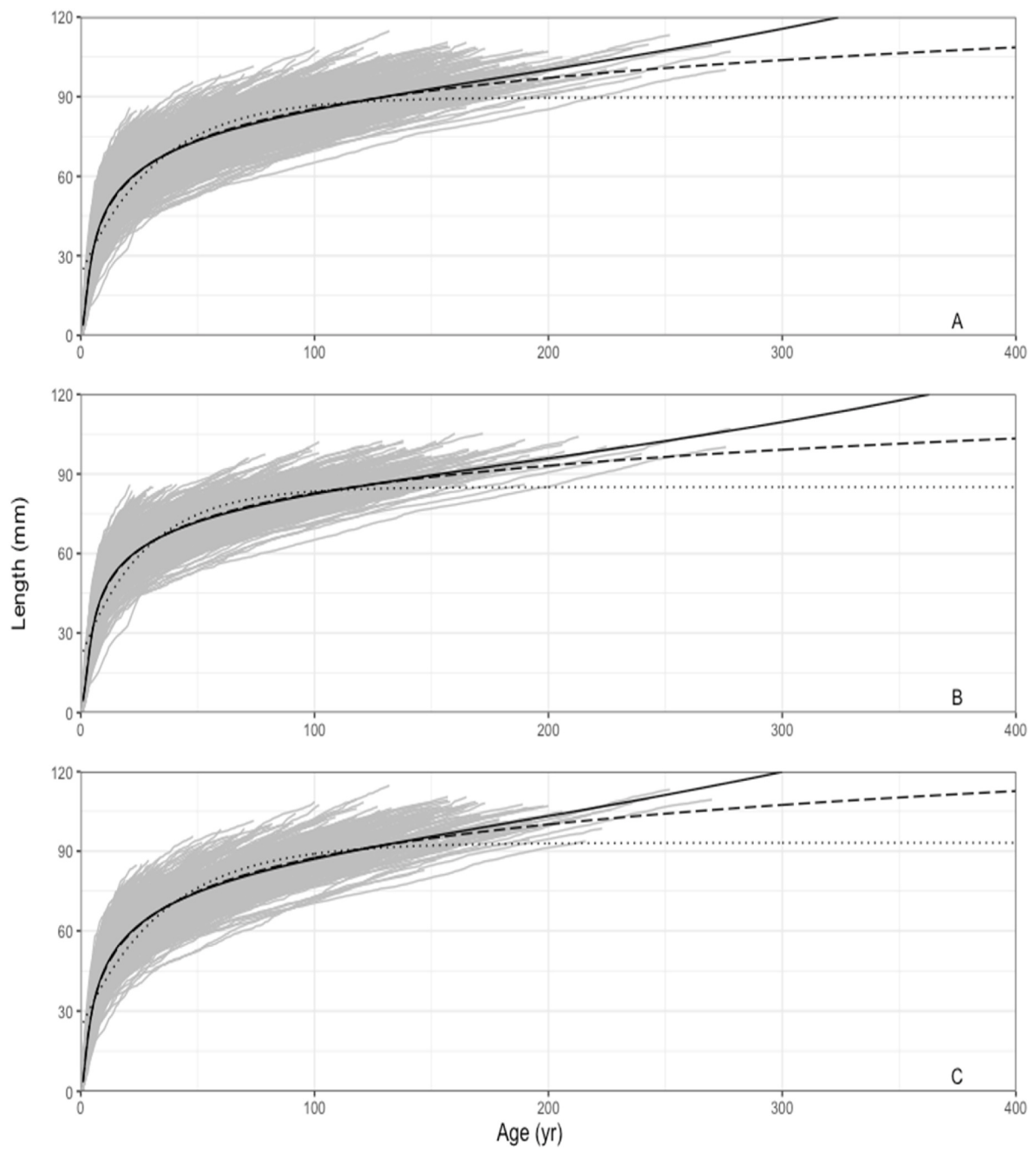
maturity at approximately 50% of their maximum body size, although considerable variability exists (Powell and Stanton, 1985). Hemeon et al., 2023 concluded in a review of the literature and through direct analysis of maturity sample data that age at maturity approximated 52 mm shell length in *A. islandica* and Sower et al. (2022) provided supporting information for the sites studied in this contribution. The second milestone size, a shell length of 80 mm, approximated to be the minimum size efficiently selected for harvest by commercial dredge (NEFSC, 2017). The number of years from birth to size at 50% maturity and the size fully selected by the fishery were analyzed using linear regression for each animal to determine whether the years taken to reach these milestones has fluctuated over the past three centuries. Time between these size milestones is referred to as the years of reproduction prior to recruitment to the fishery and was analyzed using the same method.

### 3. Results

#### 3.1. Growth models: population, males, females

Either Tanaka or modified Tanaka models fit *A. islandica* growth best, with Tanaka fitting younger ages better and modified Tanaka fitting older ages better. Von Bertalanffy, however, routinely yielded an underestimate of shell length at old age when a strong deviation existed from the other two (Figs. 2 and 3). For NJ1, the  $a$  and  $c$  parameters are always larger than in NJ2, indicating lower growth rates and higher ages at maximum growth rates (Table 1). The  $d$  parameter is larger for the population and for females at NJ2 but is smaller than males at NJ1. The  $f$  parameter is larger in all cases for NJ1, indicating lower growth rates at old age at this site.

The modified Tanaka parameters yielded somewhat different results than the original Tanaka. The  $a$ ,  $c$  and  $d$  parameters were all larger for NJ1 than for NJ2, indicating the same slower growth rates and higher ages at maximum growth. However, the  $g$  parameter, unique to the modified Tanaka model, is larger for NJ2 than for NJ1, which illustrates



**Fig. 3.** Growth models for NJ2 population (A), male (B), and female (C). Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

**Table 1**

Parameter values for von Bertalanffy, Tanaka, and modified Tanaka models of best fit. NJ1 = northern New Jersey; NJ2 = southern New Jersey; SE = standard error.

| Model           | Group      | Parameter | NJ1      |          | NJ2      |          |
|-----------------|------------|-----------|----------|----------|----------|----------|
|                 |            |           | Estimate | SE       | Estimate | SE       |
| von Bertalanffy | Population | $L_{inf}$ | 1.06E+02 | 2.18E-01 | 8.97E+01 | 7.99E-02 |
|                 |            | K         | 1.33E-02 | 8.35E-05 | 3.09E-02 | 1.48E-04 |
|                 |            | $t_0$     | 3.58E+01 | 2.31E-01 | 9.48E+00 | 9.84E-02 |
|                 | Male       | $L_{inf}$ | 8.26E+01 | 9.45E-02 | 8.50E+01 | 1.02E-01 |
|                 |            | K         | 4.91E-02 | 3.02E-04 | 3.66E-02 | 2.57E-04 |
|                 |            | $t_0$     | 3.32E+00 | 7.68E-02 | 7.61E+00 | 1.27E-01 |
|                 | Female     | $L_{inf}$ | 1.09E+02 | 3.17E-01 | 9.32E+01 | 1.14E-01 |
|                 |            | K         | 1.18E-02 | 1.04E-04 | 2.82E-02 | 1.77E-04 |
|                 |            | $t_0$     | 4.31E+01 | 3.62E-01 | 1.04E+01 | 1.37E-01 |
| Tanaka          | Population | a         | 2.71E-02 | 5.88E-04 | 1.31E-02 | 6.82E-04 |
|                 |            | c         | 3.98E+00 | 5.78E-02 | 1.58E+00 | 6.42E-02 |
|                 |            | d         | 7.85E+01 | 1.04E-01 | 7.95E+01 | 1.13E-01 |
|                 |            | f         | 4.49E-03 | 3.27E-05 | 3.65E-03 | 2.55E-05 |
|                 |            | $t_0$     | 2.62E-02 | 7.65E-04 | 1.64E-02 | 8.01E-04 |
|                 | Male       | a         | 4.11E+00 | 7.65E-02 | 2.46E+00 | 7.97E-02 |
|                 |            | c         | 7.43E+01 | 1.49E-01 | 7.40E+01 | 1.38E-01 |
|                 |            | d         | 5.11E-03 | 5.64E-05 | 4.66E-03 | 4.77E-05 |
|                 |            | f         | 2.81E-02 | 7.85E-04 | 9.12E-03 | 1.06E-03 |
|                 |            | $t_0$     | 4.23E+00 | 7.70E-02 | 8.60E-01 | 9.57E-02 |
|                 | Female     | a         | 8.00E+01 | 1.32E-01 | 8.39E+01 | 1.69E-01 |
|                 |            | c         | 4.46E-03 | 4.18E-05 | 3.07E-03 | 2.82E-05 |
|                 |            | d         | 2.69E-02 | 6.42E-04 | 1.69E-02 | 6.07E-04 |
|                 |            | f         | 3.60E+00 | 6.84E-02 | 2.40E+00 | 6.55E-02 |
|                 |            | $t_0$     | 7.99E+01 | 1.72E-01 | 7.61E+01 | 1.62E-01 |
| Modified Tanaka | Population | a         | 4.11E-03 | 4.11E-05 | 4.34E-03 | 4.30E-05 |
|                 |            | c         | 0.00E+00 | 3.55E-07 | 9.34E-06 | 3.86E-07 |
|                 |            | d         | 2.63E-02 | 7.59E-04 | 1.80E-02 | 7.20E-04 |
|                 |            | f         | 4.16E+00 | 8.31E-02 | 3.07E+00 | 8.04E-02 |
|                 |            | $t_0$     | 7.41E+01 | 2.19E-01 | 7.15E+01 | 1.93E-01 |
|                 | Male       | a         | 5.18E-03 | 7.66E-05 | 5.44E-03 | 7.63E-05 |
|                 |            | c         | 8.31E-07 | 5.97E-07 | 8.20E-06 | 5.20E-07 |
|                 |            | d         | 2.63E-02 | 8.95E-04 | 1.51E-02 | 9.36E-04 |
|                 |            | f         | 3.14E+00 | 9.53E-02 | 1.87E+00 | 9.77E-02 |
|                 |            | $t_0$     | 8.28E+01 | 2.35E-01 | 7.99E+01 | 2.48E-01 |
|                 | Female     | a         | 3.78E-03 | 4.91E-05 | 3.69E-03 | 4.94E-05 |
|                 |            | c         | 0.00E+00 | 4.33E-07 | 9.99E-06 | 5.41E-07 |
|                 |            | d         | 2.63E-02 | 8.95E-04 | 1.51E-02 | 9.36E-04 |
|                 |            | f         | 3.14E+00 | 9.53E-02 | 1.87E+00 | 9.77E-02 |
|                 |            | $t_0$     | 8.28E+01 | 2.35E-01 | 7.99E+01 | 2.48E-01 |

a less rapid decrease in growth rate at older ages for this population.

Females tend to have lower  $a$  and  $c$  values compared to males at both sites, as well as higher  $d$  and  $g$  values (Table 1), especially in the modified Tanaka model. These consistencies demonstrate that the growth rate of females is higher than that of males, which would allow them to reach the larger body sizes and dominate larger size classes as found in Hemeon et al. (2021b, 2023) and Sower et al. (2022).

### 3.2. Growth models: age-specific cohorts

Both the Tanaka and modified Tanaka models fit the 20-year cohort groups well, yet the von Bertalanffy model continued to perform poorly (Tables A1 & A2). Hemeon et al., 2023 advises that  $L_{\infty}$  parameters derived from von Bertalanffy fits should not be used due to their inherent inaccuracy. Sometimes, however, the modified Tanaka yielded overestimates for growth at age, especially for NJ2 and in 20-year cohort groups with very few animals ( $n < 10$ ) (Figs. 4–9). Nevertheless, both models indicate increasing growth trends over time. For example,  $a$  parameter values steadily decrease as birth year increases for both sites, with some fluctuation (Tables A3–A6). This indicates that maximum growth rates have increased over time.

When comparing populations within cohorts,  $a$  parameter values for NJ2 are almost always smaller than those for NJ1, indicating a more rapid growth rate early in ontogeny, except in the cases of 20-year cohort groups 1760, 1880, 1900, and 1980 (Fig. 10). Values for  $c$  (Fig. 11) and, to a lesser extent,  $d$  parameters (Fig. 12) followed similar trends. Values for  $f$  steadily increased over time (later birth years, Fig. 13), indicating that the rate at which the growth rates decline at a given old age have decreased with more recent birth years. That is, for a given old age since birth, growth rates at that age have increased with

more recent birth years. When comparing sex-based growth, females also displayed higher growth rates and lower ages at maximum size within cohorts compared to males (Figs. 10–14).

### 3.3. Growth rates

The metrics integrating growth dynamics were identified to facilitate determination of the degree of change in growth rate with birth year. The age at maturity is estimated to occur at 52 mm SL, age at recruitment to the fishery at 80 mm SL, and the number of reproductive years prior to recruiting to the fishery as the number of years elapsing between these two sizes. Linear regression analysis indicated that these three elapsed times have decreased as growth rates increased with increasing birth year.

For comparison, the age at 52 mm SL and 80 mm SL and the number of years elapsed between them was calculated for three birth years: 1800, 1900, and 2000. Sower et al. (2022) found that the size of maturity, between 50 and 55 mm SL, is often reached in the first 10–15 years of life. For individuals born in 1800, this value was somewhat higher, at age 26 for NJ1 and age 28 at NJ2 (Table 2). For individuals born in 1900, however, these ages decreased to 17 and 18 for NJ1 and NJ2, respectively. These ages decreased further for animals born in 2000, to 9 for NJ1 and 8 for NJ2 (Figs. 15 and 18). These trends are significant for both sites ( $p < 2.2E-16$ , with  $R^2$  values 0.39 and 0.37, respectively). Taking into account that variance increased by the combination of the two sexes typified by varying growth rates within this age range, these regression coefficients are surprisingly high. The rate of change for NJ1 is  $0.085 \text{ yr}^{-1}$  and is  $0.097 \text{ yr}^{-1}$  for NJ2.

Time to fishery recruitment, 80 mm SL, has decreased as birth year increased. Years required to reach 80 mm SL were calculated at 114 and

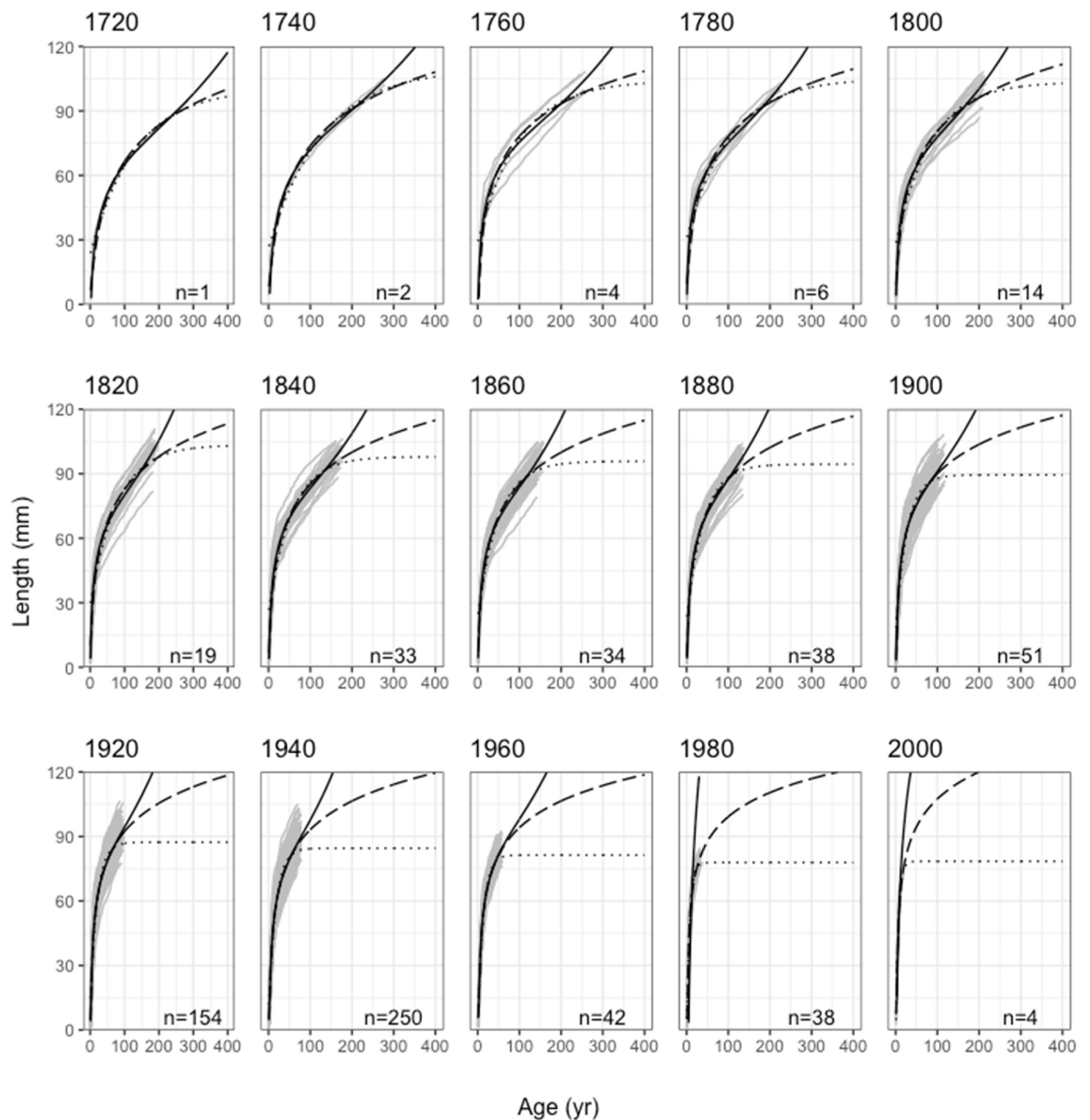


Fig. 4. Growth models for NJ1 population 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

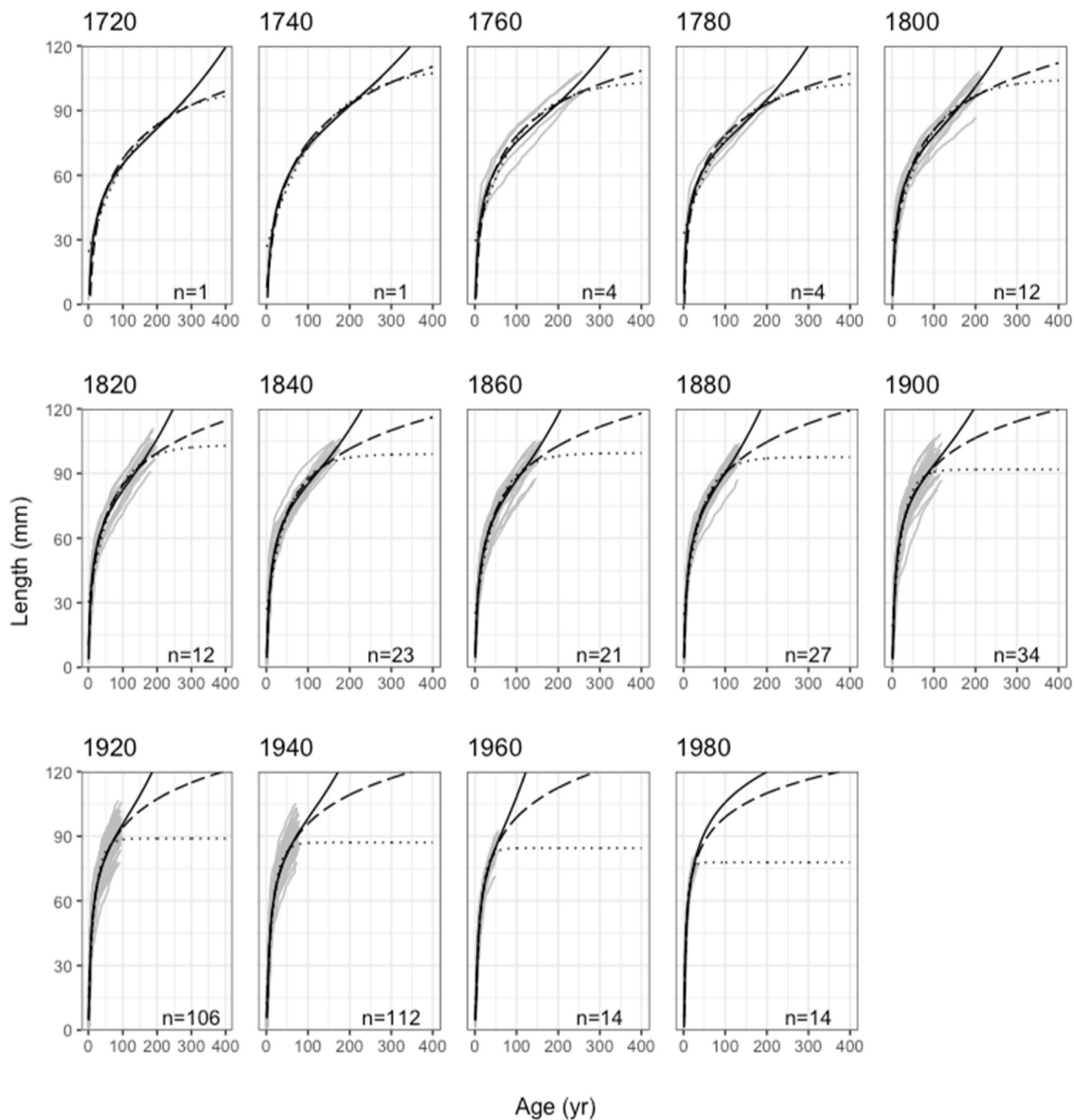


Fig. 5. Growth models for NJ1female 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

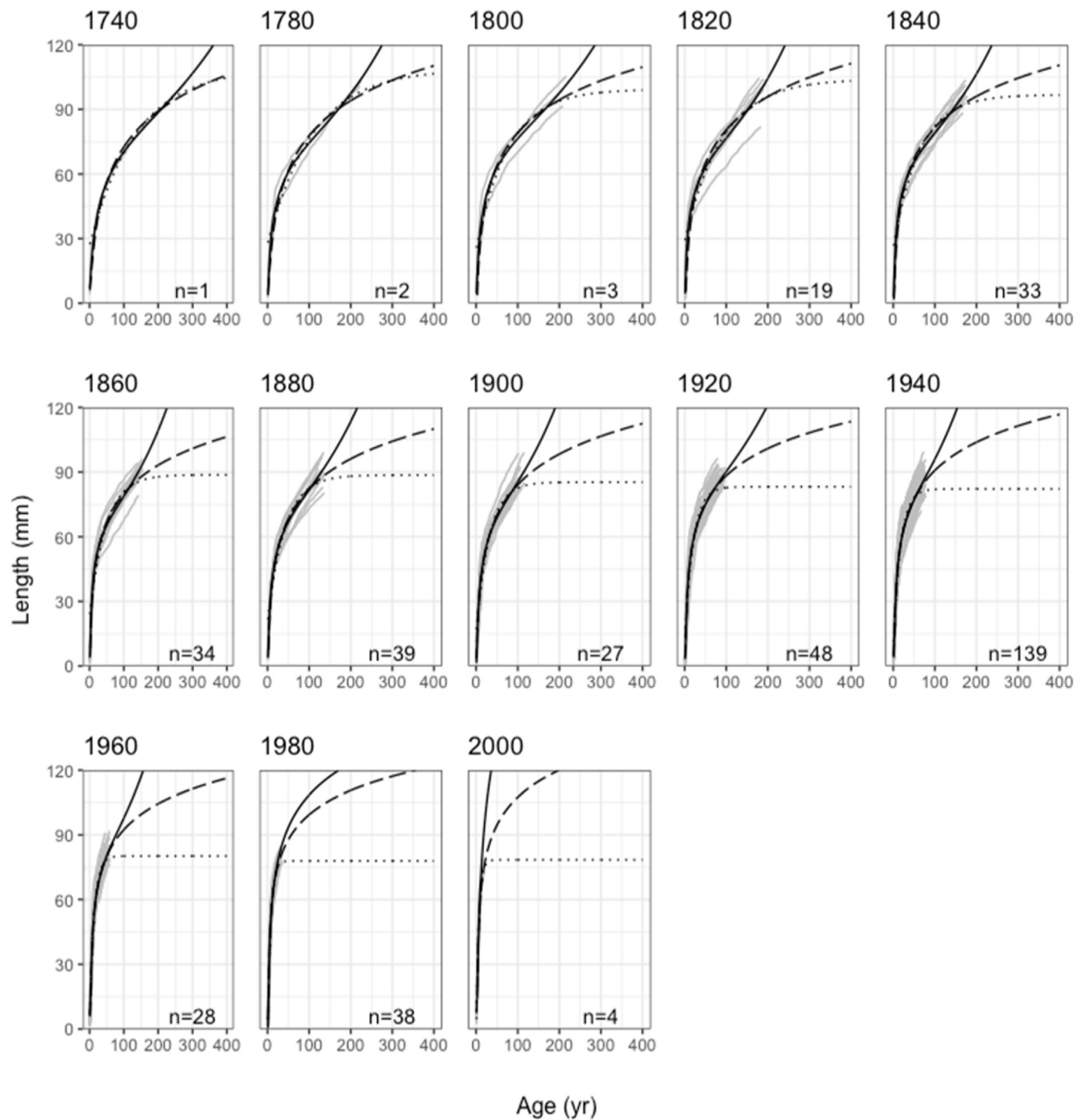


Fig. 6. Growth models for NJ1 male 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

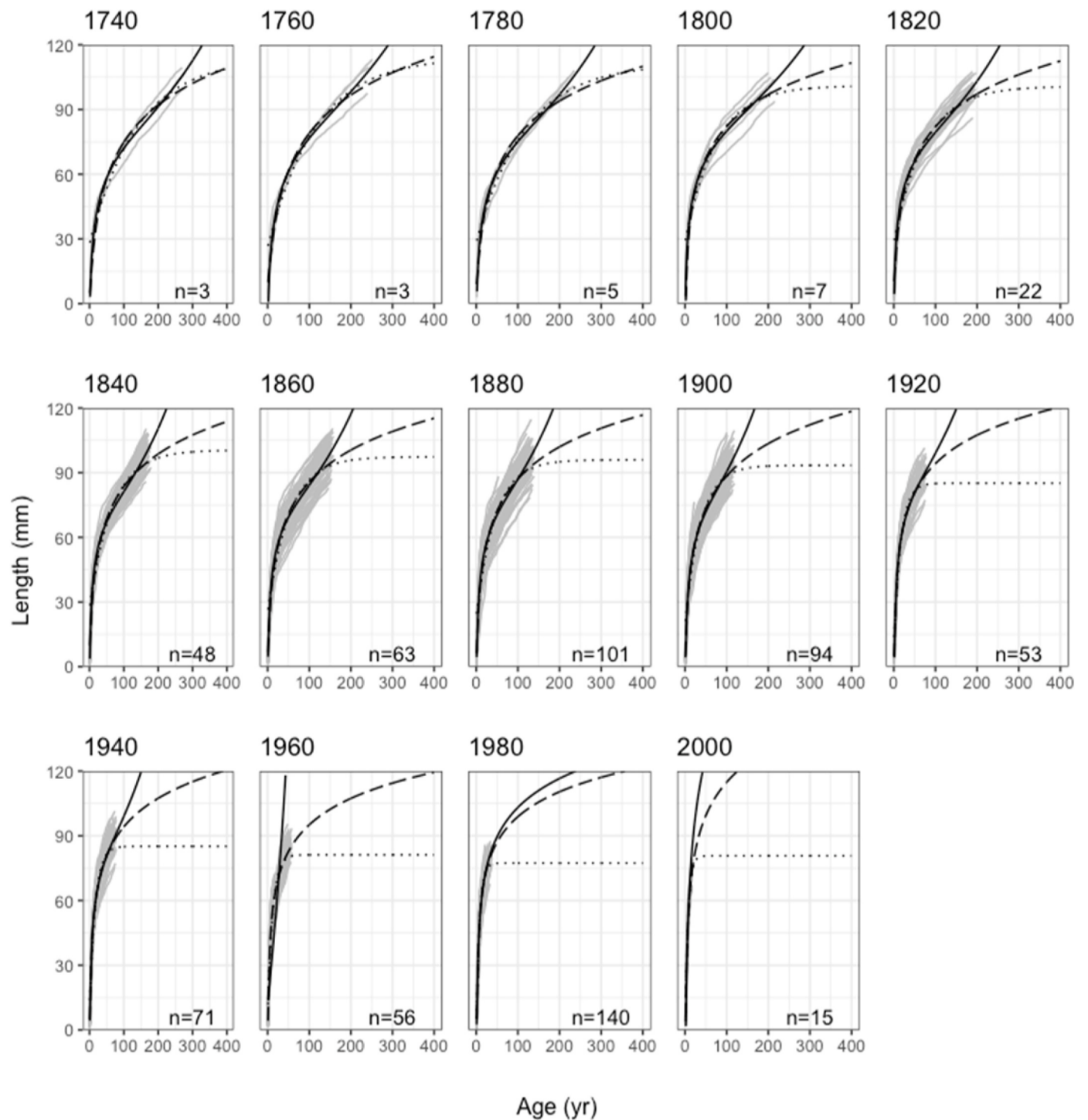


Fig. 7. Growth models for NJ2 population 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

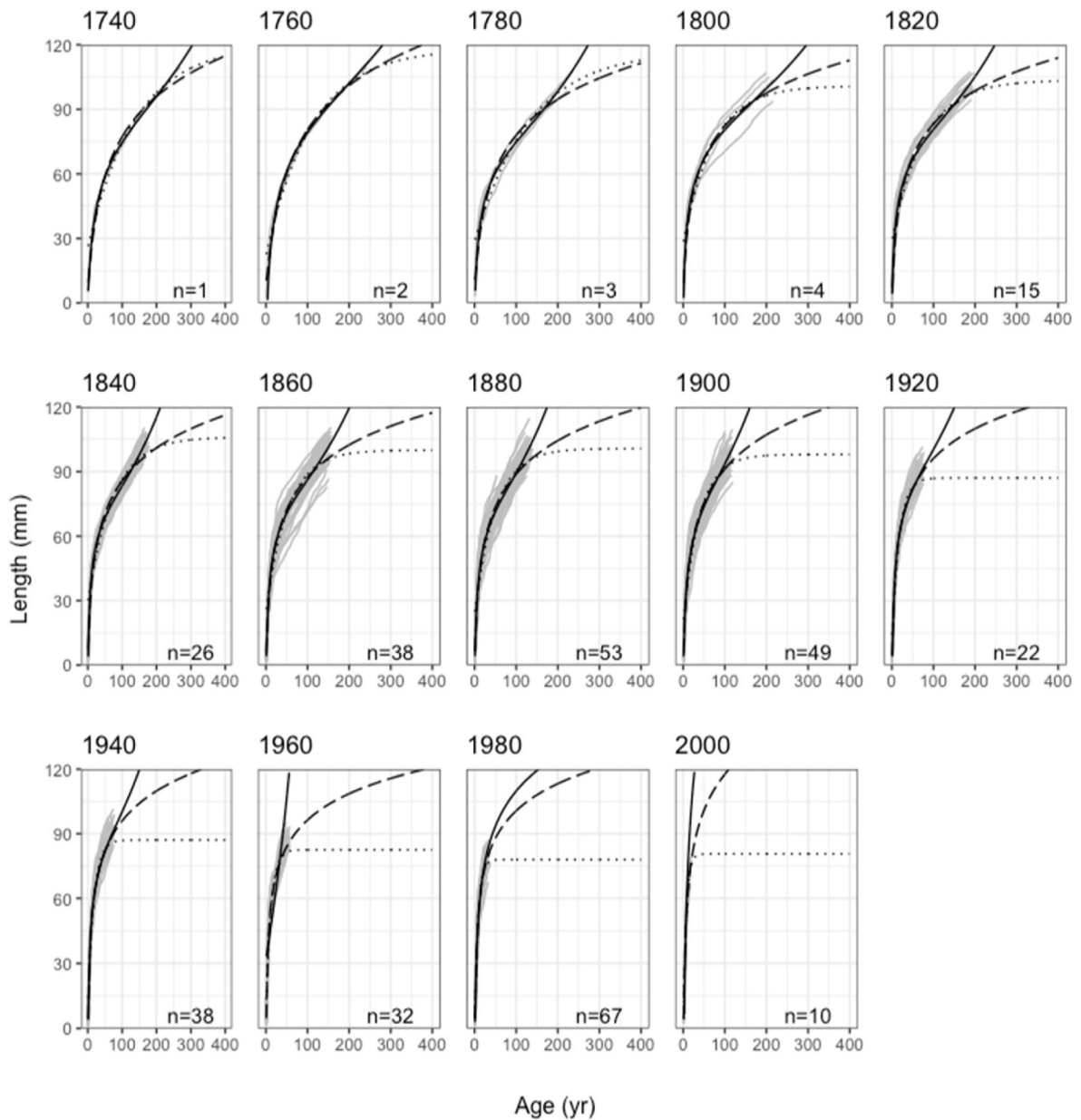


Fig. 8. Growth models for NJ2 female 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

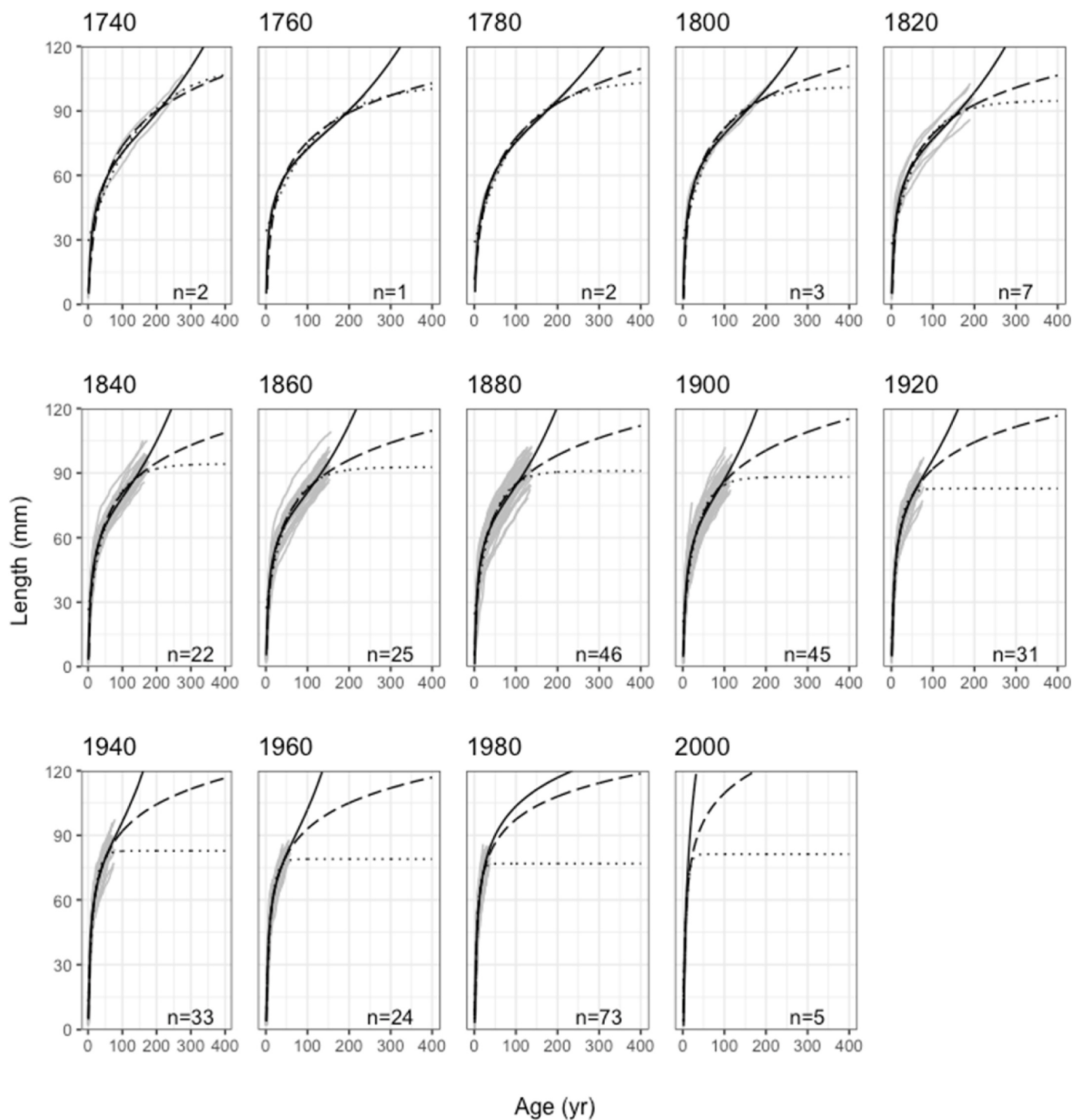
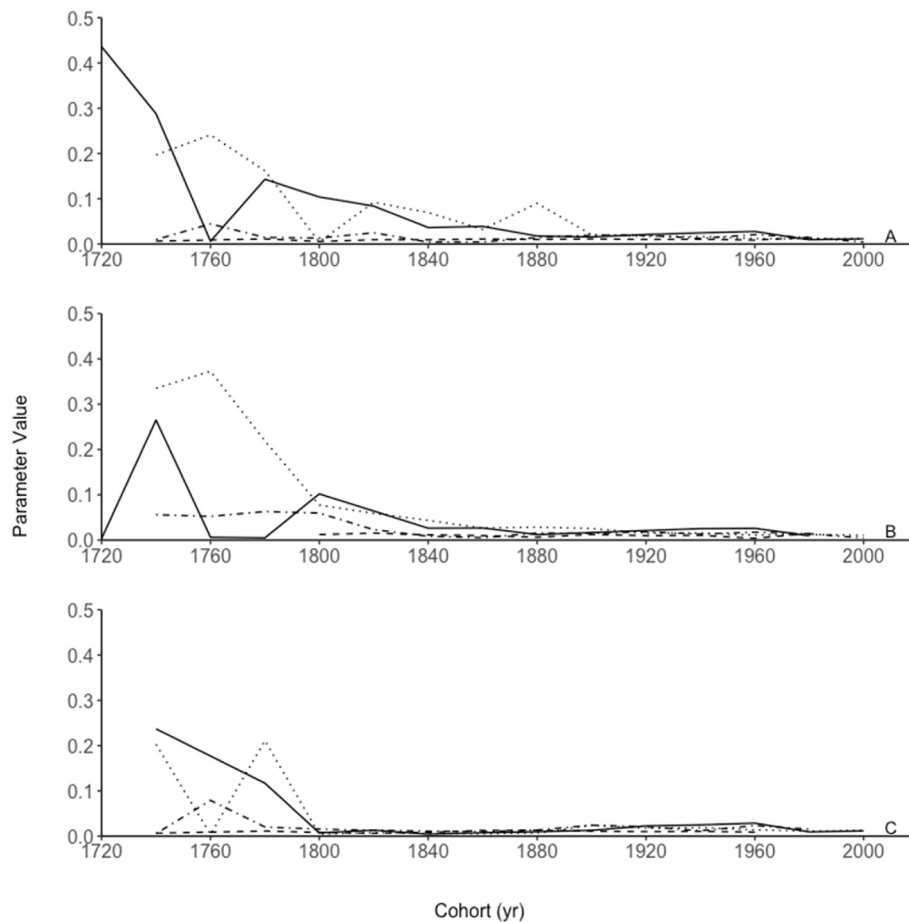


Fig. 9. Growth models for NJ2 male 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.



**Fig. 10.** Tanaka  $a$  parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line), for population (A), female (B), and male (C) groups.

118 years for NJ1 and NJ2, respectively, for individuals born in 1800. This decreased to 71 and 73 years, respectively, for individuals born in 1900, and decreased further to 28 and 26 years for animals born in 2000. The rate of change for NJ1 was  $-0.43 \text{ yr}^{-1}$  for NJ1 and  $-0.46 \text{ yr}^{-1}$  for NJ2 (Figs. 16 and 19).  $R^2$  values indicate a strong, statistically significant ( $p < 2.2\text{E-}16$ ) relationship to birth year, with values at 0.71 for NJ1, and 0.63 for NJ2.

Years of reproduction prior to recruitment to the fishery are defined as the elapsed time between individuals reaching 52 mm SL and reaching 80 mm SL. This window of time has also decreased with increasing birth year. The number of years available to reproduce for animals born in 1800 were 72 at NJ1 and 93 at NJ2. The number of years decreased to 51 and 55 for NJ1 and NJ2 respectively for individuals born in 1900 and decreased further to 30 years in NJ1 and 16 years in NJ2 for individuals born in 2000. The increase in growth rate observed in NJ2 over NJ1 is corroborated by their respective rates of change, with  $0.21 \text{ yr}^{-1}$  in NJ1 and  $-0.38 \text{ yr}^{-1}$  in NJ2 (Figs. 17 and 20). Linear regressions were also statistically significant, with  $p$ -values less than  $2.2\text{E-}16$ .  $R^2$  revealed a much stronger trend at NJ2 than NJ1, as  $R^2$  values for NJ2 were 0.77, but 0.24 for NJ1.

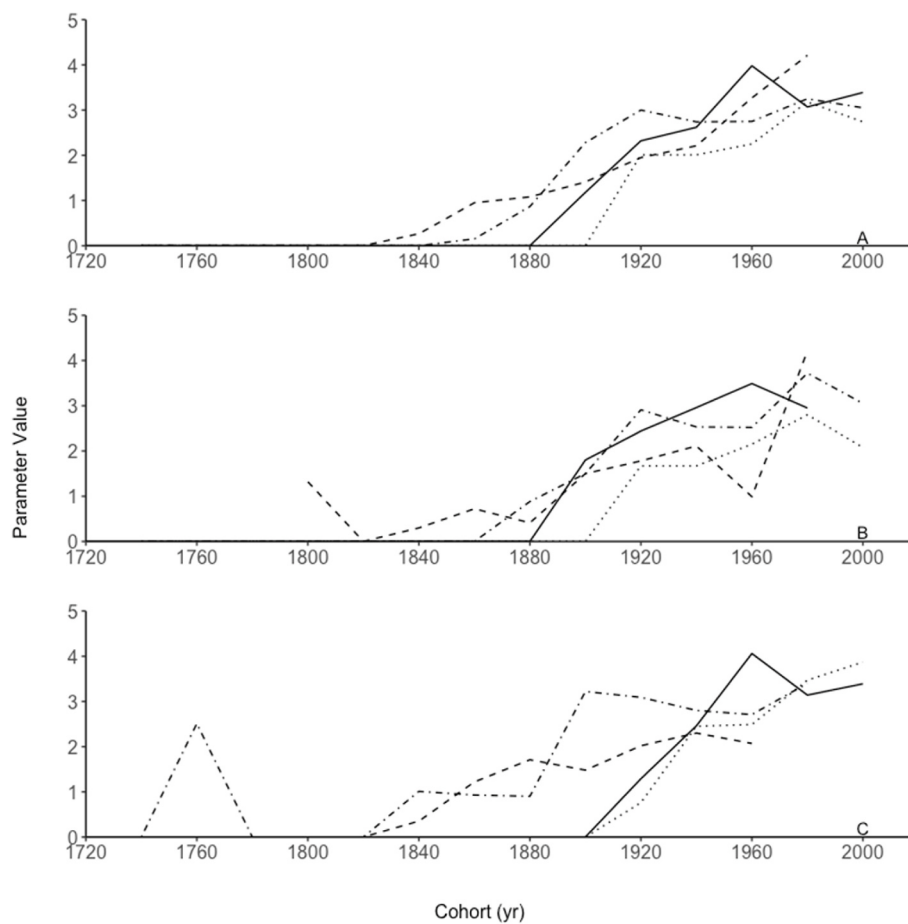
For both NJ1 and NJ2, the last two decades of birth years are characterized by a more rapid reduction in years to recruitment size and a more rapid reduction in the number of years of reproduction before recruitment to the fishery. Insufficient data are available for birth years after 2000 to confirm the presence of these apparently accelerating trends.

## 4. Discussion

### 4.1. Growth model implications

The Tanaka and modified Tanaka models for *A. islandica* growth fit the best for both populations, with the modified Tanaka often outperforming the Tanaka. The von Bertalanffy model provided the worst fit for both populations, overestimating at young ages and underestimating at old ages. This outcome was first considered by Pace et al. (2017a) and subsequently confirmed by Hemeon et al., 2023 for the Georges Bank and Long Island sites. Poor fit can lead to a substantial underestimation of length at old age, as one of the salient characteristics of *A. islandica* is the absence of asymptotic growth at old age. For this reason, the von Bertalanffy model cannot be relied upon to describe growth in this species. Thus, parameters from only the Tanaka and modified Tanaka models will be used to compare *A. islandica* across sites.

The modified Tanaka  $g$  parameter, which influences length at older ages, was higher in NJ2 than in NJ1 (Fig. 14). Modified Tanaka results are very similar to the original Tanaka in NJ1, leading to similar growth predictions. These two populations are separated by the Hudson Canyon, which influences the movement of water between these two sites (Zhang et al., 2016). Both bottom water temperature and primary productivity could be different between these two sites due to this geographic barrier. Both factors have been observed to greatly impact *A. islandica* growth (Schöne et al., 2005). As NJ2 is south of NJ1, these higher growth rates at older ages at NJ2 are potentially caused by warmer bottom water temperatures at that site. The differential in



**Fig. 11.** Tanaka  $c$  parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line), for population (A), female (B), and male (C) groups.

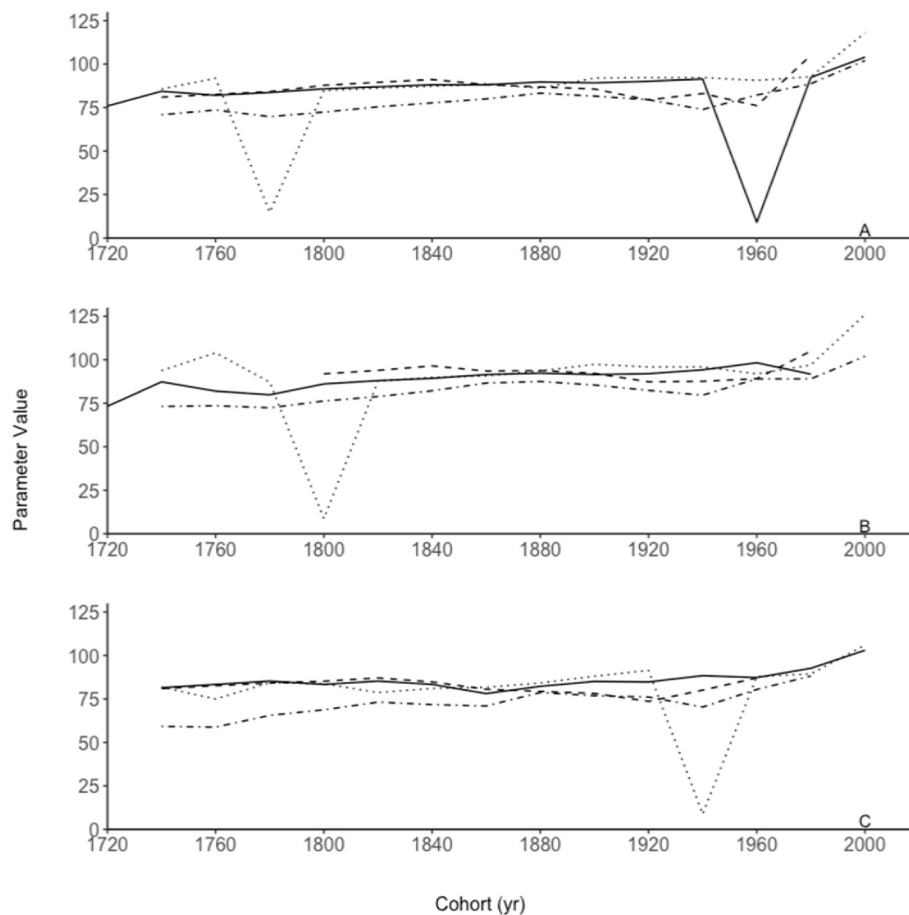
growth rate at old age, however, is not mirrored early in ontogeny. Time to maturity and time to recruitment into the fishery is very similar between the two sites.

Comparing growth model performance across the 20-year cohort groups demonstrates that the original Tanaka model often underestimates length at old age. The modified Tanaka, conversely, fits the observed data well, yet extrapolations often would appear to overestimate lengths to values unobserved in numerous studies, including Pace et al. (2017a, 2017b), Hemeon et al. (2021b, 2023), and Sower et al. (2023), leading to an apparently limited ability to extrapolate growth trends. The same limitation was also observed by Hemeon et al. (in press). However, both the original and modified Tanaka models confirm increased growth rates in both populations in recent decades, with estimates for animals born in the 1960s–2000s much higher than those born in the 1700s and 1800s (Figs. 4–9). Thus, growth rates have likely increased consistently with birth year since the late 1700s.

Females and males display distinct differences in growth, with females reaching larger sizes (Ropes et al., 1984a; Hemeon et al., 2021b, 2023; Sower et al., 2022). The higher growth rates experienced by females compared to males discussed here and in Hemeon et al., 2023 provide evidence that this species is sexually dimorphic, even though sexual dimorphism is rarely observed in bivalves. The differential rates of growth by males and females is partly responsible for the wide range of ages at length noted for most 5-mm size classes by Pace et al. (2017b), Hemeon et al. (2021b), and herein.

#### 4.2. Growth rates

Birth year is an important contributor to variation in length at age for ocean quahogs at both NJ1 and NJ2. Three elapsed time periods were used for comparison, the time between birth and maturity, the time between birth and recruitment into the fishery, and the elapsed time between the two representing the number of years of reproduction before exploitation. To compare patterns in these three metrics at all four sites, three birth years were chosen: 1800, 1900, and 2000. Each site displayed decreasing times to the three metric sizes as birthdate increased, though variation among the four sites was observed. *Arctica islandica* from Georges Bank reached 52 mm SL at the youngest age out of all four sites, at age 18 for animals born in 1800, a time span that decreased by a factor of 2 to age 9 for animals born in 2000. NJ1, NJ2, and Long Island, conversely, reached 52 mm SL by age 28 for animals born in 1800, which also decreased to age 9 for animals born in 2000, a decrease in time to maturity by a factor exceeding 3 (Table 2). At all four sites, animals born in 1900 fell almost halfway in elapsed time between the 1800 and 2000 values. Time to recruitment size (80 mm SL) followed the same trends at all four sites, with Georges Bank having the youngest age, 63 years, for animals born in 1800, whereas NJ1, NJ2, and Long Island having ages ranging from 114 to 119 years for animals born in 1800, nearly twice as long. By 2000, elapsed time to 80 mm SL had decreased to 26–28 years in NJ2 and NJ1, respectively, and 34–39 years in Long Island and Georges Bank, respectively. As for the number of years of reproduction between maturity and exploitation, NJ2 had the most drastic decrease as birth year increased, with 93 years available for animals born in 1800 decreasing by a factor of 5–16 years available for



**Fig. 12.** Tanaka  $d$  parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line), for population (A), female (B), and male (C) groups.

animals born in 2000. Georges Bank displayed the least difference, from 48 years for animals born 1800 to 41 in 2000. Long Island and NJ1 displayed very similar trends, at 79 and 72 years available for animals born in 1800, respectively, to 32 and 30 years available for animals born in 2000. Thus, the influence of birth year on time to milestone size is much more subdued in Georges Bank compared to the southern sites. These findings are also in agreement with Pace et al. (2018) who examined additional populations off southern New England and further south off Delmarva.

#### 4.3. Trends in growth

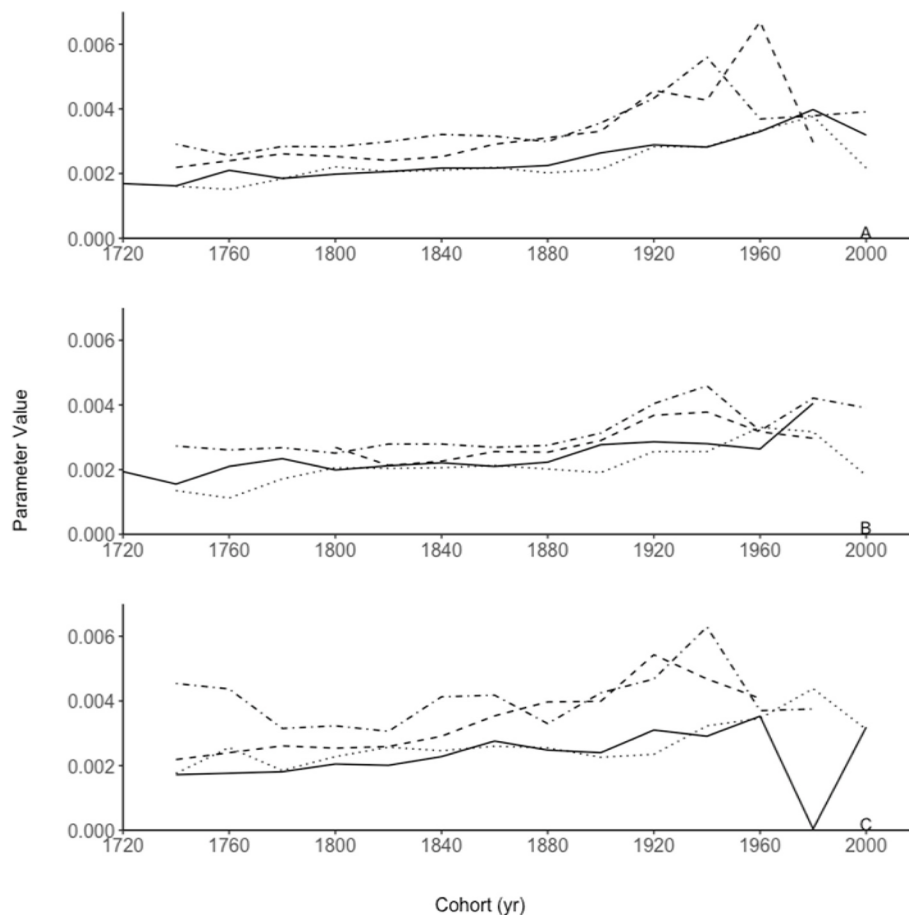
Hemeon et al. (in press) reported Tanaka model parameters for *A. islandica* from Georges Bank and Long Island (Table 3, Hemeon et al. in press). Those reported parameters can be compared directly to those for NJ1 and NJ2 to determine trends over time. At all four sites, and for both males and females (Fig. 10),  $a$  parameter values have been decreasing with slight variation since 1720. These trends indicate that maximum growth rates have increased over time at all sites. Parameter  $c$  values have increased steadily over time as well (Fig. 11); however, this parameter presents anomalous 0 values for many cohort years in the 1700s and 1800s at all four sites. Parameter  $c$  identifies the age of maximum growth rate, and the reasons behind these 0 values are unclear. The parameter  $d$  shifts the length-age curve by a constant length for all ages; that is, choosing the value of  $d$  sets the length at a specific age. Interestingly, this scaler of body size, unlike the other parameters, has remained consistent since 1720 (Fig. 12), with slight increases in the most recent decades. The  $f$  parameter values have slightly increased over

time (Fig. 13), which indicates the rate at which growth has slowed at older age has declined: growth rates are higher now at old age than would have been true in the 1700s and 1800s for animals of the same age. The  $f$  parameter is influenced by the  $g$  parameter, which additionally modulates the rate of growth rate decline with increasing age. The  $g$  parameter has increased since 1720 (Fig. 14) to a larger degree than the  $f$  parameter, potentially indicating an acceleration of growth rate at older ages not adequately compensated for by a change in  $f$ .

All four sites have displayed the same trends in parameter variation since 1720. These trends indicate that *A. islandica* growth has increased in a relatively similar fashion with some variation over this time period. One possible reason for increasing growth is increasing bottom water temperature. Although limited information exists to validate this claim, the fact that *A. islandica* growth is similarly influenced over a wide geographic scale, given the similar trends among all four sites, leads increasing weight to the assumption that increasing temperature is the probable cause.

#### 5. Conclusion

Birth year is an important contributor to variation in length at age for ocean quahogs at both NJ1 and NJ2. The impressive influence of birth year is well instantiated by regressions of age-at-specified-length relative to birth year (Figs. 14–19). Comparisons were based on the elapsed time between birth and maturity, the time between birth and recruitment into the fishery, and the period of time between the two representing the number of years of reproduction before exploitation. This latter is an important characteristic influencing the sensitivity of fishing



**Fig. 13.** Tanaka  $f$  parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line), for population (A), female (B), and male (C) groups.

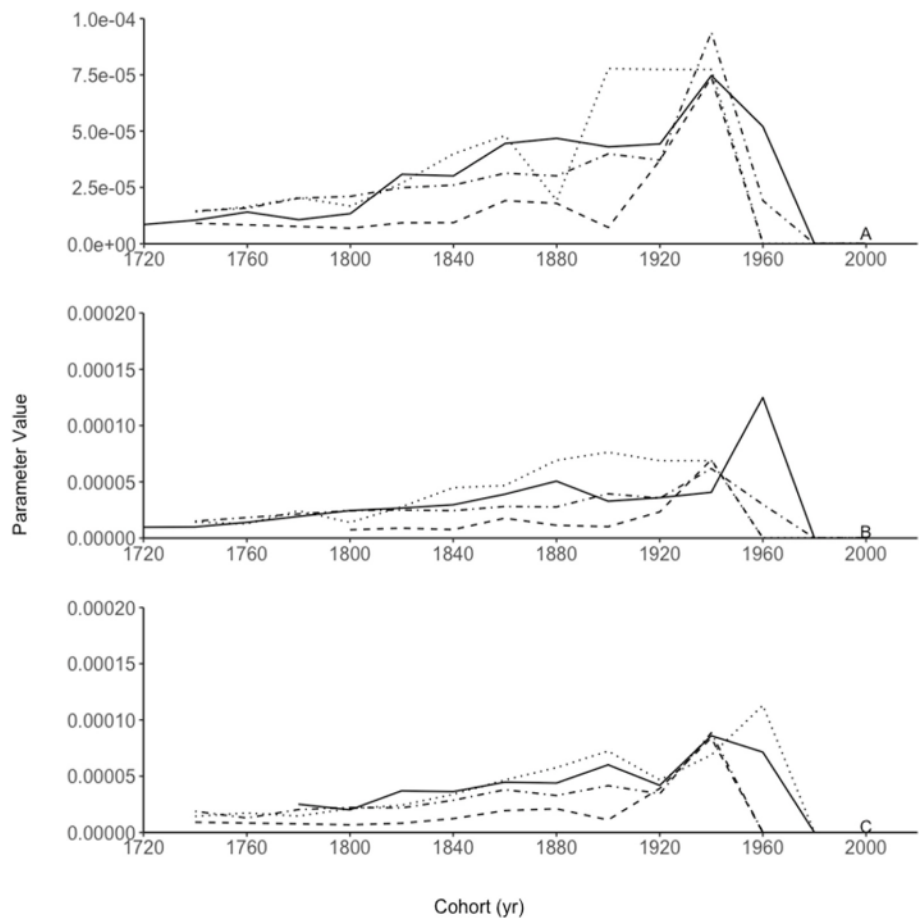
on stock sustainability (Peterson, 2002; Sissenwine and Shepherd, 1987). For comparison, three century-initiating birth years were chosen: 1800, 1900, and 2000. Year 1800 occurred in the last phase of the Little Ice Age (Cronin et al., 2010; Moore et al., 2017), whereas year 1900 occurred within a time period of consistent warming (Nixon et al., 2004). Year 2000 coincides with the initiation of a regime shift that produced rising temperatures throughout much of the Mid-Atlantic Bight (Perretti et al., 2017; Pershing et al., 2015; Powell et al., 2020).

Each site displayed decreasing times to the three metric sizes as birthdate increased, though variation among the four sites was observed. The influence of birth year on time to milestone size was much more subdued at Georges Bank (Hemeon et al. in press) compared to the southern sites. This is consistent with observations by Hemeon et al. (in press) that animals at the end of the Little Ice Age were growing fastest in this region, but that growth rates at the other three sites caught up in large measure over the following 200 years (see also Lewis et al., 2001; Ropes and Pyoas, 1982). These findings are also in agreement with Pace et al. (2018) who examined additional populations off southern New England and further south off Delmarva and, noteworthily, are in agreement with growth rates from subfossil shells measured by LeClaire et al. (in prep.) recovered from the death assemblage off Delmarva.

The latitudinal response revealed by these comparisons of elapsed time from birth to maturity and to recruitment to the fishery define a clear north-to-south gradient in increased growth rates since the end of the Little Ice Age throughout the Mid-Atlantic and Georges Bank region. The trends in growth rate as a function of birthdate may be due to increasing bottom water temperatures over the last 200 years, though due to the lack of bottom water temperature data throughout the time

period represented in the birthdates and ages reported here, one cannot be certain that temperature is the cause. However, Whitney et al. (2022) indicate that rapid warming occurred over the last 100 years in the Gulf of Maine, which may also be true for the Mid-Atlantic Bight. Of particular note is the absence of information on the long-term dynamics of the Cold Pool (Lentz 2017; Chen et al., 2018). Nonetheless, many of the *A. islandica* in this study have lived throughout the entirety of global warming since the end of the Little Ice Age, very likely leaving a record of rising temperatures in the variations in growth rate over that time.

Growth rates in most bivalves are strongly influenced by temperature, with growth rates rising over a wide temperature range, but then falling again as optimal temperatures are exceeded. The general pattern in *Venerida*, of which *A. islandica* is a member, is well described (Flye-Sainte-Marie et al., 2007; Hofmann et al., 2006; Munroe et al., 2013), with growth primarily influenced by ever rising respiration rates with rising temperatures, but a parabolic response of filtration rates leading to temperature-dependent changes in scope for growth (Beukema et al., 2017; Munroe et al., 2013). *Arctica islandica* are sensitive to variations in temperature to an even greater degree than most *Venerida* (Begum et al., 2009, 2010); thus, the presumption that the primary growth-influencing agent is rising bottom water temperatures has merit. One cannot exclude the influence of food supply, however, as food supply is an important modulator of rates of growth (Mette et al., 2016; Schöne et al., 2005; Wanamaker et al., 2009; see also LeClaire et al. in prep.), but a centuries-long increase in food supply is unlikely to be an explanatory alternative (Boyce et al., 2010). What is unique for *A. islandica*, due to their long lifespan, is that the differential in growth rate with rising temperatures can be observed within members of the



**Fig. 14.** Modified Tanaka *g* parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line), for population (A), female (B), and male (C) groups.

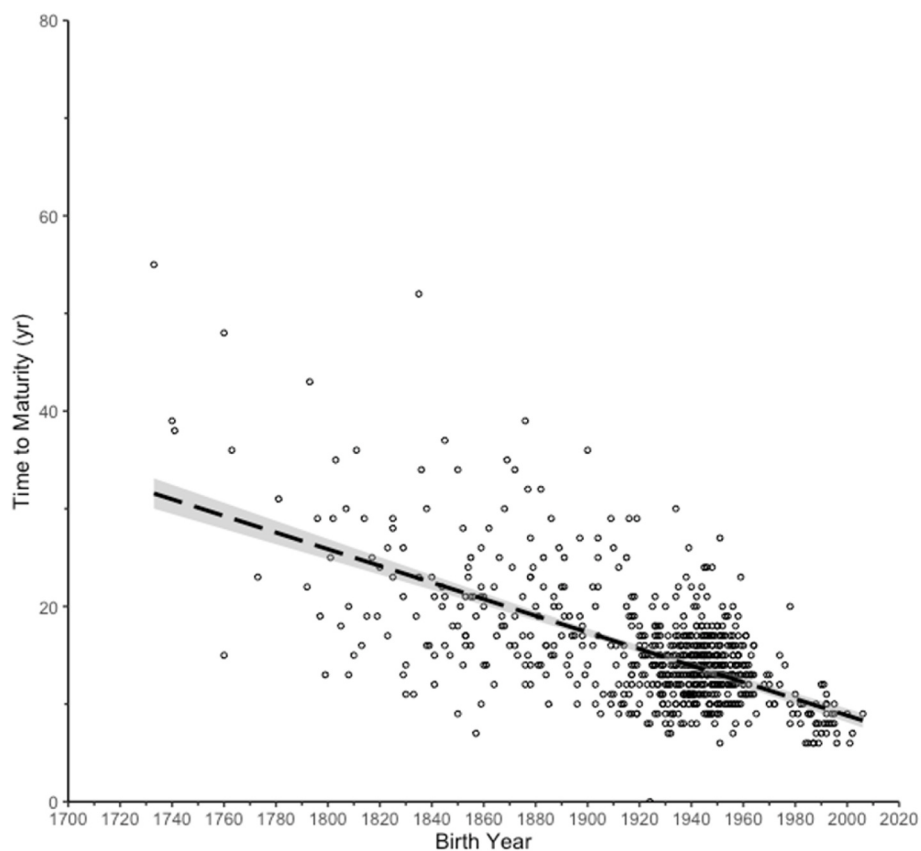
**Table 2**  
Time (yr) to milestone sizes at three birth years at northern New Jersey (NJ1), southern New Jersey (NJ2), Georges Bank (GB), and Long Island (LI), the latter two taken from Hemeon et al. (in press). Ages are reported in years.

| Milestone                           | Birth Year | NJ1 | NJ2 | GB | LI  |
|-------------------------------------|------------|-----|-----|----|-----|
| Time to 50% Maturity (52 mm)        | 1800       | 26  | 28  | 18 | 28  |
|                                     | 1900       | 17  | 18  | 12 | 16  |
|                                     | 2000       | 9   | 8   | 9  | 9   |
| Time to Commercial Size (80 mm)     | 1800       | 114 | 119 | 63 | 114 |
|                                     | 1900       | 71  | 72  | 51 | 74  |
|                                     | 2000       | 28  | 26  | 39 | 34  |
| Years of Reproduction (52 mm–80 mm) | 1800       | 72  | 93  | 48 | 79  |
|                                     | 1900       | 51  | 55  | 44 | 51  |
|                                     | 2000       | 30  | 16  | 41 | 32  |

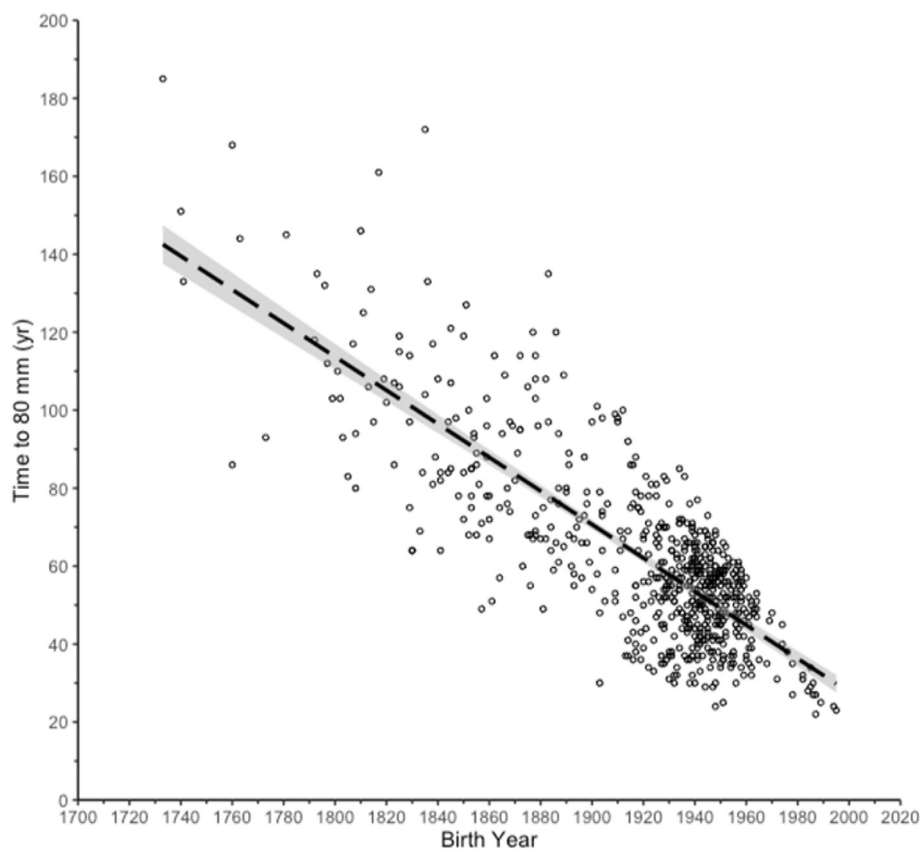
living community born across the centuries and that this record leaves a strong signal of the influence of climate change in the northwestern Atlantic. *Arctica islandica* growth rates have increased by factors of 2–3 or more since the end of the 1700s, an extraordinary physiological response to global warming.

**Declaration of competing interest**

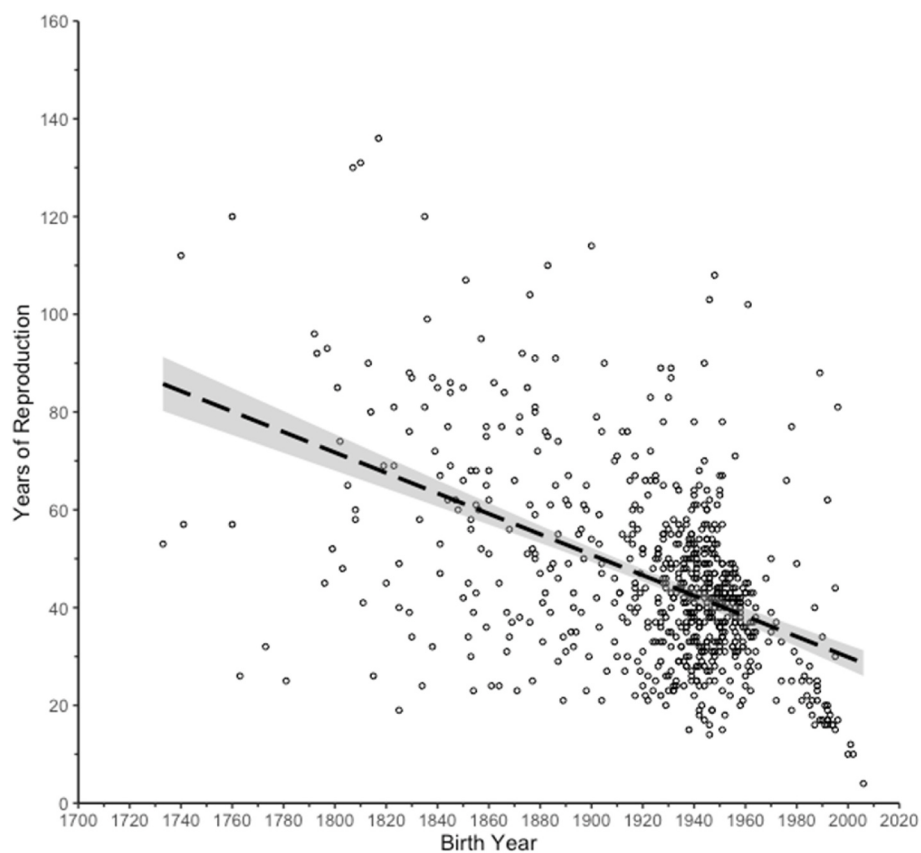
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



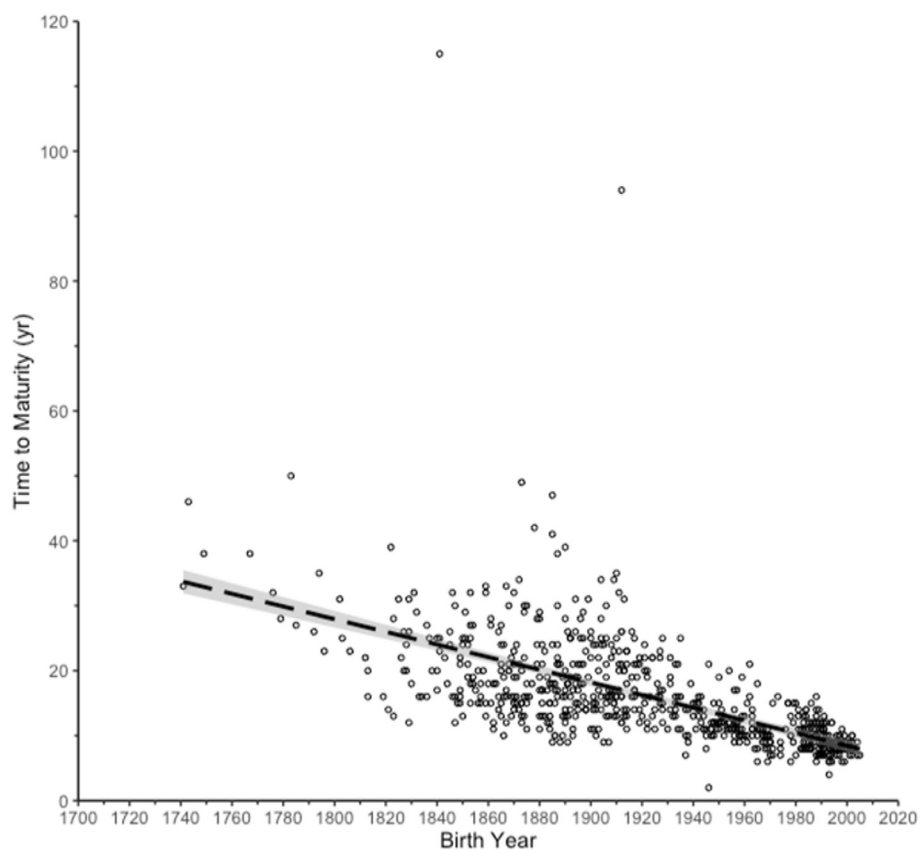
**Fig. 15.** Northern New Jersey (NJ1) time to 50% maturity (52 mm). Linear regression (dashed line) equation:  $179.12 - 0.085x$ . The shading around this line represents a 95% confidence interval.  $P < 2.2 \times 10^{-16}$ ,  $R^2 = 0.39$ .



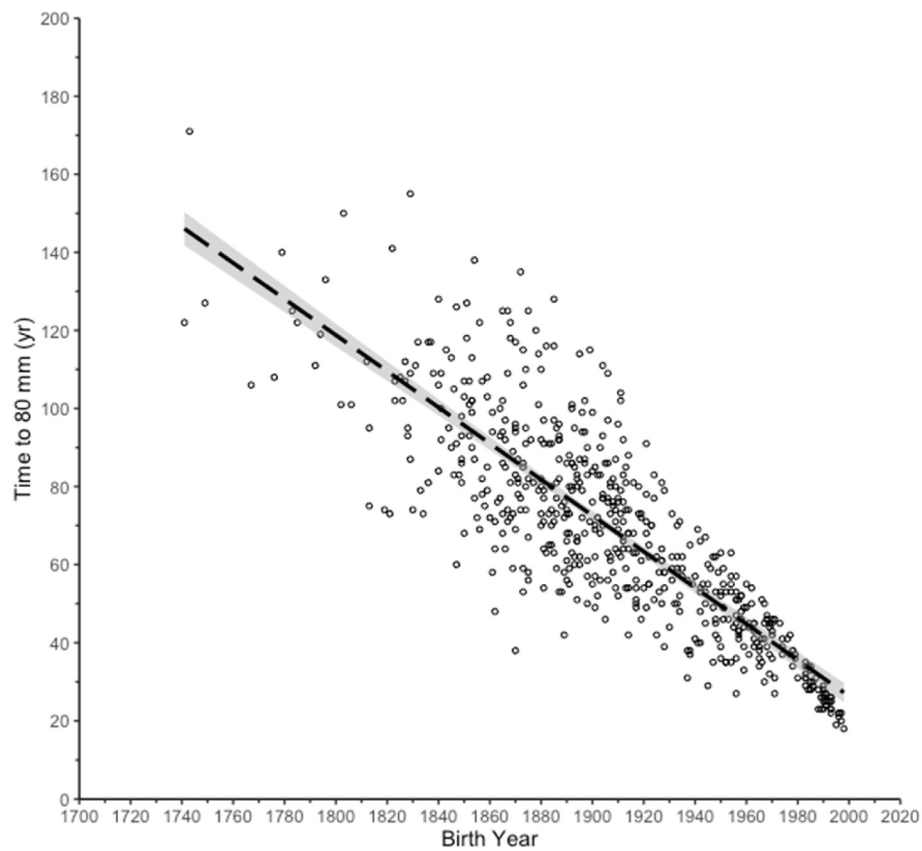
**Fig. 16.** Northern New Jersey (NJ1) time to commercial size (80 mm). Linear regression (dashed line) equation:  $888.00 - 0.43x$ . The shading around this line represents a 95% confidence interval.  $P < 2.2 \times 10^{-16}$ ,  $R^2 = 0.71$ .



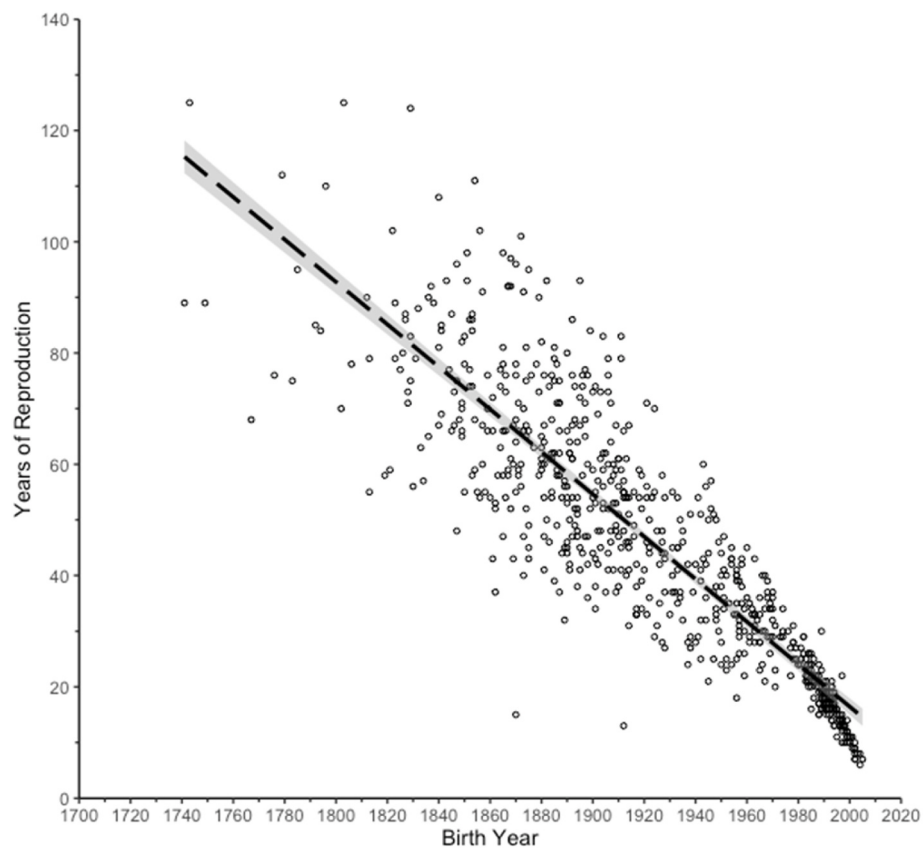
**Fig. 17.** Northern New Jersey (NJ1) years of reproduction (time between 52 mm and 80 mm). Linear regression (dashed line) equation:  $448.36 - 0.21x$ . The shading around this line represents a 95% confidence interval.  $P < 2.2 \times 10^{-16}$ ,  $R^2 = 0.24$ .



**Fig. 18.** Southern New Jersey (NJ2) time to 50% maturity (52 mm). Linear regression (dashed line) equation:  $203.18 - 0.097x$ . The shading around this line represents a 95% confidence interval.  $P < 2.2 \times 10^{-16}$ ,  $R^2 = 0.37$ .



**Fig. 19.** Southern New Jersey (NJ2) time to commercial size (80 mm). Linear regression (dashed line) equation:  $950.94 - 0.46x$ . The shading around this line represents a 95% confidence interval.  $P < 2.2 \times 10^{-16}$ ,  $R^2 = 0.63$ .



**Fig. 20.** Southern New Jersey (NJ2) years of reproduction (time between 52 mm and 80 mm). Linear regression (dashed line) equation:  $779.75 - 0.38x$ . The shading around this line represents a 95% confidence interval.  $P < 2.2 \times 10^{-16}$ ,  $R^2 = 0.77$ .

## Data availability

Data will be made available on request.

## Acknowledgements

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## Appendix A. Cohort Parameter Values per Population

**Table A1**

Northern New Jersey (NJ1) von Bertalanffy model parameter values for 20-year cohorts. SE = standard error.

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1720   | $L_{inf}$ | 1.00E+02   | 1.02E+00 | 1.00E+02 | 1.02E+00 | –        | –        |
|        | K         | 7.64E-03   | 2.56E-04 | 7.61E-03 | 2.55E-04 | –        | –        |
|        | $t_0$     | 3.45E+01   | 1.74E+00 | 3.56E+01 | 1.75E+00 | –        | –        |
| 1740   | $L_{inf}$ | 1.10E+02   | 8.74E-01 | 1.11E+02 | 1.01E+00 | 1.09E+02 | 1.18E+00 |
|        | K         | 7.76E-03   | 2.04E-04 | 8.08E-03 | 2.49E-04 | 7.39E-03 | 2.56E-04 |
|        | $t_0$     | 3.55E+01   | 1.35E+00 | 3.32E+01 | 1.55E+00 | 3.81E+01 | 1.81E+00 |
| 1760   | $L_{inf}$ | 1.04E+02   | 1.09E+00 | 1.04E+02 | 1.09E+00 | –        | –        |
|        | K         | 1.02E-02   | 4.24E-04 | 1.02E-02 | 4.24E-04 | –        | –        |
|        | $t_0$     | 3.15E+01   | 2.03E+00 | 3.15E+01 | 2.03E+00 | –        | –        |
| 1780   | $L_{inf}$ | 1.05E+02   | 8.98E-01 | 1.03E+02 | 1.01E+00 | 1.09E+02 | 1.75E+00 |
|        | K         | 9.67E-03   | 2.95E-04 | 9.90E-03 | 3.63E-04 | 9.15E-03 | 4.77E-04 |
|        | $t_0$     | 3.55E+01   | 1.42E+00 | 3.75E+01 | 1.77E+00 | 3.17E+01 | 2.22E+00 |
| 1800   | $L_{inf}$ | 1.03E+02   | 5.89E-01 | 1.05E+02 | 6.96E-01 | 9.93E+01 | 1.04E+00 |
|        | K         | 1.19E-02   | 2.59E-04 | 1.15E-02 | 2.88E-04 | 1.30E-02 | 5.49E-04 |
|        | $t_0$     | 2.64E+01   | 8.73E-01 | 2.77E+01 | 1.01E+00 | 2.21E+01 | 1.60E+00 |
| 1820   | $L_{inf}$ | 1.03E+02   | 6.23E-01 | 1.03E+00 | 6.36E-01 | 1.04E+02 | 1.28E+00 |
|        | K         | 1.29E-02   | 2.98E-04 | 1.41E-02 | 3.59E-04 | 1.12E-02 | 4.65E-04 |
|        | $t_0$     | 2.54E+01   | 8.56E-01 | 2.35E+01 | 9.34E-01 | 2.85E+01 | 1.55E+01 |
| 1840   | $L_{inf}$ | 9.79E+01   | 2.89E-01 | 9.90E+01 | 3.03E-01 | 9.67E+01 | 5.77E-01 |
|        | K         | 1.83E-02   | 2.43E-04 | 1.90E-02 | 2.69E-04 | 1.58E-02 | 3.87E-04 |
|        | $t_0$     | 1.64E+01   | 3.98E-01 | 1.56E+01 | 4.14E-01 | 1.94E+01 | 7.81E-01 |
| 1860   | $L_{inf}$ | 9.58E+01   | 3.71E-01 | 9.95E+01 | 4.29E-01 | 8.87E+01 | 4.59E-01 |
|        | K         | 2.01E-02   | 3.35E-04 | 1.99E-02 | 3.68E-04 | 2.14E-02 | 5.04E-04 |
|        | $t_0$     | 1.39E+01   | 4.33E-01 | 1.34E+01 | 4.74E-01 | 1.38E+01 | 6.06E-01 |
| 1880   | $L_{inf}$ | 9.45E+01   | 3.15E-01 | 9.76E+01 | 3.31E-01 | 8.85E+01 | 4.80E-01 |
|        | K         | 2.45E-02   | 3.65E-04 | 2.43E-02 | 3.63E-04 | 2.44E-02 | 5.88E-04 |
|        | $t_0$     | 1.07E+01   | 3.24E-01 | 1.09E+01 | 3.27E+01 | 1.04E+01 | 5.23E-01 |
| 1900   | $L_{inf}$ | 8.95E+01   | 2.67E-01 | 9.18E+01 | 2.73E-01 | 8.53E+01 | 3.91E-01 |
|        | K         | 3.82E-02   | 5.88E-04 | 4.10E-02 | 6.68E-04 | 3.24E-02 | 6.70E-04 |
|        | $t_0$     | 5.04E+00   | 2.34E-01 | 4.65E+00 | 2.39E-01 | 5.84E+00 | 3.31E-01 |
| 1920   | $L_{inf}$ | 8.73E+01   | 1.25E-01 | 8.89E+01 | 1.46E-01 | 8.32E+01 | 1.84E-01 |
|        | K         | 5.01E-02   | 3.75E-04 | 5.06E-02 | 4.40E-04 | 5.02E-02 | 5.70E-04 |
|        | $t_0$     | 2.72E+00   | 8.48E-02 | 2.71E+00 | 9.89E-02 | 2.56E+00 | 1.26E-01 |
| 1940   | $L_{inf}$ | 8.45E+01   | 1.06E-01 | 8.71E+01 | 1.52E-01 | 8.22E+01 | 1.27E-01 |
|        | K         | 5.87E-02   | 3.53E-04 | 5.98E-02 | 5.12E-04 | 5.85E-02 | 4.29E-04 |
|        | $t_0$     | 1.54E+00   | 5.34E-02 | 1.47E+00 | 7.60E-02 | 1.54E-01 | 6.48E-02 |
| 1960   | $L_{inf}$ | 8.13E+01   | 2.80E-01 | 8.45E+01 | 5.32E-01 | 8.02E+01 | 3.22E-01 |
|        | K         | 7.64E-02   | 1.17E-03 | 7.39E-02 | 1.92E-03 | 7.66E-02 | 1.40E-03 |
|        | $t_0$     | 2.30E-01   | 9.53E-02 | 1.67E-01 | 1.58E-01 | 3.11E-01 | 1.16E-01 |
| 1980   | $L_{inf}$ | 7.79E+01   | 3.12E-01 | 7.78E+01 | 4.84E-01 | 7.79E+01 | 4.04E-01 |
|        | K         | 1.42E-01   | 2.46E-03 | 1.41E-01 | 3.87E-03 | 1.42E-01 | 3.16E-03 |
|        | $t_0$     | 5.18E-01   | 5.58E-02 | 3.96E-01 | 8.99E-02 | 5.89E-01 | 7.07E-02 |
| 2000   | $L_{inf}$ | 7.85E+01   | 2.56E+00 | –        | –        | 7.85E+01 | 2.56E+00 |
|        | K         | 1.57E-01   | 1.50E-02 | –        | –        | 1.57E-01 | 1.50E-02 |
|        | $t_0$     | 6.18E-01   | 1.80E-01 | –        | –        | 6.18E-01 | 1.80E-01 |

**Table A2**

Southern New Jersey (NJ2) von Bertalanffy parameter values for 20-year cohorts. SE = standard error.

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1740   | $L_{inf}$ | 1.14E+02   | 1.35E+00 | 1.19E+02 | 1.50E+00 | 1.12E+02 | 1.70E+00 |
|        | K         | 7.13E-03   | 2.61E-04 | 7.24E-03 | 2.69E-04 | 6.85E-03 | 3.19E-04 |
|        | $t_0$     | 3.90E+01   | 1.88E+00 | 3.34E+01 | 1.76E+00 | 4.34E+01 | 2.51E+00 |
| 1760   | $L_{inf}$ | 1.14E+02   | 1.28E+00 | 1.17E+02 | 8.45E-01 | 1.02E+02 | 1.49E+00 |
|        | K         | 8.67E-03   | 3.12E-04 | 9.08E-03 | 2.06E-04 | 8.67E-03 | 4.58E-04 |

(continued on next page)

Table A2 (continued)

| Cohort | Parameter        | Population |          | Female   |          | Male     |          |
|--------|------------------|------------|----------|----------|----------|----------|----------|
|        |                  | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1780   | t <sub>0</sub>   | 2.98E+01   | 1.58E+00 | 2.25E+01 | 9.13E-01 | 4.54E+01 | 2.84E+00 |
|        | L <sub>inf</sub> | 1.11E+02   | 9.15E-01 | 1.17E+02 | 1.63E+00 | 1.04E+02 | 7.72E-01 |
|        | K                | 8.51E-03   | 2.19E-04 | 7.54E-03 | 2.99E-04 | 1.01E-02 | 2.69E-04 |
| 1800   | t <sub>0</sub>   | 3.48E+01   | 1.14E+00 | 3.74E+01 | 1.73E+00 | 3.11E+01 | 1.19E+00 |
|        | L <sub>inf</sub> | 1.01E+02   | 6.15E-01 | 1.01E+02 | 8.90E-01 | 1.01E+02 | 7.57E-01 |
|        | K                | 1.36E-02   | 3.60E-04 | 1.40E-02 | 5.47E-04 | 1.30E-02 | 4.13E-04 |
| 1820   | t <sub>0</sub>   | 2.42E+01   | 1.05E+00 | 2.27E+01 | 1.51E+00 | 2.63E+01 | 1.29E+00 |
|        | L <sub>inf</sub> | 1.01E+02   | 4.38E-01 | 1.03E+02 | 5.10E-01 | 9.48E+01 | 7.01E-01 |
|        | K                | 1.36E-02   | 2.37E-04 | 1.30E-02 | 2.49E-04 | 1.50E-02 | 4.85E-04 |
| 1840   | t <sub>0</sub>   | 2.43E+01   | 6.44E-01 | 2.52E+01 | 7.10E-01 | 2.22E+01 | 1.16E+00 |
|        | L <sub>inf</sub> | 1.00E+02   | 3.31E-01 | 1.06E+02 | 4.68E-01 | 9.43E+01 | 3.87E-01 |
|        | K                | 1.51E-02   | 1.95E-04 | 1.37E-02 | 2.21E-04 | 1.70E-02 | 2.98E-04 |
| 1860   | t <sub>0</sub>   | 2.11E+01   | 4.18E-01 | 2.34E+01 | 5.35E-01 | 1.83E+01 | 5.47E-01 |
|        | L <sub>inf</sub> | 9.73E+01   | 3.01E-01 | 9.99E+01 | 3.79E-01 | 9.28E+01 | 4.24E-01 |
|        | K                | 1.91E-02   | 2.52E-04 | 1.91E-02 | 3.04E-04 | 1.96E-02 | 3.98E-04 |
| 1880   | t <sub>0</sub>   | 1.56E+01   | 3.59E-01 | 1.47E+01 | 4.25E-01 | 1.66E+01 | 5.65E-01 |
|        | L <sub>inf</sub> | 1.02E+02   | 6.50E-01 | 1.00E+02 | 3.59E-01 | 9.10E+01 | 3.05E-01 |
|        | K                | 1.28E-02   | 3.33E-04 | 2.02E-02 | 2.73E-04 | 2.44E-02 | 3.75E-04 |
| 1900   | t <sub>0</sub>   | 2.50E+01   | 1.03E+00 | 1.29E+01 | 3.08E-01 | 1.18E+01 | 3.49E-01 |
|        | L <sub>inf</sub> | 9.34E+01   | 2.47E-01 | 9.79E+01 | 3.60E-01 | 8.82E+01 | 2.87E-01 |
|        | K                | 2.69E-02   | 2.91E-04 | 2.52E-02 | 3.58E-04 | 2.95E-02 | 4.26E-04 |
| 1920   | t <sub>0</sub>   | 8.56E+00   | 1.95E-01 | 8.74E+00 | 2.58E-01 | 8.08E+00 | 2.56E-01 |
|        | L <sub>inf</sub> | 8.51E+01   | 1.90E-01 | 8.71E+01 | 2.68E-01 | 8.66E+01 | 2.70E-01 |
|        | K                | 6.02E-02   | 6.58E-04 | 5.76E-02 | 8.42E-04 | 4.21E-02 | 6.10E-04 |
| 1940   | t <sub>0</sub>   | 1.93E+00   | 9.77E-02 | 2.10E+00 | 1.34E-01 | 3.58E+00 | 1.80E-01 |
|        | L <sub>inf</sub> | 8.51E+01   | 1.90E-01 | 8.71E+01 | 2.68E-01 | 8.28E+01 | 2.56E-01 |
|        | K                | 6.02E-02   | 6.58E-04 | 5.76E-02 | 8.42E-04 | 6.39E-02 | 1.00E-03 |
| 1960   | t <sub>0</sub>   | 1.93E+00   | 9.77E-02 | 2.10E+00 | 1.34E-01 | 1.69E+00 | 1.35E-01 |
|        | L <sub>inf</sub> | 8.11E+01   | 2.52E-01 | 8.26E+01 | 3.16E-01 | 7.89E+01 | 3.77E-01 |
|        | K                | 8.45E-02   | 1.28E-03 | 8.40E-02 | 1.61E-03 | 8.62E-02 | 1.96E-03 |
| 1980   | t <sub>0</sub>   | 8.64E-01   | 9.50E-02 | 1.07E+00 | 1.23E-01 | 5.50E-01 | 1.35E-01 |
|        | L <sub>inf</sub> | 7.73E+01   | 2.06E-01 | 7.80E+01 | 3.12E-01 | 7.69E+01 | 2.72E-01 |
|        | K                | 1.34E-01   | 1.43E-03 | 1.25E-01 | 1.94E-03 | 1.41E-01 | 2.06E-03 |
| 2000   | t <sub>0</sub>   | 4.84E-01   | 3.43E-02 | 4.16E-01 | 5.11E-02 | 5.39E-01 | 4.56E-02 |
|        | L <sub>inf</sub> | 8.07E+01   | 1.36E+00 | 8.07E+01 | 1.33E+00 | 8.13E+01 | 3.47E+00 |
|        | K                | 1.45E-01   | 6.69E-03 | 1.43E-01 | 6.62E-03 | 1.46E-01 | 1.63E-02 |
|        | t <sub>0</sub>   | 6.39E-01   | 8.51E-02 | 6.22E-01 | 8.75E-02 | 6.62E-01 | 1.92E-01 |

Table A3

Northern New Jersey (NJ1) Tanaka model parameters for 20-year cohorts. SE = standard error; - indicates cohorts with no animals.

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1720   | a         | 4.36E-01   | 1.81E-01 | 3.12E-03 | 9.71E-03 | –        | –        |
|        | c         | 0.00E+00   | 1.67E+00 | 0.00E+00 | 9.46E-01 | –        | –        |
|        | d         | 7.59E+01   | 1.18E+00 | 7.33E+01 | 1.09E+00 | –        | –        |
|        | f         | 1.69E-03   | 1.23E-04 | 1.94E-03 | 1.03E-04 | –        | –        |
| 1740   | a         | 2.88E-01   | 8.99E-02 | 2.65E-01 | 9.74E-02 | 2.37E-01 | 1.07E-01 |
|        | c         | 0.00E+00   | 1.29E+01 | 0.00E+00 | 2.63E+00 | 0.00E+00 | 2.81E+00 |
|        | d         | 8.44E+01   | 9.42E-01 | 8.73E+01 | 1.15E+00 | 8.15E+01 | 1.18E+00 |
|        | f         | 1.62E-03   | 8.39E-05 | 1.55E-03 | 9.28E-05 | 1.72E-03 | 1.15E-04 |
| 1760   | a         | 6.11E-03   | 1.03E-02 | 6.11E-03 | 1.03E-02 | –        | –        |
|        | c         | 0.00E+00   | 8.18E-01 | 0.00E+00 | 8.18E-01 | –        | –        |
|        | d         | 8.21E+01   | 8.73E-01 | 8.20E+01 | 8.73E-01 | –        | –        |
|        | f         | 2.10E-03   | 9.45E-05 | 2.10E-03 | 9.45E-05 | –        | –        |
| 1780   | a         | 1.43E-01   | 5.30E-02 | 4.92E-03 | 7.67E-03 | 1.17E-01 | 7.43E-02 |
|        | c         | 0.00E+00   | 1.61E+00 | 0.00E+00 | 6.00E-01 | 0.00E+00 | 2.53E+00 |
|        | d         | 8.37E+01   | 8.68E-01 | 7.99E+01 | 6.70E-01 | 8.53E+01 | 1.57E+00 |
|        | f         | 1.85E-03   | 9.45E-05 | 2.34E-03 | 8.58E-05 | 1.81E-03 | 1.46E-04 |
| 1800   | a         | 1.04E-01   | 3.20E-02 | 1.02E-01 | 3.58E-02 | 7.28E-03 | 1.09E-02 |
|        | c         | 0.00E+00   | 1.09E+00 | 0.00E+00 | 1.22E+00 | 0.00E+00 | 8.62E-01 |
|        | d         | 8.58E+01   | 6.97E-01 | 8.61E+01 | 7.81E-01 | 8.34E+01 | 1.07E+00 |
|        | f         | 1.98E-03   | 1.47E-05 | 1.99E-03 | 8.45E-05 | 2.05E-03 | 1.04E-04 |
| 1820   | a         | 8.39E-02   | 2.84E-02 | 6.41E-02 | 2.69E-02 | 1.33E-02 | 1.23E-02 |
|        | c         | 0.00E+00   | 1.04E+00 | 0.00E+00 | 1.06E+00 | 0.00E+00 | 8.48E-01 |
|        | d         | 8.70E+01   | 7.55E-01 | 8.80E+01 | 8.10E-01 | 8.53E+01 | 1.05E+00 |
|        | f         | 2.06E-03   | 8.27E-05 | 2.12E-03 | 9.18E-05 | 2.01E-03 | 9.58E-05 |
| 1840   | a         | 3.65E-02   | 9.06E-03 | 2.62E-02 | 7.42E-03 | 4.42E-03 | 4.49E-03 |
|        | c         | 0.00E+00   | 4.37E-01 | 0.00E+00 | 3.95E-01 | 0.00E+00 | 3.83E-01 |
|        | d         | 8.81E+01   | 4.29E-01 | 8.93E+01 | 4.22E-01 | 8.34E+01 | 5.67E-01 |

(continued on next page)

Table A3 (continued)

| Cohort | Parameter | Population |          | Female   |          | Male      |          |
|--------|-----------|------------|----------|----------|----------|-----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate  | SE       |
| 1860   | f         | 2.17E-03   | 4.67E-05 | 2.21E-03 | 4.63E-05 | 2.28E-03  | 6.20E-05 |
|        | a         | 3.91E-02   | 1.21E-02 | 2.66E-02 | 1.01E-02 | 7.60E-03  | 6.29E-03 |
|        | c         | 0.00E+00   | 5.89E-01 | 0.00E+00 | 5.70E-01 | 0.00E+00  | 4.20E-01 |
|        | d         | 8.81E+01   | 6.34E-01 | 9.15E+01 | 6.91E-01 | 7.81E+01  | 5.59E-01 |
| 1880   | f         | 2.17E-03   | 6.61E-05 | 2.10E-03 | 6.61E-05 | 2.76E-03  | 8.51E-05 |
|        | a         | 1.78E-02   | 6.27E-03 | 1.21E-02 | 4.55E-03 | 9.82E-03  | 7.08E-03 |
|        | c         | 0.00E+00   | 3.92E-01 | 0.00E+00 | 3.21E-01 | 0.00E+00  | 4.89E-01 |
|        | d         | 8.97E+01   | 5.65E-01 | 9.23E+01 | 5.11E-01 | 8.23E+01  | 7.43E-01 |
| 1900   | f         | 2.25E-03   | 5.78E-05 | 2.23E-03 | 5.03E-05 | 2.48E-03  | 8.92E-05 |
|        | a         | 1.58E-02   | 3.48E-03 | 1.65E-02 | 2.75E-03 | 1.29E-02  | 7.11E-03 |
|        | c         | 1.18E+00   | 3.13E-01 | 1.80E+00 | 2.87E-01 | 0.00E+00  | 4.87E-01 |
|        | d         | 8.92E+01   | 6.45E-01 | 9.15E+01 | 6.43E-01 | 8.51E+01  | 8.44E-01 |
| 1920   | f         | 2.64E-03   | 7.83E-05 | 2.77E-03 | 8.33E-05 | 2.40E-03  | 8.96E-05 |
|        | a         | 2.12E-02   | 1.21E-03 | 2.10E-02 | 1.34E-03 | 2.28E-02  | 1.86E-03 |
|        | c         | 2.32E+00   | 1.31E-01 | 2.44E+00 | 1.50E-01 | 1.29E+00  | 1.86E-01 |
|        | d         | 9.01E+01   | 3.37E-01 | 9.20E+01 | 3.96E-01 | 8.48E+01  | 4.53E-01 |
| 1940   | f         | 2.89E-03   | 4.45E-05 | 2.86E-03 | 5.10E-05 | 3.10E-03  | 6.82E-05 |
|        | a         | 2.48E-02   | 9.43E-04 | 2.52E-02 | 1.24E-03 | 2.49E-02  | 1.16E-03 |
|        | c         | 2.62E+00   | 1.07E-01 | 2.96E+00 | 1.51E-01 | 2.46E+00  | 1.26E-01 |
|        | d         | 9.14E+01   | 3.29E-01 | 9.42E+01 | 4.82E-01 | 8.84E+01  | 3.75E-01 |
| 1960   | f         | 2.82E-03   | 3.92E-05 | 2.80E-03 | 5.62E-05 | 2.91E-03  | 4.73E-05 |
|        | a         | 2.79E-02   | 1.59E-03 | 2.59E-02 | 2.75E-03 | 2.87E-02  | 1.94E-03 |
|        | c         | 3.98E+00   | 2.25E-01 | 3.49E+00 | 4.18E-01 | 4.06E+00  | 2.63E-01 |
|        | d         | 8.99E+00   | 9.46E-01 | 9.83E+01 | 1.94E+00 | 8.73 + 01 | 1.05E+00 |
| 1980   | f         | 3.30E-03   | 1.34E-04 | 2.64E-03 | 1.83E-04 | 3.53E-03  | 1.69E-04 |
|        | a         | 9.50E-03   | 5.50E-04 | 9.40E-03 | 8.76E-04 | 9.53E-03  | 7.01E-04 |
|        | c         | 3.07E+00   | 1.32E-01 | 2.95E+00 | 2.07E-01 | 3.14E+00  | 1.69E-01 |
|        | d         | 9.23E+01   | 1.20E+00 | 9.17E+01 | 1.83E+00 | 9.26E+01  | 1.56E+00 |
| 2000   | f         | 3.98E-03   | 1.90E-04 | 4.05E-03 | 3.02E-04 | 3.95E-05  | 2.44E-04 |
|        | a         | 1.17E-02   | 2.25E-03 | –        | –        | 1.17E-02  | 2.25E-03 |
|        | c         | 3.39E+00   | 5.99E-01 | –        | –        | 3.39E+00  | 5.99E-01 |
|        | d         | 1.04E+02   | 1.02E+01 | –        | –        | 1.03E+02  | 1.02E+01 |
|        | f         | 3.19E-03   | 9.71E-04 | –        | –        | 3.19E-03  | 9.71E-04 |

Table A4

Southern New Jersey (NJ2) Tanaka model parameters for 20-year cohorts. SE = standard error.

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1740   | a         | 1.97E-01   | 8.80E-02 | 3.35E-01 | 1.34E-01 | 2.03E-01 | 1.14E-01 |
|        | c         | 0.00E+00   | 2.58E+00 | 0.00E+00 | 3.69E+00 | 0.00E+00 | 3.10E+00 |
|        | d         | 8.57E+01   | 1.23E+00 | 9.38E+01 | 1.73E+00 | 8.18E+01 | 1.35E+00 |
|        | f         | 1.61E-03   | 1.02E-04 | 1.35E-03 | 1.06E-04 | 1.76E-03 | 1.36E-04 |
| 1760   | a         | 2.41E-01   | 1.01E-01 | 3.73E-01 | 7.76E-02 | 3.68E-03 | 1.13E-02 |
|        | c         | 0.00E+00   | 2.97E+00 | 0.00E+00 | 2.41E+00 | 0.00E+00 | 8.72E-01 |
|        | d         | 9.18E+01   | 1.55E+00 | 1.04E+02 | 1.36E+00 | 7.50E+01 | 8.94E-01 |
|        | f         | 1.51E-03   | 1.11E-04 | 1.12E-03 | 5.61E-05 | 2.56E-03 | 1.39E-04 |
| 1780   | a         | 1.62E-01   | 5.30E-02 | 2.19E-01 | 9.58E-02 | 2.11E-01 | 6.66E-02 |
|        | c         | 0.00E+00   | 1.58E+00 | 0.00E+00 | 2.73E+00 | 0.00E+00 | 1.82E+00 |
|        | d         | 1.48E+01   | 8.57E-01 | 8.71E+01 | 1.42E+00 | 8.44E+01 | 9.00E-01 |
|        | f         | 1.84E-03   | 8.60E-05 | 1.71E-03 | 1.26E-04 | 1.85E-03 | 9.34E-05 |
| 1800   | a         | 4.56E-03   | 5.65E-03 | 7.73E-02 | 5.22E-02 | 4.53E-03 | 5.77E-03 |
|        | c         | 0.00E+00   | 4.76E-01 | 0.00E+00 | 1.92E+00 | 0.00E+00 | 4.76E-01 |
|        | d         | 8.48E+01   | 6.08E-01 | 8.65E+00 | 1.30E+00 | 8.38E+01 | 5.94E-01 |
|        | f         | 2.21E-03   | 6.72E-05 | 2.06E-03 | 1.47E-04 | 2.28E-03 | 6.97E-05 |
| 1820   | a         | 9.24E-02   | 2.30E-02 | 5.91E-02 | 1.71E-02 | 7.56E-03 | 9.12E-03 |
|        | c         | 0.00E+00   | 8.17E-01 | 0.00E+00 | 7.15E-01 | 0.00E+00 | 6.16E-01 |
|        | d         | 8.62E+01   | 5.72E-01 | 8.77E+01 | 5.76E-01 | 7.87E+01 | 6.94E-01 |
|        | f         | 2.06E-03   | 6.31E-05 | 2.04E-03 | 6.00E-05 | 2.57E-03 | 1.01E-04 |
| 1840   | a         | 6.96E-02   | 1.31E-02 | 4.35E-02 | 1.06E-02 | 6.16E-03 | 4.06E-03 |
|        | c         | 0.00E+00   | 5.20E-01 | 0.00E+00 | 5.01E-01 | 0.00E+00 | 3.04E-01 |
|        | d         | 8.73E+01   | 4.33E-01 | 8.99E+01 | 4.84E-01 | 8.11E+01 | 4.09E-01 |
|        | f         | 2.10E-03   | 4.66E-05 | 2.06E-03 | 4.84E-05 | 2.46E-03 | 5.17E-05 |
| 1860   | a         | 3.26E-02   | 8.26E-03 | 2.65E-02 | 8.75E-03 | 5.32E-03 | 4.53E-03 |
|        | c         | 0.00E+00   | 4.22E-01 | 0.00E+00 | 4.85E-01 | 0.00E+00 | 3.43E-01 |
|        | d         | 8.85E+01   | 4.69E-01 | 9.07E+01 | 5.77E-01 | 8.17E+01 | 5.03E-01 |
|        | f         | 2.19E-03   | 4.95E-05 | 2.13E-03 | 5.74E-05 | 2.60E-03 | 6.77E-05 |
| 1880   | a         | 9.01E-02   | 3.62E-02 | 2.86E-02 | 6.96E-03 | 6.89E-03 | 3.93E-03 |
|        | c         | 0.00E+00   | 1.27E+00 | 0.00E+00 | 4.05E-01 | 0.00E+00 | 2.92E-01 |
|        | d         | 8.62E+01   | 8.26E-01 | 9.36E+01 | 5.61E-01 | 8.42E+01 | 4.63E-01 |

(continued on next page)

Table A4 (continued)

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1900   | f         | 2.02E-03   | 9.12E-05 | 2.02E-03 | 4.79E-05 | 2.55E-03 | 5.78E-05 |
|        | a         | 2.07E-02   | 4.65E-03 | 2.55E-02 | 6.68E-03 | 2.44E-02 | 6.96E-03 |
|        | c         | 0.00E+00   | 2.99E-01 | 0.00E+00 | 4.35E-01 | 0.00E+00 | 4.11E-01 |
|        | d         | 9.19E+01   | 4.94E-01 | 9.74E+01 | 7.31E-01 | 8.81E+01 | 6.30E-01 |
| 1920   | f         | 2.13E-03   | 4.37E-05 | 1.91E-03 | 5.32E-05 | 2.26E-03 | 6.24E-05 |
|        | a         | 1.70E-02   | 1.36E-03 | 1.54E-02 | 1.93E-03 | 1.75E-02 | 3.85E-03 |
|        | c         | 2.01E+00   | 1.65E-01 | 1.67E+00 | 2.33E-01 | 7.62E-01 | 3.22E-01 |
|        | d         | 9.22E+01   | 5.48E-01 | 9.59E+01 | 7.83E-01 | 9.14E+01 | 7.23E-01 |
| 1940   | f         | 2.83E-03   | 6.44E-05 | 2.56E-03 | 7.71E-05 | 2.35E-03 | 6.89E-05 |
|        | a         | 1.70E-02   | 1.36E-03 | 1.54E-02 | 1.93E-03 | 1.89E-02 | 1.79E-03 |
|        | c         | 2.01E+00   | 1.65E-01 | 1.67E+00 | 2.33E-01 | 2.45E+00 | 2.20E-01 |
|        | d         | 9.22E+01   | 5.48E-01 | 9.59E+01 | 7.83E-01 | 8.78E+00 | 7.17E-01 |
| 1960   | f         | 2.83E-03   | 6.44E-05 | 2.56E-03 | 7.71E-05 | 3.23E-03 | 1.06E-04 |
|        | a         | 1.21E-02   | 9.79E-04 | 1.09E-02 | 1.10E-03 | 1.42E-02 | 1.61E-03 |
|        | c         | 2.25E+00   | 1.60E-01 | 2.15E+00 | 1.86E-01 | 2.49E+00 | 2.55E-01 |
|        | d         | 9.06E+01   | 7.69E-01 | 9.19E+01 | 9.07E-01 | 8.79E+01 | 1.20E+00 |
| 1980   | f         | 3.33E-03   | 1.07E-04 | 3.31E-03 | 1.25E-04 | 3.46E-03 | 1.79E-04 |
|        | a         | 1.17E-02   | 3.91E-04 | 1.21E-02 | 6.31E-04 | 1.10E-02 | 5.06E-04 |
|        | c         | 3.18E+00   | 8.85E-02 | 2.80E+00 | 1.46E-01 | 3.47E+00 | 1.09E-01 |
|        | d         | 9.27E+01   | 7.94E-01 | 9.70E+01 | 1.28E+00 | 8.94E+01 | 9.91E-01 |
| 2000   | f         | 3.77E-03   | 1.15E-04 | 3.17E-03 | 1.40E-04 | 4.38E-03 | 1.83E-04 |
|        | a         | 1.20E-02   | 1.13E-03 | 1.05E-02 | 1.43E-03 | 1.29E-02 | 2.58E-03 |
|        | c         | 2.74E+00   | 4.02E-01 | 2.08E+00 | 4.99E-01 | 3.87E+00 | 5.97E-01 |
|        | d         | 1.18E+02   | 6.74E+00 | 1.26E+02 | 7.70E+00 | 1.06E+02 | 1.20E+01 |
|        | f         | 2.17E-03   | 3.41E-04 | 1.82E-03 | 2.97E-04 | 3.12E-03 | 1.06E-03 |

Table A5

Northern New Jersey (NJ1) modified Tanaka model parameter values for 20-year cohorts. SE = standard error.

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1720   | a         | 2.74E-02   | 3.03E-02 | 9.99E-03 | 1.21E-02 | –        | –        |
|        | c         | 0.00E+00   | 1.05E+00 | 0.00E+00 | 6.56E-01 | –        | –        |
|        | d         | 6.14E+01   | 8.36E-01 | 5.94E+01 | 7.23E-01 | –        | –        |
|        | f         | 2.92E-03   | 1.58E-04 | 3.30E-03 | 1.57E-04 | –        | –        |
| 1740   | g         | 8.54E-06   | 5.19E-07 | 9.71E-06 | 5.21E-07 | –        | –        |
|        | a         | 1.17E-02   | 1.07E-02 | 7.37E-03 | 9.71E-03 | 1.28E-01 | 4.09E-02 |
|        | c         | 0.00E+00   | 6.59E-01 | 0.00E+00 | 7.19E-01 | 0.00E+00 | 1.17E+00 |
|        | d         | 6.98E+01   | 8.60E-01 | 7.31E+01 | 1.10E+00 | 6.79E+01 | 7.98E-01 |
| 1760   | f         | 2.66E-03   | 1.21E-04 | 2.43E-03 | 1.29E-04 | 2.68E-03 | 1.35E-04 |
|        | g         | 1.05E-05   | 5.74E-07 | 9.93E-06 | 7.19E-07 | 1.04E-05 | 4.62E-07 |
|        | a         | 3.31E-02   | 2.03E-02 | 3.31E-02 | 2.04E-02 | –        | –        |
|        | c         | 1.60E+00   | 1.14E+00 | 1.60E+00 | 1.14E+00 | –        | –        |
| 1780   | d         | 6.77E+01   | 1.32E+01 | 6.77E+01 | 1.32E+00 | –        | –        |
|        | f         | 3.74E-03   | 3.47E-04 | 3.74E-03 | 3.47E-04 | –        | –        |
|        | g         | 1.41E-05   | 1.27E-06 | 1.40E-05 | 1.23E-06 | –        | –        |
|        | a         | 1.25E-02   | 1.09E-02 | 7.19E-03 | 1.04E-02 | 3.89E-02 | 2.42E-02 |
| 1800   | c         | 3.47E-01   | 5.88E-01 | 2.89E-01 | 6.10E-01 | 1.28E+00 | 1.18E+00 |
|        | d         | 6.55E+01   | 7.19E-01 | 6.52E+01 | 7.72E-01 | 6.52E+01 | 1.35E+00 |
|        | f         | 4.06E-03   | 2.12E-04 | 4.35E-03 | 2.56E-04 | 3.82E-03 | 3.61E-04 |
|        | g         | 1.07E-05   | 9.06E-07 | 1.92E-05 | 1.02E-06 | 2.51E-05 | 1.63E-06 |
| 1820   | a         | 2.48E-02   | 9.31E-03 | 2.14E-02 | 9.33E-03 | 4.55E-02 | 2.65E-02 |
|        | c         | 1.03E+01   | 5.37E-01 | 9.96E-01 | 5.61E-01 | 1.56E+00 | 1.35E+00 |
|        | d         | 6.92E+01   | 7.44E-01 | 6.92E+0  | 8.02E-01 | 6.88E+01 | 1.69E+00 |
|        | f         | 3.70E-03   | 1.77E-04 | 3.77E-03 | 1.97E-04 | 3.55E-03 | 3.84E-04 |
| 1840   | g         | 1.34E-05   | 1.02E-06 | 2.45E-05 | 1.12E-06 | 2.01E-05 | 2.17E-06 |
|        | a         | 1.72E-02   | 6.73E-03 | 1.57E-02 | 6.93E-03 | 1.90E-02 | 1.32E-02 |
|        | c         | 1.09E+00   | 4.64E-01 | 1.09E+00 | 5.15E-01 | 9.91E-01 | 7.91E-01 |
|        | d         | 6.98E+01   | 7.77E-01 | 7.32E+01 | 9.26E-01 | 6.45E+01 | 1.17E+00 |
| 1860   | f         | 3.97E-03   | 1.98E-04 | 3.70E-03 | 2.06E-04 | 4.42E-03 | 3.71E-04 |
|        | g         | 3.08E-05   | 1.38E-06 | 2.67E-05 | 1.57E-06 | 3.70E-05 | 2.24E-06 |
|        | a         | 2.41E-02   | 3.22E-03 | 2.50E-02 | 3.19E-03 | 2.47E-02 | 4.85E-03 |
|        | c         | 1.94E+00   | 2.59E-01 | 2.05E+00 | 2.64E-01 | 2.11E+00 | 3.72E-01 |
| 1880   | d         | 7.38E+01   | 5.23E-01 | 7.62E+01 | 5.53E-01 | 6.70E+01 | 6.90E-01 |
|        | f         | 3.81E-03   | 1.16E-04 | 3.66E-03 | 1.14E-04 | 4.53E-03 | 2.13E-04 |
|        | g         | 3.01E-05   | 1.14E-06 | 2.96E-05 | 1.19E-06 | 3.63E-05 | 1.60E-06 |
|        | a         | 2.72E-02   | 4.25E-03 | 2.27E-02 | 5.90E-03 | 2.88E-02 | 4.05E-03 |
| 1900   | c         | 2.17E+00   | 3.44E-01 | 1.34E+00 | 4.59E-01 | 2.92E+00 | 3.38E-01 |
|        | d         | 7.22E+01   | 7.50E-01 | 7.89E+01 | 1.02E+00 | 6.42E+01 | 7.07E-01 |
|        | f         | 4.00E-03   | 1.76E-04 | 3.17E-03 | 1.60E-04 | 5.44E-03 | 2.86E-04 |

(continued on next page)

Table A5 (continued)

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1880   | g         | 4.45E-05   | 2.11E-06 | 3.90E-05 | 2.46E-06 | 4.47E-05 | 2.48E-06 |
|        | a         | 1.97E-02   | 3.52E-03 | 1.74E-02 | 2.84E-03 | 2.70E-02 | 6.55E-03 |
|        | c         | 1.57E+00   | 3.13E-01 | 1.50E+00 | 2.71E-01 | 1.86E+00 | 5.06E-01 |
|        | d         | 7.75E+01   | 8.34E-01 | 8.05E+01 | 7.67E-01 | 7.04E+01 | 1.17E+00 |
|        | f         | 3.48E-03   | 1.45E-04 | 3.32E-03 | 1.21E-04 | 3.99E-03 | 2.65E-04 |
| 1900   | g         | 4.68E-05   | 2.83E-06 | 5.06E-05 | 2.58E-06 | 4.39E-05 | 4.14E-06 |
|        | a         | 2.43E-02   | 2.65E-03 | 2.08E-02 | 2.29E-03 | 3.31E-02 | 4.90E-03 |
|        | c         | 2.89E+00   | 3.11E-01 | 2.91E+00 | 3.02E-01 | 2.62E+00 | 4.42E-01 |
|        | d         | 8.07E+01   | 1.10E+00 | 8.53E+01 | 1.18E+00 | 7.27E+01 | 1.29E+00 |
|        | f         | 3.70E-03   | 1.96E-04 | 3.53E-03 | 1.89E-04 | 3.89E-03 | 2.60E-04 |
| 1920   | g         | 4.30E-05   | 5.69E-06 | 3.28E-05 | 6.02E-06 | 6.01E-05 | 6.51E-06 |
|        | a         | 2.39E-02   | 1.02E-03 | 2.31E-02 | 1.17E-03 | 2.56E-02 | 1.56E-03 |
|        | c         | 3.21E+00   | 1.39E-01 | 3.16E+00 | 1.65E-01 | 3.13E+00 | 1.99E-01 |
|        | d         | 8.44E+01   | 6.31E-01 | 8.73E+01 | 7.68E-01 | 7.96E+01 | 8.55E-01 |
|        | f         | 3.59E-03   | 9.91E-05 | 3.40E-03 | 1.10E-04 | 3.82E-03 | 1.50E-04 |
| 1940   | g         | 4.43E-05   | 4.77E-06 | 3.59E-05 | 5.59E-06 | 4.19E-05 | 6.80E-06 |
|        | a         | 2.69E-02   | 7.70E-04 | 2.62E-02 | 1.12E-03 | 2.75E-02 | 9.14E-04 |
|        | c         | 3.49E+00   | 1.12E-01 | 3.43E+00 | 1.72E-01 | 3.47E+00 | 1.27E-01 |
|        | d         | 8.48E+01   | 6.10E-01 | 9.05E+01 | 9.78E-01 | 8.11E+01 | 6.72E-01 |
|        | f         | 3.58E-03   | 8.98E-05 | 3.18E-03 | 1.17E-04 | 3.83E-03 | 1.12E-04 |
| 1960   | g         | 7.47E-05   | 6.79E-06 | 4.07E-05 | 1.01E-05 | 8.60E-05 | 7.87E-06 |
|        | a         | 2.76E-02   | 1.55E-03 | 2.59E-02 | 2.42E-03 | 2.82E-02 | 1.89E-03 |
|        | c         | 4.21E+00   | 2.54E-01 | 4.03E+00 | 4.38E-01 | 4.38E+00 | 2.86E-01 |
|        | d         | 8.74E+01   | 1.97E+00 | 9.20E+01 | 3.65E+00 | 8.39E+01 | 2.14E+00 |
|        | f         | 3.61E-03   | 2.69E-04 | 3.21E-03 | 4.03E-04 | 4.02E-03 | 3.51E-04 |
| 1980   | g         | 5.20E-05   | 3.78E-05 | 1.25E-04 | 7.01E-05 | 7.14E-05 | 4.24E-05 |
|        | a         | 3.05E-05   | 8.36E-04 | 4.22E-03 | 1.37E-03 | 7.47E-03 | 1.04E-03 |
|        | c         | 0.00E+00   | 1.32E+00 | 1.17E+00 | 4.09E-01 | 1.84E+00 | 3.48E-01 |
|        | d         | 3.44E+02   | 6.35E+01 | 1.06E+02 | 5.74E+00 | 1.11E+02 | 5.47E+00 |
|        | f         | 2.43E-04   | 8.21E-05 | 2.42E-03 | 3.56E-04 | 2.26E-03 | 2.96E-04 |
| 2000   | g         | 0.00E+00   | 1.53E-03 | 0.00E+00 | 2.65E-04 | 0.00E+00 | 2.62E-04 |
|        | a         | 3.70E-04   | 6.82E-03 | –        | –        | 3.70E-04 | 6.82E-03 |
|        | c         | 0.00E+00   | 5.33E+01 | –        | –        | 0.00E+00 | 5.33E+00 |
|        | d         | 2.29E+02   | 2.04E+02 | –        | –        | 2.29E+02 | 2.05E+02 |
|        | f         | 5.41E-04   | 9.50E-04 | –        | –        | 5.41E-04 | 9.50E-04 |
|        | g         | 0.00E+00   | 1.66E-02 | –        | –        | 0.00E+00 | 1.66E-02 |

Table A6

Southern New Jersey (NJ2) modified Tanaka model parameter values for 20-year cohorts. SE = standard error.

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1740   | a         | 1.38E-02   | 1.77E-02 | 1.18E-01 | 3.92E-02 | 9.16E-03 | 1.81E-01 |
|        | c         | 0.00E+00   | 9.51E-01 | 0.00E+00 | 1.32E+00 | 0.00E+00 | 9.78E-01 |
|        | d         | 6.71E+01   | 1.09E+00 | 7.59E+01 | 1.11E+00 | 6.36E+01 | 1.08E+00 |
|        | f         | 3.02E-03   | 1.99E-04 | 2.20E-03 | 1.24E-04 | 3.46E-03 | 2.54E-04 |
|        | g         | 1.42E-05   | 7.97E-07 | 1.42E-05 | 6.02E-07 | 1.44E-05 | 8.52E-07 |
| 1760   | a         | 1.28E-02   | 1.57E-02 | 8.66E-03 | 8.04E-03 | 7.38E-05 | 4.38E-03 |
|        | c         | 0.00E+00   | 1.02E+00 | 0.00E+00 | 7.63E-01 | 0.00E+00 | 2.51E-01 |
|        | d         | 7.54E+01   | 1.54E+00 | 8.76E+01 | 1.63E+00 | 6.10E+01 | 2.85E-01 |
|        | f         | 2.46E-03   | 1.80E-04 | 1.69E-03 | 9.20E-05 | 4.92E-03 | 1.23E-04 |
|        | g         | 1.64E-05   | 1.25E-06 | 1.27E-05 | 1.10E-06 | 1.73E-05 | 3.70E-07 |
| 1780   | a         | 8.56E-03   | 8.41E-03 | 8.12E-03 | 1.22E-02 | 9.58E-03 | 8.13E-03 |
|        | c         | 0.00E+00   | 5.13E-01 | 0.00E+00 | 7.41E-01 | 0.00E+00 | 4.97E-01 |
|        | d         | 6.89E+01   | 7.35E-01 | 6.78E+01 | 1.05E+00 | 7.06E+01 | 7.20E-01 |
|        | f         | 3.14E-03   | 1.32E-04 | 3.22E-03 | 1.98E-04 | 3.02E-03 | 1.21E-04 |
|        | g         | 2.04E-05   | 7.79E-07 | 2.43E-05 | 1.13E-06 | 1.46E-05 | 7.42E-07 |
| 1800   | a         | 7.33E-03   | 1.01E-02 | 8.28E-03 | 1.74E-02 | 1.98E-02 | 5.28E-03 |
|        | c         | 7.12E-02   | 6.45E-01 | 0.00E+00 | 1.12E+00 | 1.47E+00 | 3.76E-01 |
|        | d         | 7.34E+01   | 1.01E+00 | 7.57E+01 | 1.79E+00 | 6.97E+01 | 5.94E-01 |
|        | f         | 3.31E-03   | 1.93E-04 | 3.02E-03 | 2.90E-04 | 4.08E-03 | 1.63E-04 |
|        | g         | 1.67E-05   | 1.31E-06 | 1.39E-05 | 2.18E-06 | 2.12E-05 | 8.98E-07 |
| 1820   | a         | 1.40E-02   | 5.60E-03 | 6.86E-03 | 5.78E-03 | 2.85E-02 | 1.08E-02 |
|        | c         | 6.82E-01   | 3.63E-01 | 1.46E-01 | 3.77E-01 | 1.79E+00 | 6.83E-01 |
|        | d         | 6.99E+00   | 5.87E-01 | 7.19E+01 | 6.28E-01 | 6.60E+01 | 1.02E+00 |
|        | f         | 3.84E-03   | 1.42E-04 | 3.56E-03 | 1.32E-04 | 4.52E-03 | 3.36E-04 |
|        | g         | 2.69E-05   | 1.01E-06 | 2.78E-05 | 1.03E-06 | 2.42E-05 | 1.94E-06 |
| 1840   | a         | 2.06E-02   | 2.71E-03 | 1.60E-02 | 2.88E-03 | 2.56E-02 | 3.82E-03 |
|        | c         | 1.73E+00   | 2.11E-01 | 1.31E+00 | 2.28E-01 | 2.20E+00 | 2.92E-01 |
|        | d         | 6.92E+01   | 4.06E-01 | 7.15E+01 | 4.55E-01 | 6.66E+01 | 5.43E-01 |

(continued on next page)

Table A6 (continued)

| Cohort | Parameter | Population |          | Female   |          | Male     |          |
|--------|-----------|------------|----------|----------|----------|----------|----------|
|        |           | Estimate   | SE       | Estimate | SE       | Estimate | SE       |
| 1860   | f         | 4.30E-03   | 1.13E-04 | 4.03E-03 | 1.13E-04 | 4.64E-03 | 1.74E-04 |
|        | g         | 3.99E-05   | 9.44E-07 | 4.48E-05 | 1.02E-06 | 3.39E-05 | 1.31E-06 |
|        | a         | 2.41E-02   | 2.89E-03 | 2.41E-02 | 3.89E-03 | 2.31E-02 | 3.73E-03 |
|        | c         | 2.17E+00   | 2.43E-01 | 1.98E+00 | 3.28E-01 | 2.31E+00 | 3.11E-01 |
|        | d         | 7.15E+01   | 5.37E-01 | 7.54E+01 | 7.48E-01 | 6.66E+01 | 6.55E-01 |
| 1880   | f         | 4.27E-03   | 1.41E-04 | 3.72E-03 | 1.53E-04 | 5.16E-03 | 2.42E-04 |
|        | g         | 4.80E-05   | 1.56E-06 | 4.67E-05 | 1.98E-06 | 4.66E-05 | 2.17E-06 |
|        | a         | 1.22E-02   | 1.06E-02 | 1.60E-02 | 3.54E-03 | 2.53E-02 | 2.66E-03 |
|        | c         | 3.23E-01   | 6.45E-01 | 9.56E-01 | 2.90E-01 | 2.71E+00 | 2.46E-01 |
|        | d         | 7.23 + 01  | 9.73E-01 | 7.79E+01 | 7.47E-01 | 6.91E+01 | 6.14E-01 |
| 1900   | f         | 3.35E-03   | 1.91E-04 | 3.26E-03 | 1.17E-04 | 4.94E-03 | 1.98E-04 |
|        | g         | 1.92E-05   | 1.27E-06 | 6.91E-05 | 2.43E-06 | 5.76E-05 | 2.53E-06 |
|        | a         | 2.15E-02   | 2.75E-03 | 1.49E-02 | 4.68E-03 | 2.47E-02 | 2.83E-03 |
|        | c         | 1.50E+00   | 2.43E-01 | 5.16E-01 | 3.93E-01 | 2.20E+00 | 2.61E-01 |
|        | d         | 7.78E+01   | 7.19E-01 | 8.46E+01 | 1.16E+00 | 7.21E+01 | 7.64E-01 |
| 1920   | f         | 3.37E-03   | 1.13E-04 | 2.68E-03 | 1.24E-04 | 4.19E-03 | 1.75E-04 |
|        | g         | 7.78E-05   | 3.21E-06 | 7.63E-05 | 4.44E-06 | 7.23E-05 | 3.96E-06 |
|        | a         | 1.92E-02   | 1.11E-03 | 1.81E-02 | 1.63E-03 | 2.67E-02 | 3.16E-03 |
|        | c         | 2.80E+00   | 1.74E-01 | 2.45E+00 | 2.53E-01 | 2.21E+00 | 3.44E-01 |
|        | d         | 8.59E+01   | 1.00E+00 | 8.98E+01 | 1.46E+00 | 8.40E+01 | 1.34E+00 |
| 1940   | f         | 3.55E-03   | 1.44E-04 | 3.13E-03 | 1.70E-04 | 3.06E-03 | 1.65E-04 |
|        | g         | 7.74E-05   | 1.20E-05 | 6.88E-05 | 1.59E-05 | 4.67E-05 | 8.39E-06 |
|        | a         | 1.92E-02   | 1.11E-03 | 1.81E-02 | 1.63E-03 | 2.01E-02 | 1.51E-03 |
|        | c         | 2.80E+00   | 1.74E-02 | 2.45E+00 | 2.53E-01 | 3.08E+00 | 2.34E-01 |
|        | d         | 8.59E+00   | 1.00E+00 | 8.98E+01 | 1.46E+00 | 8.27E+01 | 1.35E+00 |
| 1960   | f         | 3.55E-03   | 1.44E-04 | 3.13E-03 | 1.70E-04 | 3.94E-03 | 2.30E-04 |
|        | g         | 7.74E-05   | 1.20E-05 | 6.88E-05 | 1.59E-05 | 6.89E-05 | 1.75E-05 |
|        | a         | 4.59E-10   | 4.00E-12 | 1.67E-09 | 1.03E-12 | 1.44E-02 | 1.41E-03 |
|        | c         | 1.00E+02   | 4.98E-02 | 1.37E+02 | 8.14E-02 | 2.86E+00 | 2.74E-01 |
|        | d         | 4.92E+03   | 1.40E+00 | 4.19E+03 | 1.53E+00 | 8.35E 01 | 2.24E+00 |
| 1980   | f         | 2.82E-05   | 1.51E-08 | 3.66E-05 | 1.95E-08 | 4.06E-03 | 3.68E-04 |
|        | g         | 0.00E+00   | 9.27E-05 | 0.00E+00 | 6.05E-05 | 1.13E-04 | 5.43E-05 |
|        | a         | 9.09E-03   | 4.51E-04 | 1.09E-02 | 1.30E-03 | 9.07E-03 | 6.24E-04 |
|        | c         | 2.15E+00   | 1.39E-01 | 1.58E+00 | 3.52E-01 | 2.19E+00 | 1.93E-01 |
|        | d         | 1.02E+02   | 2.08E+00 | 1.17E+02 | 4.84E+00 | 1.02E+02 | 2.90E+00 |
| 2000   | f         | 2.75E-03   | 1.57E-04 | 1.88E-03 | 1.98E-04 | 2.79E-03 | 2.23E-04 |
|        | g         | 0.00E+00   | 1.11E-04 | 0.00E+00 | 1.95E-05 | 0.00E+00 | 1.54E-04 |
|        | a         | 4.86E-04   | 3.44E-03 | 1.32E-04 | 3.19E-03 | 2.81E-03 | 1.07E-02 |
|        | c         | 0.00E+00   | 2.23E+00 | 0.00E+00 | 3.65E+00 | 0.00E+00 | 7.83E+00 |
|        | d         | 2.06E+02   | 7.60E+01 | 2.82E+02 | 1.82E+02 | 2.50E+02 | 2.87E+02 |
|        | f         | 6.48E-04   | 4.78E-04 | 3.81E-04 | 4.66E-04 | 4.62E-04 | 1.04E-03 |
|        | g         | 0.00E+00   | 6.53E-03 | 0.00E+00 | 1.42E-02 | 0.00E+00 | 2.02E-02 |

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