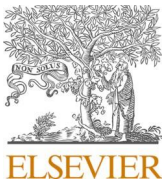
Estuarine, Coastal and Shelf Science 291 (2023) 108412



Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Regional growth rates and growth synchronicity between two populations of *Arctica islandica* in the western Mid-Atlantic (US)

Kathleen M. Hemeon [a,*], Eric N. Powell [a], John M. Klinck [b], Roger Mann [c], Sara M. Pace [a]

[a] Gulf Coast Research Laboratory, University of Southern Mississippi, 703 E Beach Dr, Ocean Springs, MS, 39564, USA
[b] Old Dominion University, 5115 Hampton Blvd, Norfolk, VA, 23529, USA
[c] Virginia Institute of Marine Science, College of William and Mary, 1370 Greate Rd, Gloucester Point, VA, 23062, USA

ARTICLE INFO

Keywords:
Arctica islandica
Ocean quahog
Growth rates
Growth indices
Georges Bank
Long Island

ABSTRACT

Arctica islandica supports an important fishery in the US Mid-Atlantic. This species is extremely slow growing and long-lived, characteristics that may make this species particularly vulnerable to fishing pressure and climate change. Understanding regional growth dynamics over time and growth responses to changing environments will improve current fishery assessments to maintain the sustainability of this stock. Two populations of *A. islandica* from Georges Bank and off Long Island on the US continental shelf with observed ages between 17 and 310 y were evaluated for age-at-length relationships and growth trends over time. Growth rates have been increasing at Georges Bank and Long Island since the 1700s. Growth rates at Long Island have been accelerating and have exceeded those at Georges Bank since the 1980s. Growth rates from this study support previous research that this species is sexually dimorphic, and females grow faster than males within a population post-maturation. Positive growth index periods at both sites may be synchronous with 32-y harmonics of the Atlantic Multi-Decadal Oscillation. A modification to the traditional Tanaka growth model that included a growth term to further increase growth at old age proved the best-fit growth model to not only each population, but also to birth-year cohorts. Both the classic and modified Tanaka models used in this study are vast improvements over the von Bertalanffy models currently applied to this species in assessment models and population dynamics models. Increasing growth rates over time resulted in fewer years of reproduction prior to recruiting to the fishery as *A. islandica* are reaching fishery size in an increasingly short period of time. The impact that reduced years of reproduction has on *A. islandica* population resiliency is yet unknown.

1. Introduction

1.1. Background

Fishery growth models are essential functions integrated into stock assessment models for the estimation of ages from subsampled length frequencies. Similar to age-length keys, growth models provide an expected relationship of length over time dependent on age and are critical components for the construction of age-frequency distributions by fisheries management (e.g., catch curves) and the modeling of population dynamics for ecological interpretation. Age-frequency distributions allow the estimation of important life-history characteristics necessary to describe a stock such as recruitment indices, mortality rates, and growth rates.

The choice of a best-fit growth model to real data does not always translate to model selection in assessment models (Flinn and Midway, 2021). The von Bertalanffy growth function (VB) is the most common growth model used in US fisheries management and, despite better fit growth models for select species, the benefit of replacing the VB in an assessment model with an alternative growth relationship must be weighed against new uncertainty introduced into assessment models by the alternative growth function (Flinn and Midway, 2021; Neves et al., 2022). The VB is an easily described model, in that model parameters have clear biological meaning in terms of age and growth (von Bertalanffy, 1938). Other models such as the Tanaka growth model (Tanaka, 1982) (i.e., power growth functions) are models well-fit to animals with indeterminate growth and have gained favor to describe marine invertebrate age-growth relationships (e.g., McShane and Anderson, 1997;

* Corresponding author. Abernathy Fish Technology Center, US Fish and Wildlife Service, 1440 Abernathy Creek Rd, Longview, WA, 98632, USA
E-mail addresses: kathleen_hemeon@fws.gov (K.M. Hemeon), eric.n.powell@usm.edu (E.N. Powell), jklinck@odu.edu (J.M. Klinck), rmann@vims.edu (R. Mann), sara.pace@deq.nc.gov (S.M. Pace).

https://doi.org/10.1016/j.ecss.2023.108412
Received 2 December 2022; Received in revised form 6 June 2023; Accepted 14 June 2023
Available online 29 June 2023

Velázquez-Abunader et al., 2016; Pace et al., 2017b). However, power functions with attenuated growth produce ambiguous model parameters with limited biological definitions (Tanaka, 1982, 1988; Sebens, 1987), a stark contrast to the k (growth rate) and L_∞ (maximum body size) parameters derived from the VB (von Bertalanffy, 1938). Despite cautionary measures required to update assessment models with new and complex growth functions, the recompense includes more accurate and precise estimates of age, maximum size, growth rates, mortality, and age frequencies.

Growth is predominantly controlled by ontogeny, genetics, and the environment (Sebens, 1987). Fishery growth data associated with a time-series can be detrended to remove ontogenetic growth and isolate environmentally driven growth over time to create standardized growth indices (Grissino-Mayer, 2001; Black et al., 2008; Peharda et al., 2018). Correlation of temporally associated growth indices to known environmental indices can uncover time periods and ecological conditions that were beneficial, neutral, or detrimental to growth. Identification of strong ecological controls on growth can improve growth projections for future climate scenarios. Wavelet analysis is a mathematical tool that can isolate periods of similar frequencies between two time series indexed to a zero-mean even when the frequency is variable through time (Torrence and Compo, 1998). When growth indices are considered, wavelets can identify common frequency power and frequency coherence between a temporal growth index and oceanographic indices derived from data such as temperature, salinity, and chlorophyll concentration (Machu et al., 1999; Kirby, 2005; Soniat et al., 2006).

1.2. Species description

Ocean quahogs (*Arctica islandica*, Linnaeus 1767) are boreal bivalves that have an expansive range in the North Atlantic, and currently occupy cold shelf waters from the White Sea at northern latitudes, through the Norwegian Sea, around the British Isles to Iceland, and finally from Newfoundland Canada to as far south as southern Virginia, US (Dahlgren et al., 2000). The last extant species of the family Arcticidae, *A. islandica* grow optimally in water temperatures between 6 and 15 °C (Golikov and Scarlato, 1973; Merrill and Ropes, 1969), with the majority of the Mid-Atlantic population being found at average summer temperatures ≤13.5 °C, and at depths conducive to cool waters, typically between 21 and 61 m (Merrill and Ropes, 1969; Serchuk et al., 1982). When conditions are suboptimal, such as during extreme temperatures, storm events, or limited food availability, this species can burrow into the sediment to an estimated mean maximum depth of 85 mm (±17 mm) and can remain buried at least to seven days during which time metabolic activity is drastically curtailed (Taylor, 1976; Oeschger, 1990; Strahl et al., 2011; Sosnowska et al., 2014; Ragnarsson and Thorarinsdóttir, 2020).

Arctica islandica is remarkable in that maximum observed ages exceed 500 y and, in the Mid-Atlantic, ages of up to 200 y have been estimated (Butler et al., 2013; Pace et al., 2017a,b; Hemeon et al., 2021a, 2023). The causation of such longevity is widely debated, but it has been postulated that longevity may be associated with reduced metabolism during deep burial that may suspend aging due to suppressed reactive oxygen production and oxidative stress (Ungvari et al., 2011), elevated antioxidant capacity (Abele et al., 2008), accumulation of nucleic acid oxidation (Gruber et al., 2014), and low somatic maintenance energy demands (Ballesta-Artero et al., 2019) possibly due to low cell turnover rates (Strahl and Abele, 2010) during such burrowing behavior; although telomere-length maintenance has also been considered (Gruber et al., 2014). Regardless of the underlying causal mechanism for this extreme longevity, *A. islandica* survive for centuries in comparatively the same location and, due to poikilothermic energetics, grow in synchrony with benthic cycles (temperature, salinity, phytoplankton abundance, physical disturbance events) and act as biorecorders capable of providing paleochronologies (Schöne et al., 2005; Butler et al., 2010; Schöne, 2013; Marali and Schöne, 2015; Mette et al., 2016; Begum et al., 2019; Poitevin et al., 2019).

Arctica islandica age is measured as the sum of the internal annuli in the hinge plate, and annual growth is measured as the length of light carbonate deposited between hinge plate annuli (Ropes, 1984). Growth in the hinge plate is proportional to growth on the outer shell valve; therefore, annual hinge plate growth can be extrapolated to annual valve growth to obtain annual growth rates in relation to the total shell length of an individual (Thompson et al., 1980a). Light carbonate growth deposition initiates in March–April when bottom water temperatures advance beyond 6 °C (Weidman et al., 1994) with rapid growth in the late spring and early summer (Jones, 1981; Thompson et al., 1980b), followed by slower growth from approximately July–August during the warmest months (Jones, 1980). The dark annuli bookmark the lighter carbonate growth and are deposited in late fall, commencing in September for many individuals, with slowest annuli growth during the coldest months (Jones, 1980). Growth rates between *A. islandica* birth-year cohorts that coexist in contemporary populations are highly variable, as growth is dependent on ambient environmental factors such as temperature, food availability, and salinity during the generational time periods specific to each cohort, whereby the conditions experienced by each cohort determine the time needed to reach a particular size (Pace et al., 2018). With each cohort reaching size classes at different ages, age compositions within a single 5-mm size class can span hundreds of years and restrict any meaningful prediction of age at size within a population. The effective use of lengths to predict age in a stock assessment model is then difficult, particularly by the traditional VB that also does not represent life-history characteristics expressed by this species (Pace et al., 2017a, 2017b, 2018; Hemeon et al., 2021a, 2023).

1.3. Objectives

The US *A. islandica* fishery is managed by length-based assessment models that contain no age data and apply a VB growth function (NEFSC, 2017, 2020). Until recently, reliable age-length keys (ALK) were not available for this species due to extreme variability in age at size data (Hemeon et al., 2021a, 2023) and ages could not be dependably estimated for the stock. The objectives of this study are to evaluate best-fit growth models for two mid-Atlantic *A. islandica* populations, estimate growth rates over time, use these models to detrend yearly growth data to create growth indices, and evaluate growth indices between site and sex using wavelet analysis. These analyses will illuminate the scale to which growth rates change over time, between populations, between sexes, and between sexes within populations; trends that may be important to inform population dynamics models for a multitude of uses.

2. Materials and methods

2.1. Growth data

Arctica islandica clams were collected in 2017 from Georges Bank (GB) (40.72767°N, 67.79850°W) at a depth of approximately 72 m and the Long Island (LI) (40.09658°N, 73.01057°W) continental shelf at a depth of approximately 48 m with a Dameron-Kubiak dredge outfitted to collect fishery-sized *A. islandica* (Hennen et al., 2016). Tissue was removed from each clam and used for sex-determination by gonadal smear slide. Shell valves were measured for length, immersed in a bleach solution, and stored dry for successive age analysis.

Prior to age determinations, each site underwent an independent age-reader error analysis that compared visual ages by two expert age readers of a random 20% subsample from each site (Hemeon et al., 2021b). This analysis increased precision between readers (<7.6% average or median coefficient of variation [CV]) and ensured that no aging bias occurred as assessed by the Evans-Hoenig test of symmetry (Hemeon et al., 2021a, 2023). Once error was minimized, the primary

age reader aged all individuals from both sites using methods of Pace et al. (2017a) and Hemeon et al. (2021a, 2021b) with ImageJ annotation software to estimate age from the shell hinge plate. Annual growth increments were measured in pixels by the ObjectJ plugin for ImageJ and data were exported as annual hinge plate growth increments in pixels. Growth increments observed on the shell hinge plate are proportional to growth of the outer shell valve (Thompson et al., 1980a); therefore, annual growth increments on the hinge plate were converted to annual growth increments of the total shell length using the proportion of total hinge plate growth in pixels for an increment to the equivalent proportion of total shell length in mm.

2.2. Growth models: Group

Growth increments for each clam were cumulatively summed to produce a shell length at age array for each individual clam and site. For each site, von Bertalanffy (VB), Tanaka, and modified Tanaka (MT) growth models were fit to the population, female, and male group growth data. The VB model was chosen as it is the standard growth function currently applied in the federal *A. islandica* fishery assessment model (von Bertalanffy, 1938; NEFSC, 2017, 2020) (Eqn (1)), and the Tanaka model was selected as it successfully fits species with indeterminate, attenuated growth at old age (Tanaka, 1982, 1988; Sebens, 1987; McShane and Anderson, 1997; Pace et al., 2017b) (Eqn (2)). The third model, the MT, contains a fifth parameter g added to the traditional Tanaka model that forced a better model fit at older age classes (Powell and Klinck, pers comm) (Eqn (3)). For old ocean quahogs, even the Tanaka model underestimates length at age. The addition of the g parameter allows the MT model to fit larger sizes at old age compared to the more conservative lengths at old age predicted by the traditional Tanaka.

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

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

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

where L_t is length in mm at time t in y. All Tanaka and modified Tanaka model parameters except d, were forced to be greater than or equal to 0 during model convergence to prevent the estimation of negative natural logarithms and/or square roots. A best-fit growth model was chosen by the Akaike information criterion (AIC).

2.3. Growth models: Cohort

As a benthic invertebrate with limited horizontal mobility, *A. islandica* adaptively grow in relative synchrony with the local environment (e.g., temperature, food availability) (Schöne et al., 2005; Harding et al., 2008; Marali and Schöne, 2015; Ballesta-Artero et al., 2018). The *A. islandica* fishery, and any alternative ecological sample, includes animals born centuries apart (Pace et al., 2017a, 2017b, 2018; Hemeon et al., 2021a, 2023), and thus growth curves are expected to vary between animals dependent on the environment into which they were born and in which they predominantly lived. To understand these temporal changes in growth, samples from each site were divided into 20-y birth-year cohorts and growth models (Eqns (1)–(3)) were subsequently fit to each cohort. A 20-y cohort grouping was chosen as it provided adequate sample sizes for old and young individuals under-represented by the sampling method used, allowing for better model convergence while also minimizing the fraction of the lifespan represented. A time slice of 20 y represented only 6% of the total lifespan of Mid-Atlantic populations (Hemeon et al., 2023) and 4% of the total lifespan of the species (Butler et al., 2013) and is comparable to yearly cohort analyses of shorter-lived marine species.

2.4. Growth rates

Growth rates were evaluated by the time required to reach important fishery or biological size milestones. For *A. islandica*, these were the time needed to reach size at 50% maturity, the time needed to recruit into the fishery, and the number of reproductive years prior to entering the fishery. The size milestone at which 50% of the population was mature was derived from maturity data obtained from animals that recruited over the last few decades from a sample collected in 2017 from GB and LI (Mann, unpublished). This sample included 103 immature and 227 mature *A. islandica* between 16 and 91 mm. A binomial logistic regression identified the mean size at 50% population maturity as 52-mm with a 95% confidence interval of 50.4–53.0 mm (Appendix Figure A.1). These results are comparable to those by Thompson et al. (1980b) and Thorarinsdóttir and Steingrímsson (2000), who observed maximum immature sizes of 47 mm and 60 mm (respectively) and a mature minimum size between 36 and 44 mm (Thorarinsdóttir and Steingrímsson, 2000). The degree to which the 52-mm milestone is representative for recruits over the last several centuries is unknown, but 52 mm is consistent with the estimate of average maturity size for bivalves of 44% of maximum size (Powell and Stanton, 1985), as the estimated maximum size of 118 mm from this relationship is consistent with the maximum sizes observed at GB (116 mm; Hemeon et al., 2021a) and LI (111 mm; Hemeon et al., 2023). Thus, an assumption of maturity at this size being a stable property of ontogeny in *A. islandica* is consistent with the known ontogenetics of bivalves. The size milestone selected for time to reach fishable size was set at 80 mm as this is the size that commercial fishery dredge selectivity nears 80% (Appendix Figure A.2, see also NEFSC, 2017 Table 15). Years of reproduction before recruitment to the fishery were approximated as the number of years needed for each animal to grow from size at 50% maturity (52 mm) to size at fishery recruitment (80 mm).

Individual clams from GB and LI were plotted by birth year versus the time to each of the three size milestones, and regression analyses were fit to these data by site and sex. In addition, population best-fit models for birth-year cohorts were also used to estimate time to size milestones, and subsequent growth rates were also recorded. Time to size and growth rates derived from the regression and growth models were compared.

2.5. Growth periodicity

Growth synchrony and periodicity were evaluated by Morlet wavelet analyses with Bartlett window transformations (Torrence and Compo, 1998; Kirby, 2005; Soniat et al., 2006) processed from the R package WaveletComp (Rösch and Schmidbauer, 2018). Prior to wavelet analysis, growth data were detrended and standardized. Ontogenetic growth was removed from each individual clam by subtracting cohort-specific modified Tanaka growth curves from every individual growth curve and resulted in a residual for each individual clam for each calendar year of life. Mean and unit variance were calculated for each calendar year across individuals to standardize growth over time and created a unitless growth index for each site by total population, and each sex within each site.

Cross wavelet analyses compared paired data series for significant power relationships at alpha = 0.10. A 10% significance level was chosen as multiple phases of data reduction likely resulted in accumulated error. Within-region analyses compared GB and LI population growth indices, and a parallel analysis applied a 15-y *loess* (Cleveland and Devlin, 1988) smoother to test smoothing on frequency resolution. Within-sex analyses compared GB females with LI females, and GB males with LI males. Finally, within-site analyses compared GB males to females, and LI males to females. A lead/lag evaluation of period phase shifts identified which data series led the other over time within a

known, significant power period. The lead/lag analysis, also known as phase difference, measured the angle between two time series that were then converted into time (see Rösch and Schmidbauer, 2018, Eqn (4)).

$$LeadLag = Phase * \frac{PP * 0.5}{\pi}, \quad \text{Eqn (4)}$$

where *LeadLag* is the number of years one time series leads or lags a second time series, *Phase* is the phase difference between the two time series in radians, and *PP* is the significant power period in years.

3. Results

3.1. Growth models: group

The modified Tanaka (MT) model was the best fit model to all groups (population, female, male) at both Long Island (LI) and Georges Bank (GB) (Table 1, Fig. 1) using AIC model selection criteria. von Bertalanffy (VB) models consistently overfit early ages near the origin (less than 5 y), and drastically underfit mid to late ages (greater than approximately 120 y) as the VB produces a model asymptote when one did not exist. The Tanaka and MT models fit similarly until approximately 160 y, after which the two models diverged and the Tanaka model slightly underestimated size at old age. Attenuated, or indeterminate, growth at mid to old age (greater than approximately 160 y) was best captured by a Tananka model, with the MT model fitting marginally better.

Tanaka (1988) described Tanaka model parameters as such: a influences maximum growth rate, and a larger a lessens the maximum growth rate; c represents age at maximum growth rate; f is the rate of change in growth rate; and d is a scaler of body size. When GB and LI were compared by group, GB had a larger maximum growth rate than LI, i.e., smaller a (Appendix Table A1). Age at maximum growth rate, c, was younger at GB than LI. A scale of body size, d, was larger at GB than LI across all groups. The f parameter is a more cryptic model coefficient, and a clear ecological comparison between sites cannot be made at this time. The MT model had an additional term g that increased length at larger t (i.e., at older ages) and resulted in larger length estimates at older ages.

3.2. Growth models: Cohort

Individual clams were assigned to birth-year cohorts dependent on 20-y blocks of time where, for example, a clam with a birth year of 1910 was grouped with other individuals with birth years between 1900 and 1919. Growth models were fit to these 20-y cohort age-length data to identify if growth model parameters changed between 20-year cohorts and therefore growth dynamics changed over time. Modified Tanaka models were fit to 20-y birth-year cohorts for LI and GB using a Levenberg-Marquardt algorithm (Appendix Tables A.2-A.3, Figs. 2 and 3). Tanaka and VB models were also fit to each cohort to present model comparisons that included time-varying k and t_0 values for future comparisons with existing VB growth models in *A. islandica* assessment models (Appendix Tables A.4-A.7), but it is strongly advised that L_∞ parameters not be used in analyses due to obvious inaccuracies (Figs. 2 and 3, Appendix Figures A.3-A.6).

When evaluated by 20-y cohorts, the cohort model fits are similar to those of the group model fits, in that the VB model overfit young ages and underfit mid to old ages, and the Tanaka and MT were similar until the end of the data series where the MT became increasingly unstable at extrapolated ages where no length data existed (Figs. 2 and 3). Quite obviously, length at age by cohort using any of the models presented here cannot be extrapolated beyond the observed lengths and ages as the upper limits of the models are no longer constrained (e.g., projections of length data at ages older than 117 y for the 1900 cohort). Faster growth was observed in recent cohorts based on the increased slope of the growth curves near the origin and younger ages at which the growth curves began to attenuate (Figs. 2 and 3). Attenuated growth at large size occurred at earlier ages for cohorts from the 1900s when compared to cohorts of the 1800s.

Modified Tanaka cohort-specific growth parameters were evaluated over time to understand temporal trends across the sample time series (Appendix Figure A.7). Parameter values were divided into median delineated quadrats (Rothschild and Mullen, 1985) and parameter value distribution probabilities were evaluated using chi-square goodness of fit with expected probabilities for each of the four quadrats set to 0.25. Parameters with significant chi-square results indicate that the parameter is non-random over time and that those parameters are changing over time. Only the c parameter for population and female growth models at GB and LI, and the LI population d parameter were significantly different than a 0.25 probability occurrence over time (Table 2). The age at maximum growth rate (c) at GB and LI (population and female) has changed over time, as did the body size scaler (d) at LI which is an indication that body size has likely increased for males at LI since approximately 1880 (Appendix Figure A.8). When parameters over time (i.e., by cohort) were compared to the parameters derived from the group growth models (see Appendix Figures A.8-A.9), it was revealed that group model parameters (Fig. 1) often did not adequately represent modern cohorts (Figs. 2 and 3) and that model parameters fluctuated over time often with unpredictable trends (Appendix Tables A.1-A.7; Appendix Figure A.7-A.9).

Table 1
Georges Bank and Long Island best fit growth models.

Site	Sex	*N*	Model	Δ *AIC*
Georges Bank	Population	569	von Bertalanffy	20,039
			Tanaka	189
			Modified Tanaka	0
	Female	284	von Bertalanffy	11,907
			Tanaka	94
			Modified Tanaka	0
	Male	285	von Bertalanffy	12,634
			Tanaka	517
			Modified Tanaka	0
Long Island	Population	865	von Bertalanffy	12,689
			Tanaka	350
			Modified Tanaka	0
	Female	426	von Bertalanffy	11,485
			Tanaka	82
			Modified Tanaka	0
	Male	439	von Bertalanffy	12,045
			Tanaka	335
			Modified Tanaka	0

N, sample size; Δ *AIC*, difference in Akaike information criterion (AIC) from best fit AIC.

3.3. Growth rates

Growth rates can be conveyed as the time it takes an *A. islandica* clam to reach a milestone size. In other words, the time needed for *A. islandica* to grow between two sizes with the omittance of underlying ontogeny. The age (i.e., number of years elapsed) when the animal reached fishable size as estimated by the size highly selected by harvest gear (80 mm, NEFSC, 2017), the age of an animal when the population was at the modern (birth years post 1987) length for 50% maturity (52 mm, Mann et al., unpublished), and the years of reproduction approximated as the time from maturation to recruitment to the fishery (52 mm–80 mm), are important metrics for the fishery and US Mid-Atlantic *A. islandica* populations.

When GB and LI time to milestones were evaluated by group by two-sample Wilcoxon tests, regardless of birth year or sex, GB reached size at 50% maturity (median = 13 y, range = 7–55 y) slightly faster (W = 3.01E5, $p < 0.0001$) than LI (median = 16 y, range = 6–70 y), GB recruited to the fishery (median = 53 y, range = 16–127 y) faster (W = 1.22E5, $p < 0.0001$) than LI (median = 66 y, range = 17–178 y), and as a result of faster fishery recruitment, GB had fewer reproductive years

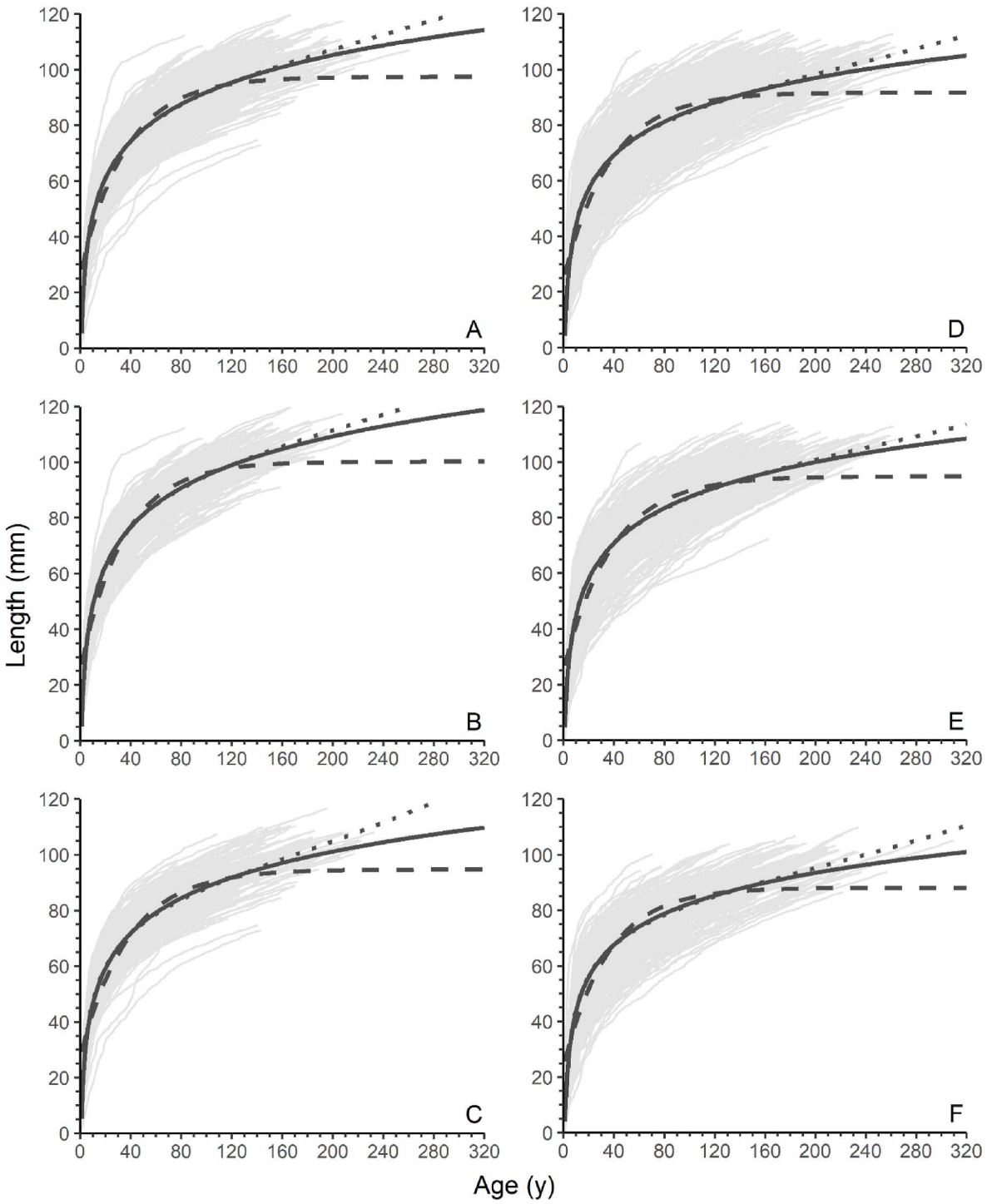


Fig. 1. Regional growth models. Individual clam age-length data (grey), von Bertalanffy growth models (dashed line), Tanaka growth models (solid line), and modified Tanaka growth models (dotted line) for Georges Bank (A) population, (B) female, (C) male, and Long Island (D) population, (E) female, (F) male groups.

(median = 45 y, range = 14–99 y) than LI (median = 56 y, range = 17–129 y) ($W = 4.79E4$, $p < 0.0001$) (Fig. 4). At GB, time needed to reach each size milestone was less for female *A. islandica* than males (maturity: $W = 2.08E4$, $p = < 0.01$; W = 2.08E4, fishery: $p < 0.0001$; years of reproduction: $W = 6.54E3$, $p < 0.0001$). Likewise, LI females also reached the fishery at a younger age ($W = 3.77E4$, $p < 0.0001$) and had fewer years of reproduction ($W = 1.54E4$, $p < 0.0001$) than males, but LI males and females matured at similar ages ($W = 3.58E4$, $p = 0.14$).

Regression models were fit to the age at size milestone, by birth year, and were expressed for GB and LI (Fig. 5). The youngest *A. islandica* sampled at GB had a birth year of 1984 and the youngest *A. islandica* sampled from LI had a birth year of 2000. Growth rate change over time was small considering the size and longevity of *A. islandica*, thus, regression coefficients required high precision to remain accurate for model estimation (Table 3). Regressions for GB were significant for maturity and fishery milestones for all groups, but birth year accounted for less than 20% of the variation in growth rates. Birth year explained more variation in small animal growth rates (up to 52 mm) than large animal growth rates (up to 80 mm) at GB; however, regression of

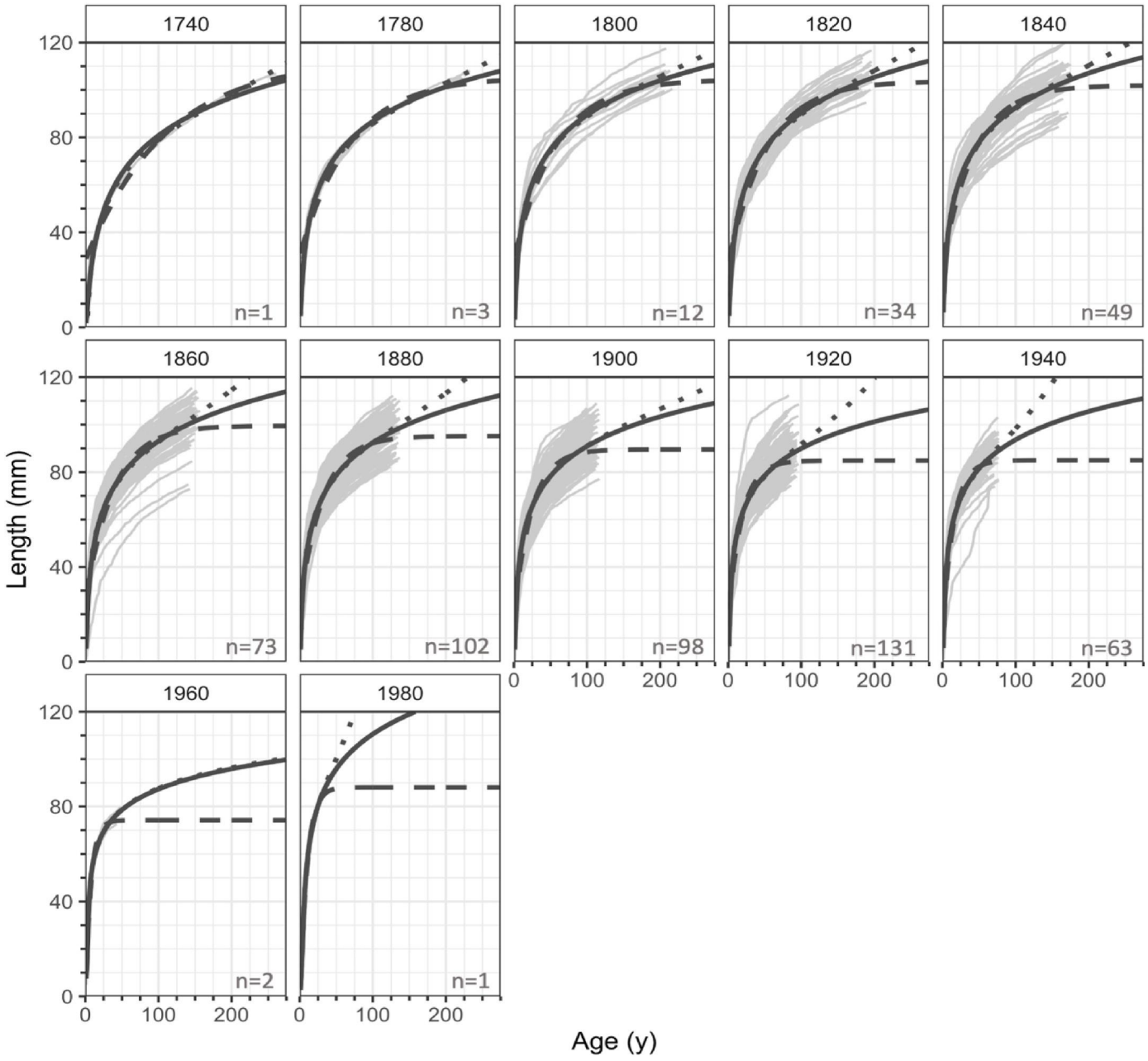


Fig. 2. Georges Bank population growth models by cohort. Estimated Tanaka (solid line), modified Tanaka (dotted line), and von Bertalanffy (dashed line) models from individual sample age-length data (light grey) by 20-y birth-year cohorts (plot header).

reproductive years by birth year was not significant. Regression models for LI were significant for all milestones and all groups ($p < 0.0001$), and birth year accounted for greater than 43% of the growth rate variance. At LI, growth rate was strongly related to birth year at larger sizes such as when animals recruited to the fishery, and the weakest relationship between birth year and growth rate occurred prior to assumed maturation (assumed since it is not known if maturity consistently occurred at 52 mm in previous centuries).

Birth year was a poor predicter of growth rate at GB (adjusted $R^2 <$ 21%), while birth year was a strong predictor of growth rate for LI *A. islandica* (adjusted $R^2 >$ 40%) (Fig. 5). Growth rates not only increased with increasing birth year at LI, but growth rates have been accelerating over time (Fig. 5). When age at length data were grouped by site and sex, GB clearly had faster growth rates than LI (Fig. 4), but when birth year is considered, recent LI cohorts have similar growth rates to recent GB cohorts and LI growth rates may have even exceeded GB growth rates since the 1950s (Fig. 5).

To validate that the MT growth models captured changing growth rates over time by birth year, cohort-specific MT models were used to estimate time needed to reach identical milestones and were compared with time estimates derived from Fig. 5 regression models. Specifically, population regression models (Table 3) and cohort-specific MT models (Appendix Tables A.2-A.3) were used to estimate time to size milestones using 40-y time slices to compare changes over time by birth year, by site, and by model (Table 4). Regression estimates for time to maturity were identical (8 y) for cohorts post 1980, but these estimates represented projected time to size for future 2020 cohorts. When time to maturity of 1740 cohorts at GB and LI (23 y and 38 y, respectively) were compared to projected modern cohorts in 2020 (8 y), GB experienced a 65% decrease in time and LI a 79% decrease in time to maturity over the past three centuries (Table 4). Modified Tanaka models cannot be used to estimate predicted data outside the bounds of the observed data due

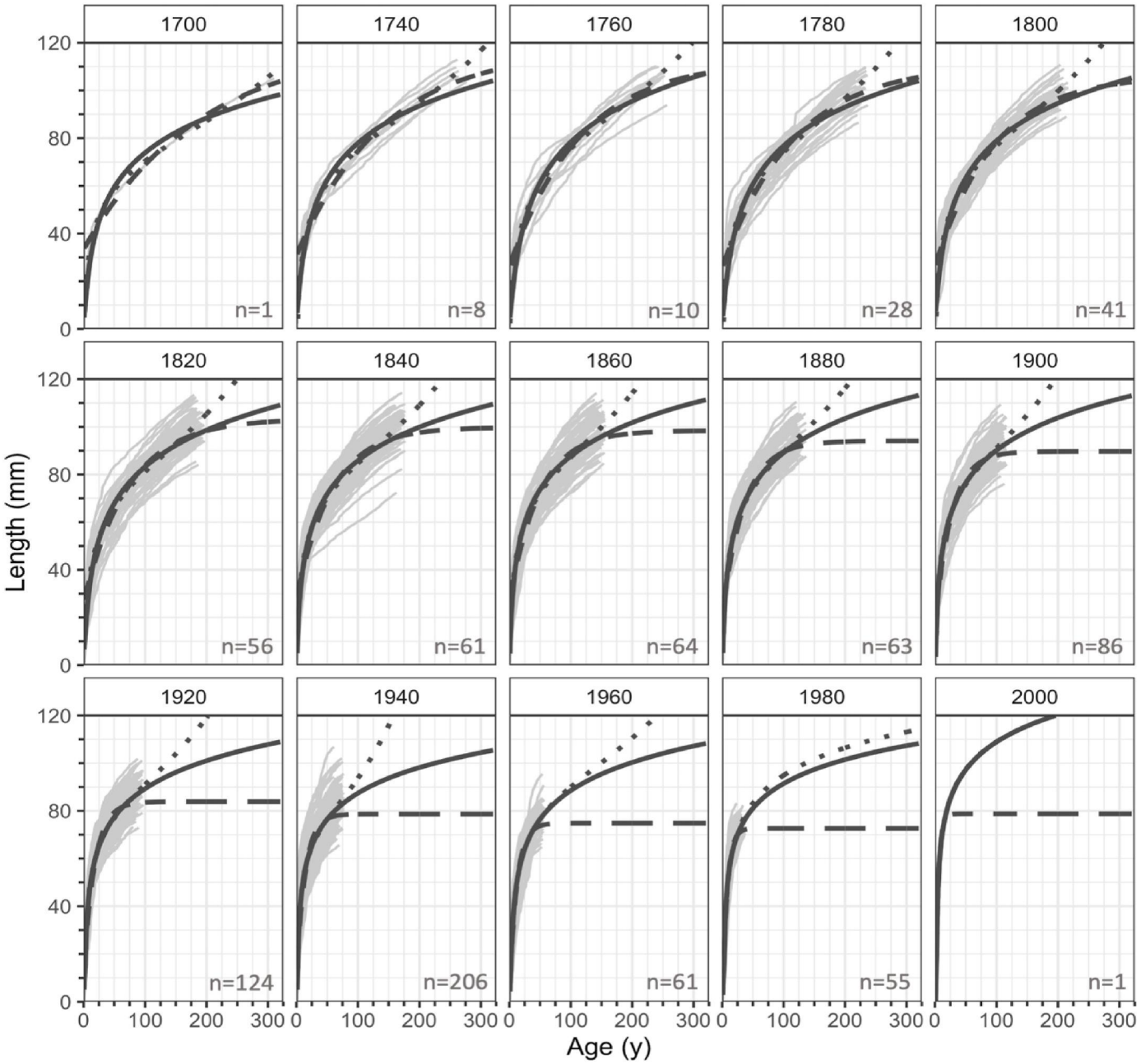


Fig. 3. Long Island population growth models by cohort. Estimated Tanaka (solid line), modified Tanaka (dotted line), and von Bertalanffy (dashed line) models from individual clam age-length data (light grey) by 20-y birth-year cohorts (plot header).

Table 2
Cohort parameter chi-square goodness of fit analysis to modified Tanaka growth model parameters over time (see Appendix Figures A.7-A.9).

Site	Group	*P*-Value				
		a	*c*	*d*	*f*	*g*
Georges Bank	Population	0.97	0.003	0.067	0.067	0.838
	Female	0.463	0.003	0.067	0.067	0.557
	Male	1	0.463	0.463	0.973	0.557
Long Island	Population	1	0.003	0.024	0.094	0.973
	Female	0.463	0.003	0.094	0.067	0.463
	Male	1	0.463	0.463	0.973	0.557

to model instability; however, between 1780 and 1940 at GB, model estimates were slightly more conservative than the regression models, but GB MT estimates were often only 0–1 y larger than those derived from regression. At LI, MT time estimates were identical to, or 2 y larger than, regression model estimates post 1700. All in all, both regression models and cohort specific MT models performed similarly for estimated time to size at 50% maturity at both sites.

When time needed to reach fishable size is considered, regression models estimated that LI experienced an 81% decrease in time to reach 80 mm between 1740 and 2020 with a time of 138 y required for a 1740 *A. islandica* to recruit to the fishery versus the 26 y projected for 2020 (Table 4). *Arctica islandica* at GB only experienced a 41% decrease in time needed to reach fishable size in that same time period, with a modern time to the fishery of 37 y. The 1980 cohorts at both GB and LI have demonstrated similar time to 80 mm (41 and 42 y, respectively), an indication that LI growth rates of mature *A. islandica* have matched those at GB despite centuries of lagged growth rates at LI compared to GB, and regression model projections suggest LI growth rates may now be

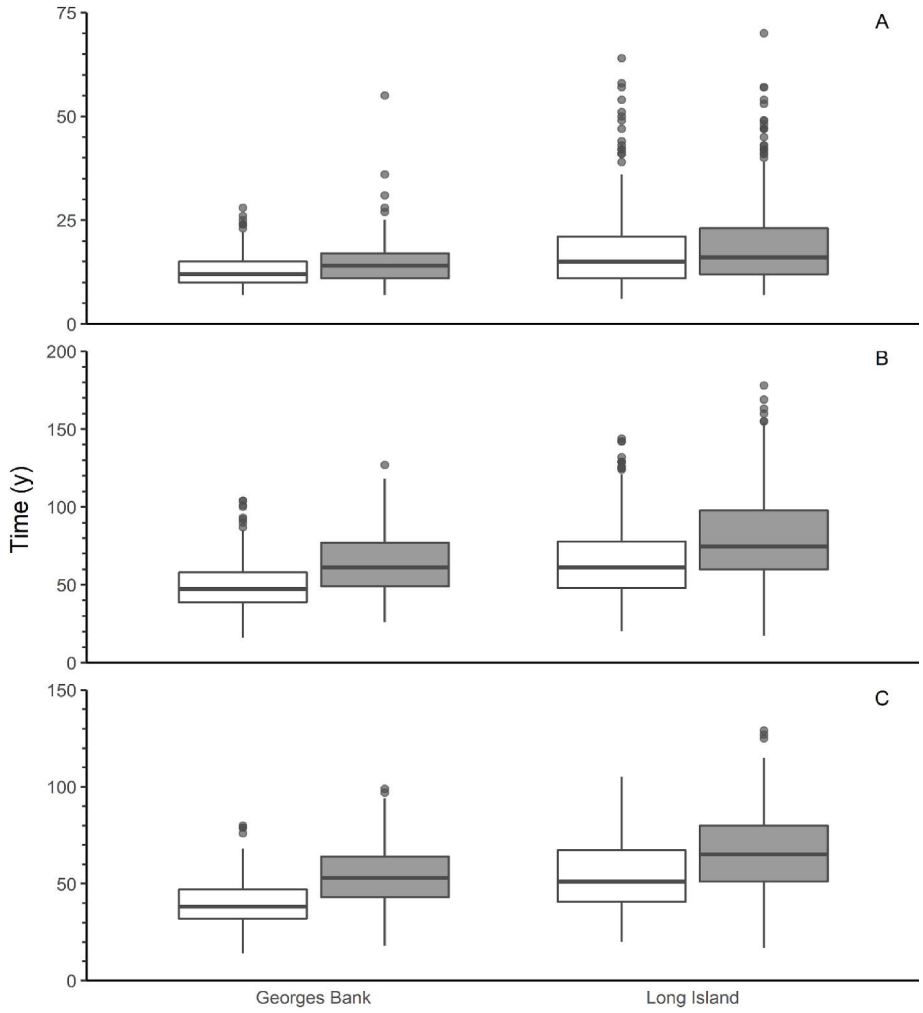


Fig. 4. Time to milestone sizes by sex and site. Female (white, left) and male (grey, right), by site, for (A) time to 50% maturity, (B) time to fishable size, (C) time (years) of reproduction before reaching fishable size. Boxes represent the interquartile range (IQR) with 50th percentile bar (median), whiskers represent 1.5 × IQR, and points are outliers (>1.5 × IQR).

surpassing those at GB in modern cohorts. Time estimates derived from MT models at both sites are comparable to those of the regression models and once again support the integrity of the MT growth models. Number of reproductive years prior to recruitment into the fishery is the time needed to grow between the maturity and fishery size milestones and represents growth of mature but relatively unfishable portions of the population (i.e., reproductive time). Reproductive time has been greater for LI *A. islandica* across most of the cohorts until 1940 when reproductive time was equal between GB and LI, and between 1980 and 2020 when reproductive years were estimated to be fewer at LI than GB as the adult growth rates at LI appear to exceed those at GB. Modified Tanaka growth model estimates for reproductive time are once again more conservative than the regression estimates and may represent life-history stages where *A. islandica* growth becomes more variable post maturity and over time. Age-length variability post-maturity may also reflect the emergence age of sexual dimorphism characteristics of this species, where male and female growth trajectories begin to diverge (Hemeon et al., 2021a, 2023).

Model estimated times to milestone size were also used to calculate growth rates (mm y^{-1}) to those size milestones for 20-y birth-year cohorts to compare trends over time (Fig. 6). These growth rates are coarse estimates of growth per year to reach specific milestone sizes and do not take into consideration ontogenetic growth. Regression models were used to predict growth rates for future cohorts (1980, 2000, and 2020), whereas MT models cannot be used to predict growth rates beyond the extent of observed data. Root-mean-square deviation (RMSE) was used to evaluate the extent that observed data deviated from model estimates for both regression and MT growth rates. Although true data are variable over time, and RMSE bounds often overlap between GB and LI, clear growth rate trends are observed for all three size milestones. Both regression and MT observed and estimated growth rates have been increasing relative to previous cohorts for all three size milestones. Regression estimates also suggest that GB *A. islandica* exhibit higher growth rates than LI until approximately 1960 when growth rates appear to have equalized between sites, and predicted growth rates at LI may have exceeded those at GB for mature clams since the 1980s (Fig. 6B and C). The MT model growth rates were derived from unique MT growth functions for each 20-y birth-year cohort estimated in this analysis and resulted in variable trends through time (Fig. 6D–F); however, growth rate values are comparable between MT and regression models and observed greater growth rates at LI in the late 20th century are also evident in modeled MT outputs for mature *A. islandica*. Overall, however, both the regression and MT models appeared to be adequate representations of changing growth rates over time providing additional support for the use of MT models to describe *A. islandica* growth.

3.4. Growth periodicity

With confidence in the MT cohort growth models, cohort growth models were used to detrend biological growth from each corresponding

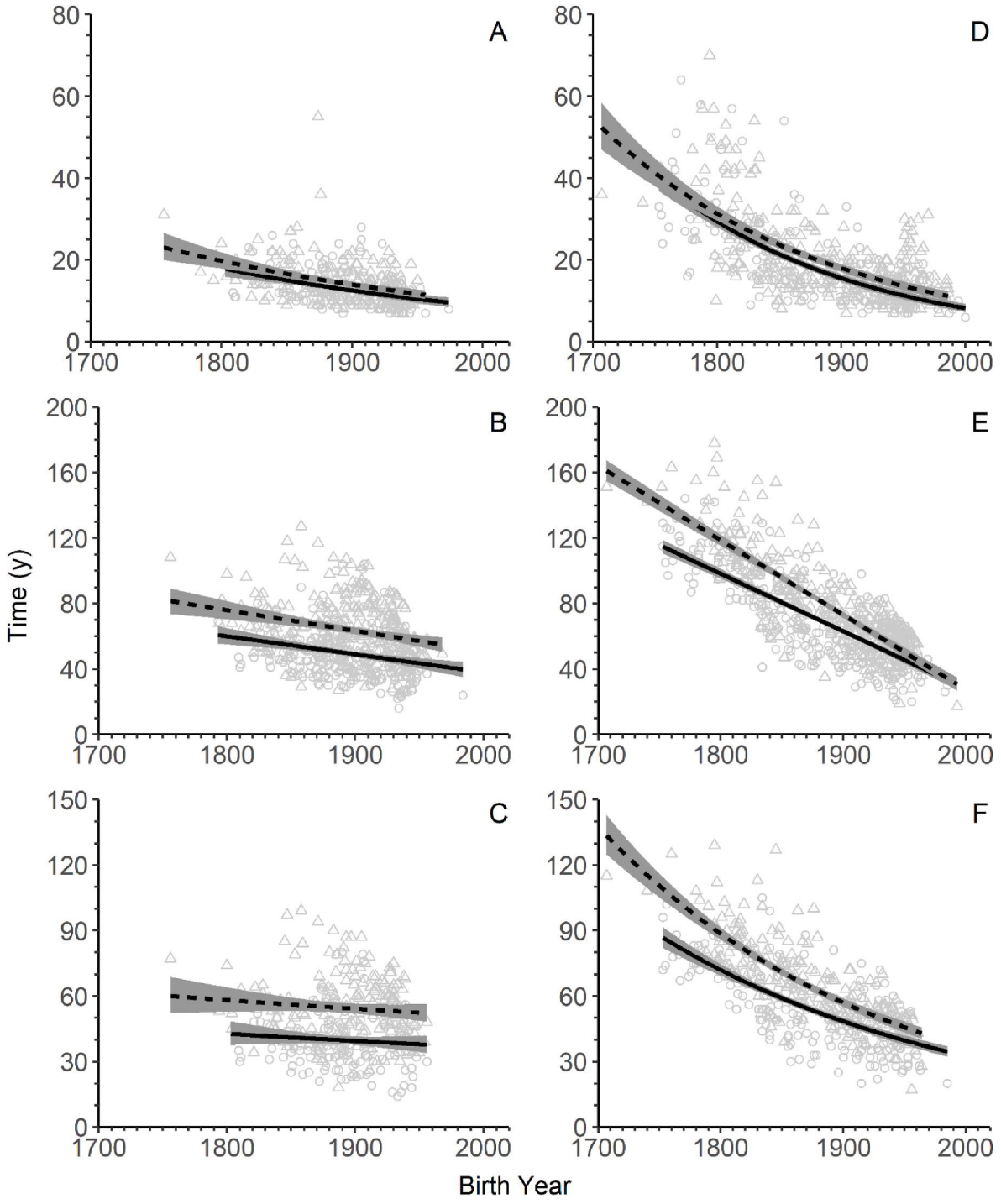


Fig. 5. Time to milestone sizes by birth year for Georges Bank (A–C) and Long Island (D–F) by sex with best-fit regression models. Individual female (solid line, circles) and male (dashed line, triangles) observed time to reach maturity (52 mm) fitted with negative exponential regression (A, D), time to reach fishable size (80 mm) fitted with linear regression (B, E), and estimated years of reproduction prior to recruitment to the fishery (52–80 mm) fitted with negative exponential regression (C, F), and 95% confidence intervals (grey shading).

individual clam by birth year to create a growth residual for each calendar year of life per clam. A mean residual was calculated for each calendar year by group (i.e., site and sex), and a unit variance was calculated by dividing each calendar year mean residual by the total standard deviation of mean residuals across all years specific to each group. Unit variance was retained as a growth index for each group (i.e., population, female, male) for cross-wavelet analyses. Growth indices were compared in three combinations: within-region analyses to identify common growth signatures between two populations in separate geospatial areas of an inhabited range (GB population vs LI population), within-sex analyses (GB female vs LI female, GB male vs LI male) were used to identify if the dimorphic sexes were growing in synchrony despite geospatial differences, and within-site analyses to identify if female and male *A. islandica* were growing similarly within populations in response to common environmental conditions (GB female vs GB male, LI female vs LI male).

Within-region cross wavelets of GB and LI population growth indices (Fig. 7 A, D) revealed a significant power period of 31 y (Fig. 8 A).

Table 3
Regression models fit to time to recruitment to the fishery, maturity, and reproductive size milestones. Fishery milestone models were fit with linear regression, while maturity and reproductive time milestone models were fit with exponential regressions. Model parameters *a* and *b* were presented with high precision due to size and longevity of *A. islandica*, where X represented birth year and regression models were presented with associated adjusted R^2 (R^2) and *p*-values.

Milestone	Site	Group	*a*	*b*	R^2	*P*-Value
Fishery $aX + b$	Georges Bank	Population	−0.12	279	0.06	<0.0001
		Female	−0.11	258	0.06	<0.0001
		Male	−0.13	302	0.07	<0.0001
	Long Island	Population	−0.4	834	0.63	<0.0001
		Female	−0.35	730	0.61	<0.0001
		Male	−0.46	939	0.70	<0.0001
Maturity ab^X	Georges Bank	Population	1.278550 E+04	0.9963682	0.19	<0.0001
		Female	2.384999 E+04	0.99601	0.19	<0.0001
		Male	1.045765 E+04	0.9964996	0.20	<0.0001
	Long Island	Population	4.320093 E+05	0.9946469	0.48	<0.0001
		Female	1.097935 E+06	0.9941226	0.56	<0.0001
		Male	2.570220 E+05	0.9949479	0.43	<0.0001
Reproductive Time ab^X	Georges Bank	Population	2.294765 E+02	0.9991366	0.01	0.08
		Female	3.697061 E+02	0.998795	0.01	0.10
		Male	2.053312 E+02	0.9992778	0.01	0.17
	Long Island	Population	2.309810 E+05	0.9955760	0.52	<0.0001
		Female	1.021612 E+05	0.9959637	0.48	<0.0001
		Male	3.714926 E+05	0.9953745	0.63	<0.0001

Within-sex cross-wavelet analyses demonstrated that female growth indices between sites (Fig. 7 B, E) had significant power frequencies at approximately 24- and 42-y periods (Fig. 8 B), while male growth indices (Fig. 7 C, F) have significant frequency powers at approximately 23- and 39-y periods (Fig. 8 C). The similar power frequency periods between sexes, indicated that males and females at both sites are growing in similar growth cycles. Within-site cross wavelets compared male and female growth indices at GB (Fig. 8 D) and male and female growth indices at LI (Fig. 8 E). Both sites presented power frequencies at approximately 22-y periods, but LI had an additional power frequency at a 39-y period while GB had additional power frequencies at 12-, 32-, and 62-y periods (Fig. 8D and E). Common positive and negative growth indices, or patterns, existed between sites and among sexes. Negative growth indices occurred at both Mid-Atlantic sites approximately between 1990 and 1999 and again beginning in 2015 (Fig. 7). Georges Bank also had negative growth indices between 1850 and 1900 and from 1900 to 1940 (Fig. 7A–C). Long Island incurred a long series of negative growth indices between 1840 and 1940 (Fig. 7D–F). The 1940–1990 period generally produced positive growth indices across sites and sexes.

Significant high-power periods were analyzed for phase shifts by the same set of paired data series discussed previously. A phase shift represented a lead or lag of one time series (i.e., growth index) in relation to the other for a specific frequency period. When GB and LI were evaluated, GB lagged LI for the 31-y period frequency until the early 1940s, but once the lag was too large (50% of time period, i.e., 15.5 y) the relationship inverted, and GB led LI until the end of the time series when the animals were collected in 2017 (Appendix Figure A.10). Between 1760 and 1840, and again between 1970 and 2017, GB and LI were in-phase meaning the two sites were growing in relative synchrony (phase shift less than $\frac{\pi}{2}$ or lead/lag difference less than 8 y).

4. Discussion

4.1. Growth rates

Studies by Ropes (1984), Thorarinsdóttir and Steingrímsson (2000), Fritz (1991), Hemeon et al. (2021a), and Hemeon et al. (2023) have posited that *A. islandica* are sexually dimorphic. Clearly, from this study, growth rates differ between sexes and between populations in the Mid-Atlantic Bight. Females from both populations grow faster than males within the same population as indicated by number of years needed to reach life-history and fishery milestones sizes, and by the modified Tanaka (MT) *a*, and von Bertalanffy (VB) *k* estimated parameters (Table A1). Faster growing female *A. islandica* support findings by Hemeon et al. (2021a; 2023). Despite the rapid march of female *A. islandica* into the fishery compared to males, the fishery demographics of LI are highly male biased (Hemeon et al., 2023). At LI, males dominated small size classes up to 85 mm within a length frequency collected by fishery equipment (60 mm–120 mm) but the mature population sex-ratio was 1:1.4 (F:M) (Hemeon et al., 2023). As females grow to larger sizes faster than males, a fishery that targets large animals would be expected to land proportionately more females leading to size and age truncation. No evidence exists for this outcome, possibly due to the low fishing mortality rate under current management restrictions (NEFSC, 2020). For example, LI does not have a higher female total mortality rate that might reduce the number of females in a population and create a skewed sex ratio (Hemeon et al., 2023).

One explanation for a limited impact of a fishery on female mortality is better dredge evasion by large *A. islandica*. If large *A. islandica* are, in fact, deeper or more frequent burrowers than smaller animals, and large *A. islandica* are predominantly female, an under-sampling of large females could result. Positive correlations between shell length and burrowing depth of clams support this hypothesis (e.g., Zaklan and Ydenberg, 1997; Ragnarsson and Thorarinsdóttir, 2020). This explanation would be plausible if it was also true that *A. islandica* at LI also have higher burrowing rates than GB due to local environmental variability that is not observed at GB since GB does not show a deficit in fishery-sized females.

Additionally, a length truncation is not observed at LI once again suggesting that a fishery bias towards large females is not predominant. One cannot exclude, however, the simpler explanation that a skewed sex ratio originates from the sampling of a patchy population, where a larger tow-area would be required to sample a more complete demographic distribution. This study sampled a coverage area greater than 1.764 km^2 and samples collected in this spatial extent were assumed to be representative of the population. If patchy demographics exist, the scale would be larger than approximately 2 km^2.

The MT growth model proved to be the best fit growth model for *A. islandica* as the VB growth model drastically overestimated size at young age, rarely approached the origin, and underestimated size at old age and large size. The MT growth models also change with birth year. As birth-year cohorts advanced through time, the model parameters also changed through time. Georges Bank *A. islandica* exhibited faster growth rates than those at LI based on the MT and VB parameters listed previously, as well as growth rates to milestones sizes when age-length data were aggregated by sex. Findings that *A. islandica* grow faster at GB than at LI confirm age at size relationships identified in Hemeon et al. (2023), but also previous findings by Pace et al. (2018) that GB growth rates

Table 4
Modeled time to size milestones. Regression results were calculated from best-fit linear and non-linear data regressions (Table 3). Modified Tanaka results were calculated from cohort-specific modified Tanaka model parameters (Appendix Tables A.2-A.3). Modified Tanaka reproductive time estimates were calculated as the difference between Time to Fishable Size Time and Time to 50% Maturity. Bold values represent projected time to milestones using the regression models assuming growth trends endure post 1980.

Growth Milestone	Growth Model	Birth Year	Time to Size (y)	
			Georges Bank	Long Island
50% Maturity (Growth: 0–52 mm)	Regression	1740	23	38
		1780	20	31
		1820	17	25
		1860	15	20
		1900	13	16
		1940	11	13
		1980	10	10
		2020	**8**	**8**
		Δ (%)	−65	−79
	Modified Tanaka	1740	NA	32
		1780	20	35
		1820	18	25
		1860	15	18
		1900	14	16
		1940	11	13
		1980	NA	12
		Δ (%)	−45	−63
Fishable Size (Growth: 0–80 mm)	Regression	1740	70	138
		1780	65	122
		1820	61	106
		1860	56	90
		1900	51	74
		1940	46	58
		1980	41	42
		2020	**37**	**26**
		Δ (%)	−47	−81
	Modified Tanaka	1740	NA	124
		1780	77	127
		1820	66	97
		1860	56	75
		1900	57	63
		1940	48	62
		1980	NA	43
		Δ (%)	−38	−65
Reproductive Time (Growth: 52–80 mm)	Regression	1740	58	103
		1780	49	86
		1820	48	72
		1860	46	61
		1900	44	51
		1940	43	42
		1980	41	36
		2020	**40**	**30**
		Δ (%)	−31	−71
	Modified Tanaka	1740	NA	92
		1780	57	92
		1820	48	72
		1860	41	57
		1900	43	47
		1940	37	49
		1980	NA	31
		Δ (%)	−35	−66

Δ (%), Percent change; NA, Data not available and/or model constraints prevent estimation.

were higher than other locations in the Mid-Atlantic Bight. Factors that may covary with calendar year that also affect growth, such as bottom water temperatures, could have a stronger effect on LI *A. islandica* growth rates than those at GB, particularly for larger animals with sizes greater than 52 mm due to strong LI relationships between growth rate and time.

In this study, growth rates of immature animals at LI increased by 63% over 240 y and by 45% over 160 y at GB using MT models. Growth rates were the fastest for animals up to 52 mm and predictably declined after maturation as energy allotment was diverted to reproduction (Ballesta-Artero et al., 2018). Increased growth rates over time, as observed in the regression and cohort-specific MT model estimates, not only reduced the amount of time needed to reach fishable size, but also the number of reproductive years prior to potential fishery harvest. For instance, GB lost between 31 and 35% of reproductive years over the time period, while LI lost between 66 and 71% of potential reproductive years. Additional reproductive years per animal at LI compared to GB through the 1940s would indicate that LI may be resilient to a commercial fishery if the time to maturity was low and fecundity constant; however, model trends point to increased adult growth rates at LI and thus reduced reproductive time in modern cohorts, an important consideration for assessment models and future study.

Long Island displayed a clear relationship between birth year and growth rates, whereas GB showed more subtle birth-year dependent change in growth rates. For instance, the time to recruit to the fishery at GB decreased from 70 y to 37 y by regression model predictions, while LI time to recruit to the fishery dropped from 138 y to 26 y by regression model predictions (results comparable to MT estimates). An 81% decrease in years to fishable size at LI compared to only a 47% decrease in time to fishable size at GB over the temporal extent of this study. This study also provides strong evidence that growth rates have been accelerating at LI and LI growth rates have recently matched those of the more growth-stable GB population, data that support previous findings by Pace et al. (2018). The faster growth rates of adult *A. islandica* at LI compared to GB in the past 40 y also provides an explanation for why the 2017 samples at GB included very few young animals (minimum age of sample: 33 y [85 mm], birth year: 1984) as opposed to LI (minimum age of sample: 17 y [77 mm], birth year: 2000) and suggests that younger *A. islandica* at LI will contribute more and more to fishery harvests and scientific sampling in coming years (Hemeon et al., 2021a, 2023).

4.2. Growth indices over time

Regional similarities in growth anomalies existed between GB and LI. An anomaly in this case refers to a positive or negative growth index that deviates from the zero-mean. A frequency period of 31 y has significant power in the GB and LI population time series. Generally, GB lagged behind LI in timing. In the case of the 31-y period, GB *A. islandica* lagged LI by less than 15 y, but has been in phase since the 1970s. The in-phase 31-y periods are an indication that growth frequencies were in synchrony on either side of the Great South Channel in recent decades. The Atlantic Multidecadal Oscillation (AMO) is a well-described, low-frequency oceanographic cycle with flexible periods ranging between 20 and 80 y (Knudsen et al., 2014; Moore et al., 2017) but often centered around a 60-y period (Kilbourne et al., 2014). The frequency of the AMO is variable over time, and could drive the repeating approximately 20-, 30-, 40-y power periods observed at GB and LI that are simply harmonics of the larger AMO cycle. It is also possible, that the North Atlantic Oscillation (NAO) plays a role as it cycles between 7, 13, 20, 26, and 34 y (Seip et al., 2019), but the NAO is extremely noisy (Seip et al., 2019) and would require direct cross wavelet analyses to distinguish positive (negative) NAO phases with positive (negative) *A. islandica* growth.

Arctica islandica from the western Mid-Atlantic demonstrate clear trends of increasing growth rates over the past three centuries and increasing growth rate trends are modulated by long-term climate cycles with periods shorter than the long lifespan of the species, namely the AMO and possibly the NAO. It is important to note that large-period (i.e., long-term) climate cycles such as the AMO are often first detrended by removing the underlying increasing temperature trend from the 20th century prior to the development of independent climate-cycle indices. Whitney et al. (2022) have supported evidence that warming in the northwest Atlantic over the past century has immensely surpassed any previous warming rates from the past 1000 y, with the Gulf of Maine warming more significantly than the global average. *Arctica islandica* growth rates and indices clearly demonstrate increasing growth rates

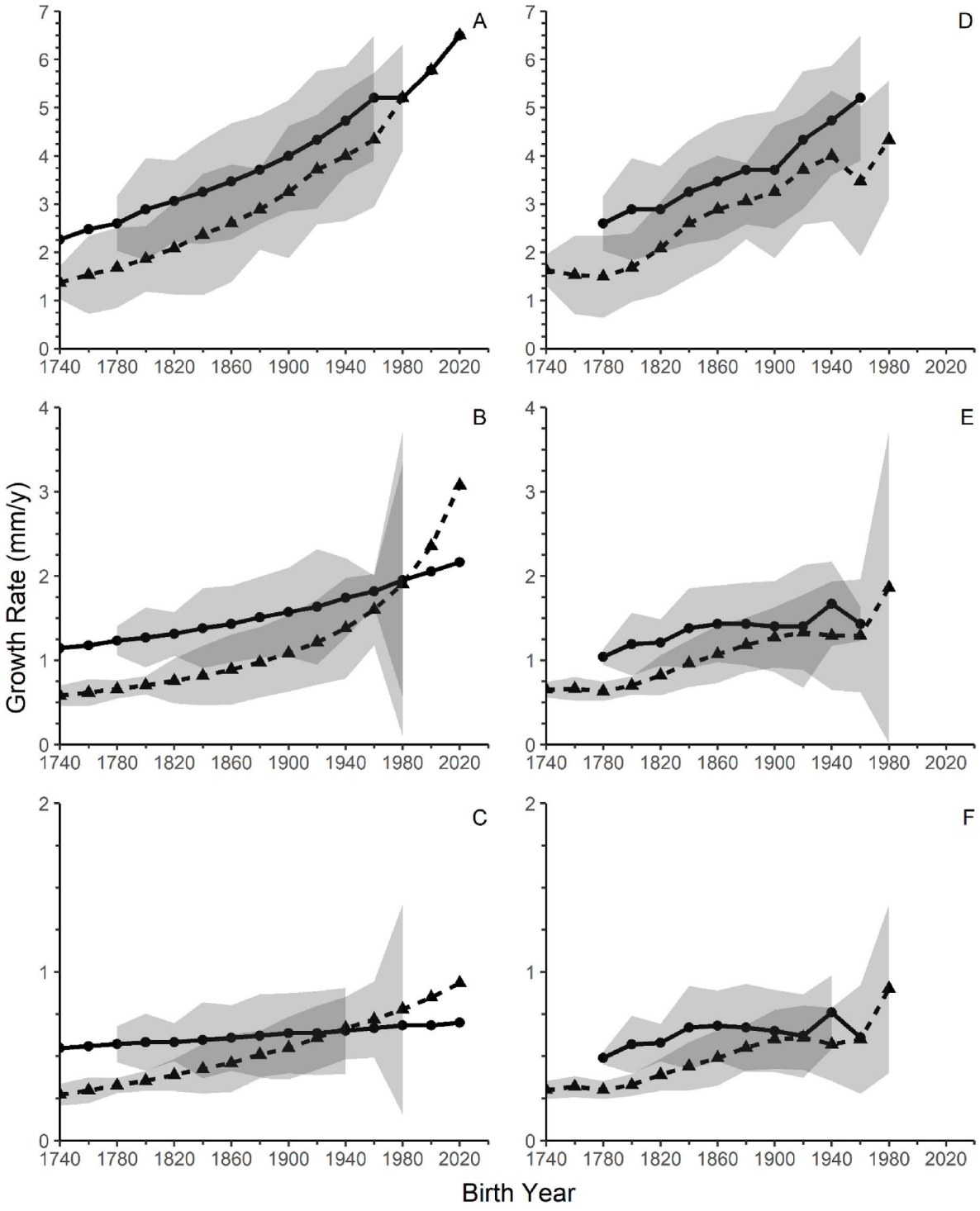


Fig. 6. Regional growth rates by birth year. Regression (A–C) and modified Tanaka (D–F) growth rate models estimated for Georges Bank (solid lines, circles) and Long Island (dashed lines, triangles). Growth rates are milestone size/time (mm/y) by birth year for 50% maturity (52 mm) (A, D), fishable size (80 mm) (B, E), and reproductive years between the onset of maturity and fishable size (52–80 mm) (C, F) size milestones. Grey shading represents root-mean-square deviation (RMSE) of observed data to models. Values outside the grey shading were predicted using the regression growth models but observed data are not available to determine RMSE; modified Tanaka models cannot be used to predict values outside of observed data range. Regression growth rates estimated from group-specific regression equations for observed data (see Fig. 5); modified Tanaka growth rates estimated from cohort-specific models fit to observed data (see Appendix Tables A.2-A.3).

over time in parallel with the consistent warming of the western Mid-Atlantic, particularly since the early 1900s. Long-lived, sedentary, and carbonate-producing marine species provide exceptional glimpses into past oceanographic environments through internal growth records, and potentially amplify changing environmental dynamics not yet observed at a regional scale.

5. Conclusions

This study found that Tanaka growth models best the fit age and growth data of *Arctica islandica* at Georges Bank (GB) and Long Island (LI) and strongly suggest that the traditional von Bertalanffy (VB) growth model will seriously underestimate size at old age and growth

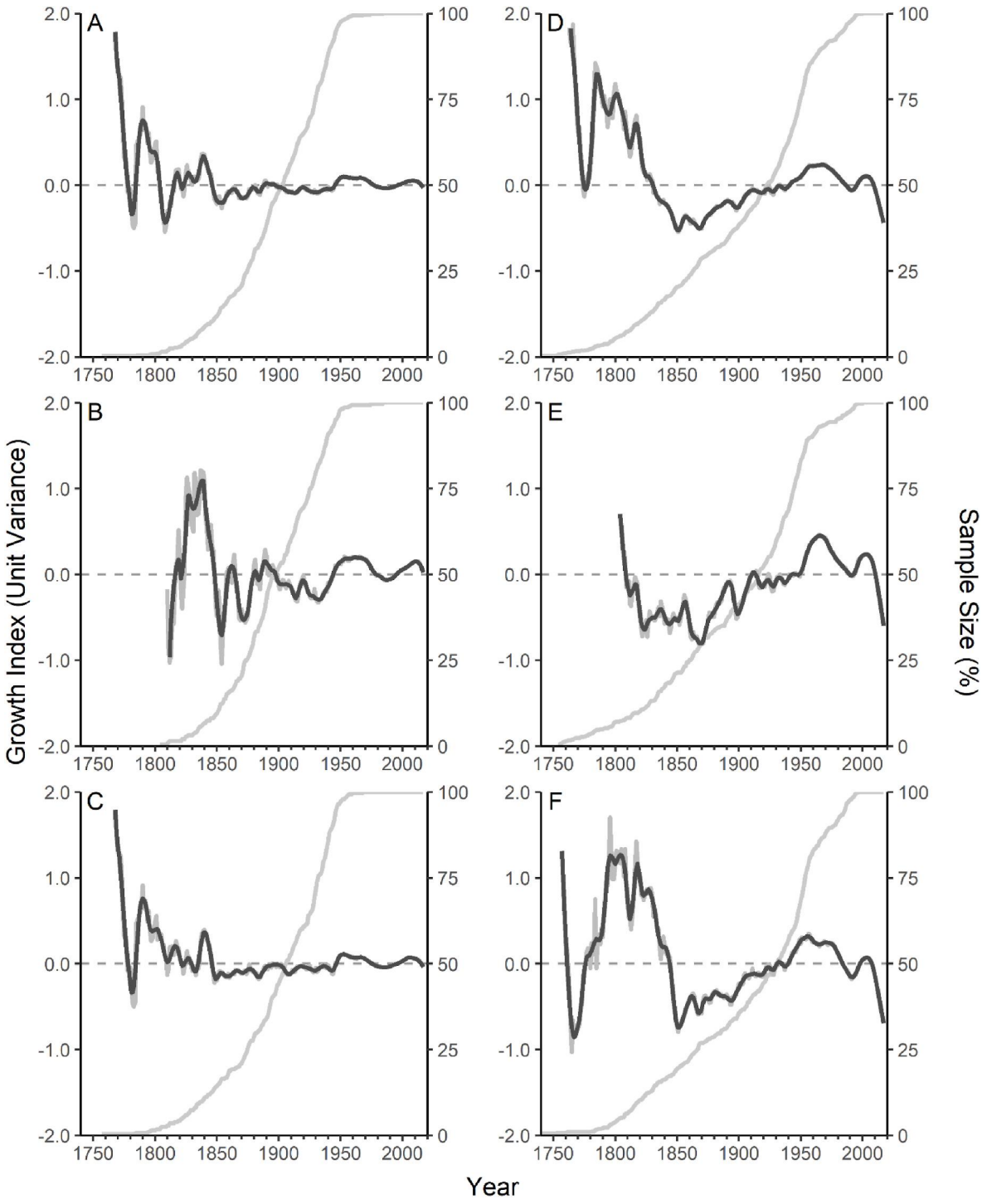


Fig. 7. Regional population growth indices and sample size (as a percent of total sample) over time. Population (A, D), female (B, E), and male (C, F) growth indices (oscillating light grey line), and growth indices with a 15-y *loess* smoother (black line), derived from Georges Bank (A–C) and Long Island (D–F) samples. Sample size (ascending light grey line; second y-axis) represented percent of total samples specific to each group used to estimate growth indices for each calendar year.

rate post maturity. Model performance between the original and modified Tanaka models are similar, and either model would be a vast improvement for the estimation of *A. islandica* age at length compared to the VB growth model. Due to assessment model limitations, and the integration of VB parameters to estimate other stock metrics, VB k, t_0, and L_∞ parameters were listed by cohort to offer time-varying conditions, but clearly the L_∞ parameter should not be used to estimate maximum body size, as this parameter vastly underestimates the true length at age. Similarity in model performance between regression and cohort-specific MT growth models support the application of cohort-conscious MT growth models in population dynamics models as a surrogate for the VB.

Female growth rates exceed those of males, and GB growth rates exceed growth rates at LI until recent decades. These results support findings by Hemeon et al. (2023) that area-specific age-length keys and growth models should be used when estimating ages for different *A. islandica* management areas and populations in the US Mid-Atlantic. Also of note is the accelerating growth rate of *A. islandica* at LI and the

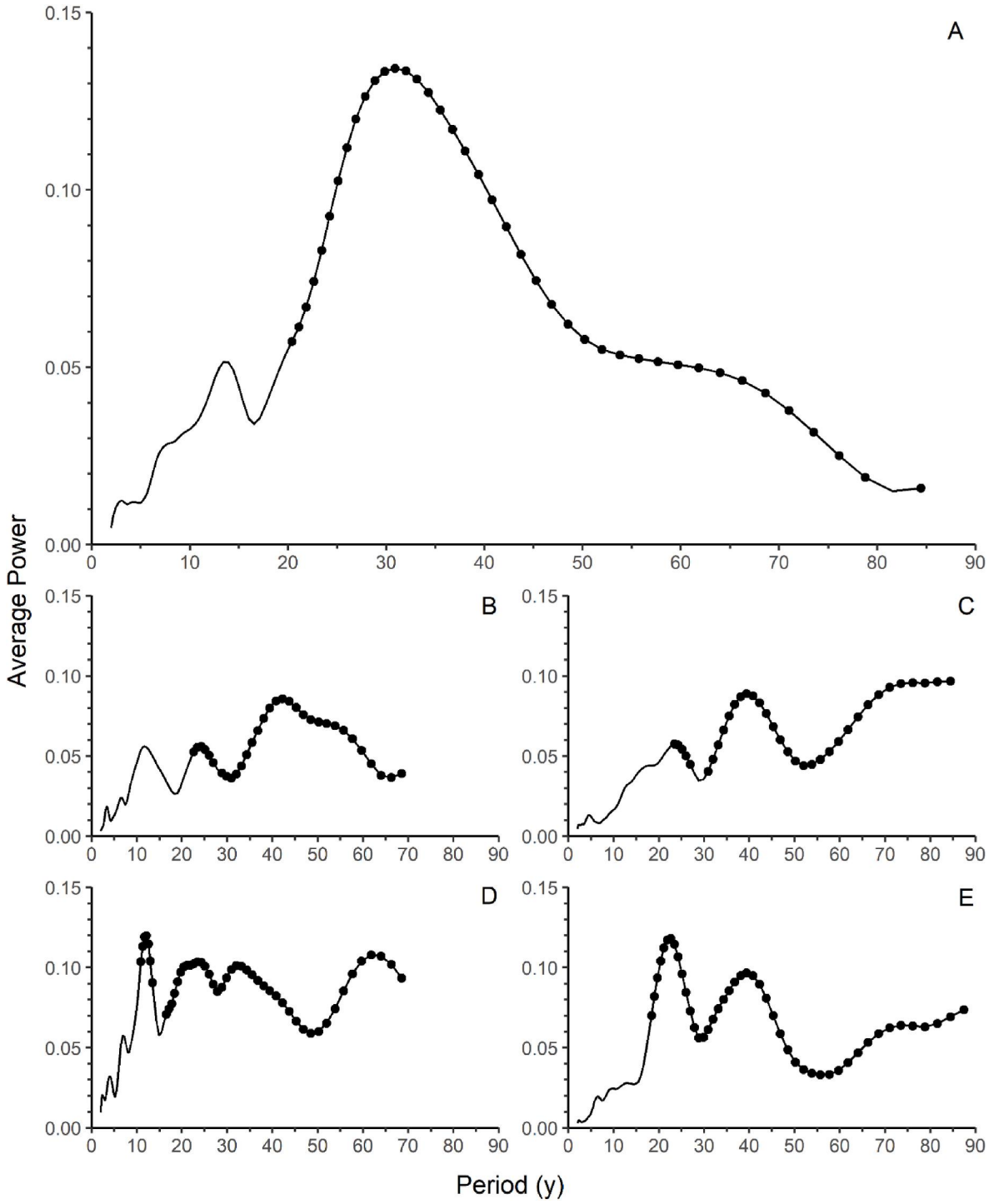


Fig. 8. Cross-wavelet analysis of significantly similar growth periods between Georges Bank and Long Island populations (A), Georges Bank and Long Island females (B), Georges Bank and Long Island males (C), Georges Bank males and females (D), and Long Island males and females (E). Wavelet power analyzed for average frequency by period (y). Significance represented by black points (alpha = 0.10).

consequent implications for population resilience. Not only are LI animals recruiting into the fishery faster over time, but this fact also implies that fewer reproductive years are available before a higher probability of being harvested. If fecundity does not decrease with age, important spawning stock biomass may be removed from the population faster than replacement in future climate scenarios. An increasing growth rate over time also implies that a single growth curve is not sufficient to represent the LI population. Finally, growth indices at GB and LI varied significantly on 31-y periods, and GB growth rates often lag LI in response to these periods.

Whether to model growth for a single stock or by population and cohort is an important decision because if birth year is ignored, model parameters do not reflect contemporary growth of upcoming generations. Inaccurate growth estimates would likely underestimate stock biomass productivity and overestimate the number of spawning years prior to *A. islandica* recruitment to the fishery. Additionally, understanding how these growth relationships correlate with environmental cycles will assist in accurate forecasts of future growth conditions and

growth responses to anomalous temperatures. The continuation of cross wavelet analyses between *A. islandica* growth indices with both basin-wide (e.g., AMO, NAO, Atlantic Meridional Overturning Circulation) and local temperature variability (Cold Pool strength, ENSO), may provide insight into fishery milestone timing and conditions necessary for successful growth and recruitment. Additional wavelet analyses between *A. islandica* growth indices and temperature, salinity, chlorophyll-a derived datasets can inform future growth trends in response to projected climate scenarios.

Long-term temperature trends show that the North Atlantic has been warming since the Little Ice Age, which ended in the early 1800s. This warming is well recorded in the increasing growth rate of *A. islandica* at both LI and GB, with the implication that the scale of warming has been distinctly larger at LI. *Arctica islandica* has received considerable attention as a recorder of long-term changes in bottom water temperature. For the region covered by this study, the scale of change in growth rates strongly demonstrates the sensitivity of this species to warming temperatures and implies that a more extensive regional evaluation of growth trends both latitudinally and with depth, may provide an unparalleled record of the geographic trends in temperature change over time, and likely the dynamics of the Cold Pool, one of the primary hydrographic features of the northwestern Atlantic continental shelf since the end of the Little Ice Age.

CRediT authorship contribution statement

Kathleen M. Hemeon: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eric N. Powell:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **John M. Klinck:** Writing – review & editing, Validation, Methodology. **Roger Mann:** Writing – review & editing, Resources, Funding acquisition, Data curation, Conceptualization. **Sara M. Pace:** Validation, Resources.

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.

Data availability

Data will be made available on request.

6. Acknowledgments

The authors thank the Seawatch International crew from the F/V E.S. S. Pursuit for their time, expertise, and resources necessary for offshore benthic sampling. The authors also acknowledge and thank the reviewers for their comments and edits. This research was supported by a Non-academic Research Internship for Graduate Students from the National Science Foundation (NSF) to the first author and the NSF Industry/University Cooperative Research Center, Science Center for Marine Fisheries (SCEMFIS), under NSF awards 1841435 and 1841112 and through membership fees provided by the SCEMFIS Industry Advisory Board.

APPENDIX

Table A.1
Regional group model parameters.

Model	Group	Parameter	Georges Bank		Long Island	
			Estimate	*SE*	Estimate	*SE*
von Bertalanffy	Population	L_∞	9.73 E+01	7.78E-02	9.17 E+01	6.92E-02
		k	2.80E-02	1.16E-04	2.70E-02	1.07E-04
		t_0	−1.12 E+01	9.47E-02	−1.15 E+01	9.53E-02
	Female	L_∞	1.00 E+02	9.71E-02	9.48 E+01	9.84E-02
		k	2.93E-02	1.48E-04	2.61E-02	1.40E-04
		t_0	−9.91 E+00	1.10E-01	−1.18 E+01	1.33E-01
	Male	L_∞	9.47 E+01	1.11E-01	8.80 E+01	9.07E-02
		k	2.63E-02	1.57E-04	2.85E-02	1.58E-04
		t_0	−1.31 E+01	1.47E-01	−1.10 E+01	1.28E-01
Tanaka	Population	a	2.70E-03	7.50E-04	1.11E-02	7.61E-04
		c	1.31E-01	6.92E-02	1.06 E+00	6.35E-02
		d	9.03 E+01	1.26E-01	7.98 E+01	9.69E-02
		f	2.71E-03	1.69E-05	3.44E-03	2.05E-05
	Female	a	4.60E-03	9.24E-04	9.69E-03	1.14E-03
		c	2.54E-01	8.86E-02	7.99E-01	9.44E-02
		d	9.56 E+01	1.71E-01	8.38 E+01	1.45E-01
		f	2.46E-03	1.90E-05	3.09E-03	2.55E-05
	Male	a	6.08E-04	1.02E-03	1.32E-02	9.16E-04
		c	0.00 E+00	9.01E-02	1.47 E+00	7.74E-02
		d	8.51 E+01	1.53E-01	7.52 E+01	1.17E-01
		f	3.00E-03	2.50E-05	3.98E-03	3.18E-05
Modified Tanaka	Population	a	7.36E-03	7.34E-04	1.57E-02	7.29E-04
		c	7.62E-01	7.62E-02	1.77 E+00	6.88E-02
		d	8.78 E+01	2.03E-01	7.73 E+01	1.53E-01
		f	3.00E-03	2.82E-05	3.90E-03	3.48E-05
		g	6.04E-06	4.29E-07	5.07E-06	2.66E-07
	Female	a	8.73E-03	9.27E-04	1.36E-02	1.14E-03
		c	8.50E-01	1.01E-01	1.34 E+00	1.06E-01
		d	9.31 E+01	2.91E-01	8.19 E+01	2.38E-01
		f	2.70E-03	3.28E-05	3.37E-03	4.21E-05
		g	6.37E-06	6.41E-07	3.47E-06	3.74E-07
	Male	a	9.21E-03	8.52E-04	1.77E-02	8.45E-04
		c	1.18 E+00	8.84E-02	2.27 E+00	8.15E-02

(*continued on next page*)

Table A.1 (*continued*)

Model	Group	Parameter	Georges Bank		Long Island	
			Estimate	*SE*	Estimate	*SE*
		d	8.06 E+01	2.20E-01	7.24 E+01	1.77E-01
		f	3.71E-03	4.48E-05	4.68E-03	5.55E-05
		g	1.14E-05	4.87E-07	6.56E-06	3.51E-07

SE, standard error; *a,c,d,f,g*, modified Tanaka growth coefficients.

Table A.2
Georges Bank 20-y cohort modified Tanaka model parameters.

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1740	*a*	6.55E-03	9.64E-03			6.55E-03	9.64E-03
	c	0.00 E+00	8.07E-01			0.00 E+00	8.07E-01
	d	8.10 E+01	1.45 E+00			8.10 E+01	1.45 E+00
	f	2.19E-03	1.34E-04			2.19E-03	1.34E-04
	g	9.14E-06	1.01E-06			9.14E-06	1.01E-06
1780	*a*	1.14E-02	6.26E-03			1.14E-02	6.26E-03
	c	0.00 E+00	4.09E-01			0.00 E+00	4.09E-01
	d	8.42 E+01	6.49E-01			8.42 E+01	6.49E-01
	f	2.61E-03	8.21E-05			2.61E-03	8.21E-05
	g	7.67E-06	6.34E-07			7.67E-06	6.34E-07
1800	*a*	5.74E-03	6.39E-03	1.22E-02	5.18E-03	8.31E-03	6.74E-03
	c	0.00 E+00	5.14E-01	1.32 E+00	5.48E-01	0.00 E+00	4.95E-01
	d	8.78 E+01	1.01 E+00	9.19 E+01	1.28 E+00	8.52 E+01	9.11E-01
	f	2.53E-03	1.15E-04	2.69E-03	1.56E-04	2.54E-03	1.06E-04
	g	6.91E-06	1.17E-06	7.37E-06	1.59E-06	6.78E-06	1.04E-06
1820	*a*	9.56E-03	4.31E-03	1.52E-02	7.51E-03	6.22E-03	4.69E-03
	c	0.00 E+00	3.24E-01	0.00 E+00	5.46E-01	0.00 E+00	3.71E-01
	d	8.95 E+01	6.58E-01	9.39 E+01	1.10 E+00	8.71 E+01	7.69E-01
	f	2.41E-03	6.72E-05	2.13E-03	9.03E-05	2.59E-03	8.89E-05
	g	9.31E-06	8.87E-07	8.87E-06	1.36E-06	8.22E-06	1.09E-06
1840	*a*	9.48E-03	4.35E-03	1.14E-02	4.27E-03	8.38E-03	6.66E-03
	c	2.64E-01	3.63E-01	2.99E-01	3.67E-01	3.52E-01	5.44E-01
	d	9.11 E+01	8.51E-01	9.65 E+01	8.96E-01	8.48 E+01	1.22 E+00
	f	2.52E-03	8.96E-05	2.26E-03	7.77E-05	2.91E-03	1.66E-04
	g	9.38E-06	1.50E-06	7.56E-06	1.49E-06	1.23E-05	2.32E-06
1860	*a*	1.12E-02	2.63E-03	9.82E-03	2.63E-03	1.27E-02	4.55E-03
	c	9.50E-01	2.62E-01	7.21E-01	2.70E-01	1.22 E+00	4.31E-01
	d	8.82 E+01	7.35E-01	9.35 E+01	7.90E-01	8.06 E+01	1.12 E+00
	f	2.91E-03	9.38E-05	2.56E-03	8.04E-05	3.54E-03	2.05E-04
	g	1.91E-05	1.87E-06	1.77E-05	1.87E-06	1.94E-05	3.20E-06
1880	*a*	1.01E-02	1.67E-03	6.29E-03	2.33E-03	1.29E-02	2.02E-03
	c	1.08 E+00	1.84E-01	4.11E-01	2.49E-01	1.71 E+00	2.27E-01
	d	8.69 E+01	5.93E-01	9.38 E+01	8.15E-01	7.94 E+01	7.09E-01
	f	3.11E-03	8.17E-05	2.54E-03	7.93E-05	3.97E-03	1.49E-04
	g	1.79E-05	2.04E-06	1.14E-05	2.46E-06	2.10E-05	2.85E-06
1900	*a*	1.13E-02	1.71E-03	1.23E-02	2.16E-03	1.10E-02	1.84E-03
	c	1.41 E+00	2.07E-01	1.50 E+00	2.76E-01	1.48 E+00	2.15E-01
	d	8.57 E+01	7.81E-01	9.22 E+01	1.11 E+00	7.82 E+01	7.58E-01
	f	3.31E-03	1.14E-04	2.90E-03	1.27E-04	3.99E-03	1.54E-04
	g	7.25E-06	3.84E-06	1.02E-05	5.15E-06	1.12E-05	4.08E-06
1920	*a*	1.01E-02	8.86E-04	9.83E-03	1.39E-03	1.01E-02	8.75E-04
	c	1.95 E+00	1.33E-01	1.78 E+00	2.17E-01	2.02 E+00	1.27E-01
	d	7.94 E+01	6.25E-01	8.73 E+01	1.08 E+00	7.36 E+01	5.66E-01
	f	4.57E-03	1.48E-04	3.68E-03	1.74E-04	5.43E-03	1.81E-04
	g	3.71E-05	5.76E-06	2.33E-05	8.74E-06	3.91E-05	5.78E-06
1940	*a*	1.06E-02	9.45E-04	1.05E-02	1.25E-03	1.07E-02	1.23E-03
	c	2.21 E+00	1.65E-01	2.11 E+00	2.23E-01	2.30 E+00	2.11E-01
	d	8.31 E+01	9.85E-01	8.76 E+01	1.39 E+00	8.01 E+01	1.23 E+00
	f	4.27E-03	1.93E-04	3.78E-03	2.20E-04	4.68E-03	2.84E-04
	g	7.39E-05	1.30E-05	6.97E-05	1.76E-05	8.40E-05	1.69E-05
1960	*a*	8.76E-03	1.52E-03	3.75E-03	5.45E-03	9.07E-03	2.02E-03
	c	3.27 E+00	2.82E-01	9.90E-01	1.20 E+00	2.07 E+00	4.32E-01
	d	7.61 E+01	2.79 E+00	8.91 E+01	1.17 E+01	8.71 E+01	3.83 E+00
	f	6.70E-03	1.01E-03	3.17E-03	1.22E-03	4.08E-03	6.25E-04
	g	0.00 E+00	1.15E-04	0.00 E+00	3.67E-04	0.00 E+00	1.08E-04
1980	*a*	1.48E-02	1.09E-03	1.48E-02	1.09E-03		
	c	4.21 E+00	2.42E-01	4.21 E+00	2.42E-01		
	d	1.05 E+02	4.64 E+00	1.05 E+02	4.64 E+00		
	f	2.97E-03	3.78E-04	2.97E-03	3.78E-04		
	g	3.77E-04	2.57E-04	3.77E-04	2.57E-04		

SE, standard error; *a,c,d,f,g*, modified Tanaka growth coefficients.

Table A.3
Long Island 20-y cohort modified Tanaka model parameters.

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1700	*a*	2.41E-02	2.15E-02			2.41E-02	2.15E-02
	c	0.00 E+00	8.08E-01			0.00 E+00	8.08E-01
	d	6.23 E+01	5.97E-01			6.23 E+01	5.97E-01
	f	3.84E-03	1.91E-04			3.84E-03	1.91E-04
	g	1.19E-05	3.98E-07			1.19E-05	3.98E-07
1740	*a*	9.91E-03	9.63E-03	5.59E-02	2.71E-02	5.71E-03	1.22E-02
	c	0.00 E+00	5.85E-01	0.00 E+00	1.02 E+00	0.00 E+00	5.89E-01
	d	7.09 E+01	7.68E-01	7.32 E+01	9.29E-01	5.92 E+01	5.54E-01
	f	2.91E-03	1.26E-04	2.73E-03	1.49E-04	4.54E-03	2.22E-04
	g	1.46E-05	5.97E-07	1.51E-05	6.48E-07	1.88E-05	5.39E-07
1760	*a*	4.46E-02	2.83E-02	5.24E-02	3.09E-02	7.90E-02	8.87E-03
	c	0.00 E+00	1.22 E+00	0.00 E+00	1.25 E+00	2.51 E+00	3.53E-01
	d	7.36 E+01	1.29 E+00	7.36 E+01	1.26 E+00	5.88 E+01	2.93E-01
	f	2.56E-03	1.76E-04	2.61E-03	1.79E-04	4.37E-03	1.11E-04
	g	1.58E-05	9.69E-07	1.82E-05	9.48E-07	1.29E-05	2.96E-07
1780	*a*	1.46E-02	8.31E-03	6.29E-02	2.21E-02	2.04E-02	1.80E-02
	c	0.00 E+00	4.77E-01	0.00 E+00	8.44E-01	0.00 E+00	8.68E-01
	d	6.98 E+01	6.71E-01	7.24 E+01	8.53E-01	6.56 E+01	1.04 E+00
	f	2.84E-03	1.01E-04	2.68E-03	1.26E-04	3.15E-03	1.97E-04
	g	2.02E-05	6.73E-07	2.14E-05	7.51E-07	2.03E-05	1.09E-06
1800	*a*	1.33E-02	5.85E-03	5.96E-02	2.73E-02	1.56E-02	7.66E-03
	c	0.00 E+00	3.52E-01	0.00 E+00	1.14 E+00	0.00 E+00	4.00E-01
	d	7.24 E+01	5.46E-01	7.63 E+01	1.33 E+00	6.88 E+01	5.42E-01
	f	2.83E-03	7.92E-05	2.51E-03	1.67E-04	3.23E-03	1.02E-04
	g	2.10E-05	6.53E-07	2.45E-05	1.34E-06	2.22E-05	6.87E-07
1820	*a*	2.50E-02	9.59E-03	2.29E-02	1.13E-02	1.32E-02	8.49E-03
	c	0.00 E+00	4.73E-01	0.00 E+00	6.00E-01	0.00 E+00	4.93E-01
	d	7.54 E+01	6.61E-01	7.89 E+01	9.05E-01	7.32 E+01	7.81E-01
	f	2.99E-03	1.07E-04	2.79E-03	1.27E-04	3.06E-03	1.27E-04
	g	2.49E-05	9.34E-07	2.50E-05	1.24E-06	2.19E-05	1.15E-06
1840	*a*	4.37E-03	4.27E-03	8.51E-03	6.96E-03	1.11E-02	3.70E-03
	c	0.00 E+00	3.12E-01	0.00 E+00	4.94E-01	1.01 E+00	3.04E-01
	d	7.77 E+01	6.29E-01	8.22 E+01	1.00 E+00	7.18 E+01	6.25E-01
	f	3.21E-03	1.04E-04	2.79E-03	1.30E-04	4.13E-03	1.60E-04
	g	2.60E-05	1.24E-06	2.44E-05	1.80E-06	2.86E-05	1.46E-06
1860	*a*	4.62E-03	3.72E-03	5.33E-03	5.16E-03	9.82E-03	3.15E-03
	c	1.51E-01	3.05E-01	0.00 E+00	4.29E-01	9.29E-01	2.69E-01
	d	8.00 E+01	7.24E-01	8.66 E+01	1.06 E+00	7.10 E+01	6.10E-01
	f	3.16E-03	1.11E-04	2.69E-03	1.23E-04	4.18E-03	1.54E-04
	g	3.13E-05	1.78E-06	2.81E-05	2.40E-06	3.80E-05	1.77E-06
1880	*a*	1.43E-02	3.30E-03	1.54E-02	4.35E-03	1.37E-02	4.20E-03
	c	8.66E-01	2.89E-01	8.82E-01	3.91E-01	9.01E-01	3.59E-01
	d	8.33 E+01	8.02E-01	8.75 E+01	1.12 E+00	7.87 E+01	9.62E-01
	f	2.99E-03	1.06E-04	2.75E-03	1.27E-04	3.30E-03	1.52E-04
	g	3.01E-05	2.59E-06	2.77E-05	3.44E-06	3.28E-05	3.29E-06
1900	*a*	1.97E-02	1.63E-03	1.46E-02	2.59E-03	2.43E-02	1.70E-03
	c	2.28 E+00	1.88E-01	1.50 E+00	2.92E-01	3.22 E+00	2.03E-01
	d	8.16 E+01	6.72E-01	8.55 E+01	1.06 E+00	7.69 E+01	7.13E-01
	f	3.57E-03	1.12E-04	3.13E-03	1.40E-04	4.25E-03	1.61E-04
	g	3.99E-05	3.42E-06	3.94E-05	5.00E-06	4.16E-05	4.02E-06
1920	*a*	1.94E-02	9.52E-04	1.83E-02	1.10E-03	2.11E-02	1.54E-03
	c	3.00 E+00	1.31E-01	2.91 E+00	1.59E-01	3.09 E+00	1.99E-01
	d	7.95 E+01	5.90E-01	8.24 E+01	7.45E-01	7.61 E+01	8.49E-01
	f	4.33E-03	1.27E-04	4.04E-03	1.42E-04	4.68E-03	2.11E-04
	g	3.71E-05	5.11E-06	3.55E-05	6.22E-06	3.44E-05	7.65E-06
1940	*a*	1.25E-02	5.62E-04	1.31E-02	9.01E-04	1.20E-02	6.79E-04
	c	2.74 E+00	9.12E-02	2.53 E+00	1.48E-01	2.80 E+00	1.08E-01
	d	7.39 E+01	5.22E-01	7.97 E+01	8.56E-01	7.04 E+01	6.18E-01
	f	5.60E-03	1.63E-04	4.59E-03	1.90E-04	6.29E-03	2.35E-04
	g	9.39E-05	8.46E-06	6.18E-05	1.20E-05	8.86E-05	1.11E-05
1960	*a*	2.09E-02	1.85E-03	1.74E-02	2.30E-03	2.35E-02	2.66E-03
	c	2.75 E+00	3.04E-01	2.52 E+00	4.18E-01	2.71 E+00	4.07E-01
	d	8.22 E+01	2.17 E+00	8.90 E+01	3.21 E+00	8.05 E+01	2.78 E+00
	f	3.69E-03	3.11E-04	3.20E-03	3.59E-04	3.70E-03	4.03E-04
	g	1.91E-05	4.73E-05	2.99E-05	6.38E-05	0.00 E+00	6.08E-05
1980	*a*	1.41E-02	9.61E-04	1.39E-02	1.44E-03	1.56E-02	1.29E-03
	c	3.25 E+00	2.18E-01	3.72 E+00	2.76E-01	3.40 E+00	2.81E-01
	d	8.87 E+01	3.23 E+00	8.90 E+01	4.51 E+00	8.82 E+01	4.08 E+00
	f	3.79E-03	4.11E-04	4.21E-03	6.67E-04	3.75E-03	5.10E-04
	g	0.00 E+00	2.00E-04	0.00 E+00	3.24E-04	0.00 E+00	2.42E-04
2000	*a*	4.45E-03	6.19E-04	4.45E-03	6.19E-04		
	c	3.05 E+00	1.57E-01	3.05 E+00	1.57E-01		
	d	1.02 E+02	7.43 E+00	1.02 E+02	7.43 E+00		

(*continued on next page*)

Table A.3 (*continued*)

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
	f	3.91E-03	7.96E-04	3.91E-03	7.96E-04		
	g	0.00 E+00	2.09E-03	0.00 E+00	2.09E-03		

SE, standard error; *a,c,d,f,g*, modified Tanaka growth coefficients.

Table A.4
Georges Bank 20-y cohort Tanaka growth models.

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1740	*a*	5.54E-02	3.61E-02			5.54E-02	3.61E-02
	c	0.00 E+00	1.51 E+00			0.00 E+00	1.51 E+00
	d	8.74 E+01	9.89E-01			8.74 E+01	9.89E-01
	f	1.88E-03	9.88E-05			1.88E-03	9.88E-05
1780	*a*	1.99E-02	8.34E-03			1.99E-02	8.34E-03
	c	0.00 E+00	4.47E-01			0.00 E+00	4.47E-01
	d	8.87 E+01	3.81E-01			8.87 E+01	3.81E-01
	f	2.28E-03	4.93E-05			2.28E-03	4.93E-05
1800	*a*	9.55E-03	6.59E-03	3.84E-03	5.74E-03	7.62E-03	5.07E-03
	c	0.00 E+00	4.48E-01	0.00 E+00	5.08E-01	0.00 E+00	3.77E-01
	d	9.13 E+01	4.88E-01	9.74 E+01	6.76E-01	8.99 E+01	4.45E-01
	f	2.29E-03	5.89E-05	2.18E-03	7.22E-05	2.20E-03	4.92E-05
1820	*a*	1.53E-02	4.49E-03	2.18E-02	7.53E-03	1.06E-02	4.94E-03
	c	0.00 E+00	2.83E-01	0.00 E+00	4.63E-01	0.00 E+00	3.25E-01
	d	9.37 E+01	3.20E-01	9.85 E+01	5.31E-01	9.05 E+01	3.72E-01
	f	2.14E-03	3.36E-05	1.88E-03	4.39E-05	2.35E-03	4.59E-05
1840	*a*	9.83E-03	4.34E-03	1.11E-02	4.14E-03	7.40E-03	6.40E-03
	c	0.00 E+00	3.06E-01	0.00 E+00	3.03E-01	0.00 E+00	4.61E-01
	d	9.46 E+01	4.06E-01	9.98 E+01	4.23E-01	8.99 E+01	6.08E-01
	f	2.27E-03	4.45E-05	2.06E-03	3.85E-05	2.45E-03	7.64E-05
1860	*a*	5.55E-03	2.95E-03	6.28E-03	2.85E-03	4.21E-03	5.33E-03
	c	0.00 E+00	2.40E-01	0.00 E+00	2.41E-01	0.00 E+00	4.10E-01
	d	9.43 E+01	3.87E-01	9.90 E+01	4.05E-01	8.69 E+01	6.10E-01
	f	2.36E-03	4.26E-05	2.16E-03	3.80E-05	2.74E-03	8.90E-05
1880	*a*	2.50E-03	1.84E-03	4.09E-03	2.26E-03	5.97E-03	2.33E-03
	c	0.00 E+00	1.67E-01	0.00 E+00	2.05E-01	5.81E-01	2.14E-01
	d	9.19 E+01	3.09E-01	9.70 E+01	3.92E-01	8.45 E+01	3.82E-01
	f	2.57E-03	3.77E-05	2.29E-03	3.90E-05	3.15E-03	6.74E-05
1900	*a*	9.97E-03	1.65E-03	1.05E-02	2.11E-03	8.90E-03	1.84E-03
	c	1.16 E+00	1.69E-01	1.14 E+00	2.26E-01	1.11 E+00	1.82E-01
	d	8.71 E+01	3.66E-01	9.43 E+01	5.25E-01	8.01 E+01	3.65E-01
	f	3.13E-03	5.96E-05	2.70E-03	6.48E-05	3.65E-03	7.92E-05
1920	*a*	8.16E-03	9.88E-04	8.44E-03	1.45E-03	8.32E-03	9.93E-04
	c	1.40 E+00	1.22E-01	1.41 E+00	1.87E-01	1.48 E+00	1.18E-01
	d	8.32 E+01	3.29E-01	8.99 E+01	5.40E-01	7.73 E+01	3.01E-01
	f	3.85E-03	7.11E-05	3.31E-03	8.85E-05	4.51E-03	8.69E-05
1940	*a*	8.95E-03	1.11E-03	8.78E-03	1.44E-03	8.95E-03	1.50E-03
	c	1.59 E+00	1.54E-01	1.52 E+00	2.05E-01	1.60 E+00	2.04E-01
	d	8.84 E+01	5.33E-01	9.28 E+01	7.39E-01	8.60 E+01	6.86E-01
	f	3.45E-03	8.79E-05	3.12E-03	1.01E-04	3.64E-03	1.25E-04
1960	*a*	8.59E-03	1.34E-03	6.01E-03	6.12E-04	8.22E-03	8.74E-04
	c	3.32 E+00	2.45E-01	4.03 E+00	1.02E-01	2.60 E+00	1.65E-01
	d	7.55 E+01	1.29 E+00	6.86 E+01	6.02E-01	8.04 E+01	8.29E-01
	f	6.94E-03	6.16E-04	1.02E-02	5.48E-04	5.60E-03	2.79E-04
1980	*a*	1.57E-02	9.55E-04	1.57E-02	9.55E-04		
	c	4.00 E+00	2.42E-01	4.00 E+00	2.42E-01		
	d	1.11 E+02	2.31 E+00	1.11 E+02	2.31 E+00		
	f	2.51E-03	1.70E-04	2.51E-03	1.70E-04		

SE, standard error; *a,c,d,f*, Tanaka growth coefficients.

Table A.5
Long Island 20-y cohort Tanaka growth models.

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1700	*a*	9.24E-02	8.29E-02			9.24E-02	8.29E-02
	c	0.00 E+00	2.47 E+00			0.00 E+00	2.47 E+00
	d	7.59 E+01	9.96E-01			7.59 E+01	9.96E-01
	f	2.27E-03	1.67E-04			2.27E-03	1.67E-04
1740	*a*	1.06E-01	4.00E-02	1.42E-01	4.60E-02	1.00E-01	7.54E-02

(*continued on next page*)

Table A.5 (*continued*)

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
	c	0.00 E+00	1.28 E+00	0.00 E+00	1.46 E+00	0.00 E+00	2.23 E+00
	d	8.31 E+01	6.50E-01	8.81 E+01	7.65E-01	7.57 E+01	9.89E-01
	f	1.98E-03	7.71E-05	1.73E-03	7.01E-05	2.30E-03	1.61E-04
1760	*a*	1.37E-01	4.68E-02	1.51E-01	4.89E-02	7.24E-02	4.23E-02
	c	0.00 E+00	1.58 E+00	0.00 E+00	1.64 E+00	0.00 E+00	1.32 E+00
	d	8.88 E+01	9.19E-01	9.07 E+01	9.50E-01	7.01 E+01	6.27E-01
	f	1.64E-03	7.37E-05	1.58E-03	7.17E-05	2.55E-03	1.20E-04
1780	*a*	1.31E-01	2.87E-02	1.34E-01	3.14E-02	1.21E-01	4.47E-02
	c	0.00 E+00	9.42E-01	0.00 E+00	1.05 E+00	0.00 E+00	1.44 E+00
	d	8.42 E+01	5.56E-01	8.74 E+01	6.37E-01	8.01 E+01	8.23E-01
	f	1.82E-03	5.28E-05	1.74E-03	5.56E-05	1.95E-03	8.92E-05
1800	*a*	1.09E-01	1.91E-02	1.70E-01	4.16E-02	9.20E-02	1.99E-02
	c	0.00 E+00	6.52E-01	0.00 E+00	1.44 E+00	0.00 E+00	6.71E-01
	d	8.45 E+01	4.20E-01	9.40 E+01	9.73E-01	8.07 E+01	4.19E-01
	f	1.95E-03	4.34E-05	1.53E-03	6.46E-05	2.17E-03	5.28E-05
1820	*a*	5.72E-02	1.17E-02	7.95E-02	1.91E-02	7.01E-02	1.95E-02
	c	0.00 E+00	4.97E-01	0.00 E+00	7.57E-01	0.00 E+00	7.25E-01
	d	8.80 E+01	4.13E-01	9.17 E+01	6.00E-01	8.30 E+01	5.23E-01
	f	2.02E-03	4.18E-05	1.89E-03	5.50E-05	2.23E-03	6.56E-05
1840	*a*	2.10E-02	6.64E-03	3.08E-02	1.10E-02	1.15E-02	6.54E-03
	c	0.00 E+00	3.56E-01	0.00 E+00	5.70E-01	0.00 E+00	3.79E-01
	d	8.65 E+01	3.74E-01	9.13 E+01	5.98E-01	8.13 E+01	4.08E-01
	f	2.42E-03	4.86E-05	2.13E-03	6.17E-05	2.80E-03	6.84E-05
1860	*a*	1.33E-02	5.11E-03	1.59E-02	6.74E-03	1.05E-02	5.58E-03
	c	0.00 E+00	3.21E-01	0.00 E+00	4.33E-01	0.00 E+00	3.38E-01
	d	8.83 E+01	4.14E-01	9.41 E+01	5.84E-01	8.11 E+01	4.08E-01
	f	2.43E-03	5.08E-05	2.18E-03	5.86E-05	2.81E-03	6.56E-05
1880	*a*	1.09E-02	3.89E-03	1.09E-02	4.84E-03	1.02E-02	5.20E-03
	c	0.00 E+00	2.73E-01	0.00 E+00	3.54E-01	0.00 E+00	3.53E-01
	d	9.04 E+01	4.33E-01	9.43 E+01	5.86E-01	8.62 E+01	5.37E-01
	f	2.36E-03	4.69E-05	2.22E-03	5.65E-05	2.53E-03	6.65E-05
1900	*a*	1.07E-02	2.06E-03	4.80E-03	3.17E-03	1.84E-02	2.25E-03
	c	6.99E-01	1.85E-01	0.00 E+00	2.81E-01	1.73 E+00	2.07E-01
	d	8.94 E+01	3.84E-01	9.34 E+01	5.94E-01	8.44 E+01	4.16E-01
	f	2.62E-03	4.59E-05	2.36E-03	5.91E-05	3.05E-03	6.55E-05
1920	*a*	1.78E-02	1.09E-03	1.67E-02	1.25E-03	1.95E-02	1.74E-03
	c	2.38 E+00	1.21E-01	2.32 E+00	1.46E-01	2.51 E+00	1.83E-01
	d	8.35 E+01	3.07E-01	8.65 E+01	3.86E-01	7.97 E+01	4.39E-01
	f	3.62E-03	6.01E-05	3.41E-03	6.75E-05	3.95E-03	1.01E-04
1940	*a*	1.17E-02	6.89E-04	1.21E-02	1.04E-03	1.16E-02	8.07E-04
	c	2.09 E+00	9.13E-02	2.04 E+00	1.37E-01	2.26 E+00	1.08E-01
	d	7.95 E+01	2.97E-01	8.39 E+01	4.52E-01	7.52 E+01	3.48E-01
	f	4.29E-03	7.19E-05	3.84E-03	9.01E-05	4.92E-03	1.07E-04
1960	*a*	2.08E-02	1.89E-03	1.72E-02	2.36E-03	2.35E-02	2.34E-03
	c	2.67 E+00	2.46E-01	2.40 E+00	3.39E-01	3.00 E+00	2.91E-01
	d	8.29 E+01	1.01 E+00	9.03 E+01	1.50 E+00	7.80 E+01	1.14 E+00
	f	3.58E-03	1.63E-04	3.06E-03	1.84E-04	4.12E-03	2.35E-04
1980	*a*	1.49E-02	8.98E-04	1.37E-02	1.23E-03	1.58E-02	1.17E-03
	c	4.07 E+00	1.52E-01	3.68 E+00	2.41E-01	4.23 E+00	1.87E-01
	d	8.22 E+01	1.23 E+00	8.76 E+01	2.12 E+00	8.03 E+01	1.46 E+00
	f	5.04E-03	2.95E-04	4.37E-03	3.92E-04	5.23E-03	3.76E-04
2000	*a*	4.42E-03	4.22E-04	4.42E-03	4.22E-04		
	c	2.98 E+00	1.41E-01	2.98 E+00	1.41E-01		
	d	1.02 E+02	3.09 E+00	1.02 E+02	3.09 E+00		
	f	3.86E-03	3.85E-04	3.86E-03	3.85E-04		

SE, standard error; *a,c,d,f*, Tanaka growth coefficients.

Table A.6
Georges Bank 20-y cohort von Bertalanffy growth models. The L_∞ parameter is not reliable for these growth datasets and should not be used to estimate maximum length. The k and t0 parameters may be useful for estimating growth at young age/small size.

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1740	L_∞	1.13 E+02	9.02E-01			1.13 E+02	9.02E-01
	k	9.18E-03	2.66E-04			9.18E-03	2.66E-04
	t_0	−3.14 E+01	1.40 E+00			−3.14 E+01	1.40 E+00
1780	L_∞	1.05 E+02	4.55E-01			1.05 E+02	4.55E-01
	k	1.46E-02	3.11E-04			1.46E-02	3.11E-04
	t_0	−2.30 E+01	8.74E-01			−2.30 E+01	8.74E-01
1800	L_∞	1.04 E+02	3.55E-01	1.08 E+02	5.15E-01	1.02 E+02	3.59E-01
	k	1.76E-02	3.19E-04	1.92E-02	5.25E-04	1.69E-02	3.03E-04

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Table A.6 (*continued*)

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
	t_0	−1.80 E+01	6.42E-01	−1.69 E+01	9.46E-01	−1.84 E+01	6.41E-01
1820	L_∞	1.04 E+02	2.06E-01	1.06 E+02	3.06E-01	1.02 E+02	2.66E-01
	k	1.92E-02	1.94E-04	1.92E-02	2.73E-04	1.92E-02	2.62E-04
	t_0	−1.52 E+01	3.16E-01	−1.38 E+01	4.29E-01	−1.65 E+01	4.40E-01
1840	L_∞	1.02 E+02	2.20E-01	1.05 E+02	2.29E-01	9.87 E+01	3.58E-01
	k	2.30E-02	2.69E-04	2.35E-02	2.77E-04	2.24E-02	4.37E-04
	t_0	−1.29 E+01	3.18E-01	−1.20 E+01	3.12E-01	−1.41 E+01	5.51E-01
1860	L_∞	9.95 E+01	2.02E-01	1.03 E+02	2.14E-01	9.43 E+01	3.40E-01
	k	2.63E-02	2.88E-04	2.62E-02	2.90E-04	2.67E-02	5.34E-04
	t_0	−1.11 E+01	2.60E-01	−1.07 E+01	2.59E-01	−1.18 E+01	4.85E-01
1880	L_∞	9.52 E+01	1.52E-01	9.85 E+01	1.87E-01	9.06 E+01	2.11E-01
	k	3.18E-02	2.85E-04	3.11E-02	3.21E-04	3.35E-02	4.59E-04
	t_0	−8.86 E+00	1.80E-01	−8.65 E+00	2.08E-01	−8.85 E+00	2.73E-01
1900	L_∞	8.95 E+01	1.62E-01	9.41 E+01	2.19E-01	8.50 E+01	1.87E-01
	k	4.17E-02	4.44E-04	4.11E-02	5.45E-04	4.19E-02	5.55E-04
	t_0	−5.77 E+00	1.66E-01	−5.51 E+00	2.04E-01	−6.19 E+00	2.11E-01
1920	L_∞	8.48 E+01	1.46E-01	8.92 E+01	2.19E-01	8.09 E+01	1.54E-01
	k	5.42E-02	5.72E-04	5.36E-02	7.90E-04	5.54E-02	6.69E-04
	t_0	−4.51 E+00	1.31E-01	−4.22 E+00	1.80E-01	−4.68 E+00	1.50E-01
1940	L_∞	8.50 E+01	2.03E-01	8.73 E+01	2.82E-01	8.36 E+01	2.68E-01
	k	6.50E-02	8.90E-04	6.48E-02	1.18E-03	6.49E-02	1.20E-03
	t_0	−2.75 E+00	1.31E-01	−2.59 E+00	1.71E-01	−2.87 E+00	1.79E-01
1960	L_∞	7.42 E+01	5.75E-01	7.01 E+01	5.54E-01	7.73 E+01	4.99E-01
	k	1.32E-01	6.26E-03	1.56E-01	7.48E-03	1.20E-01	4.87E-03
	t_0	1.38E-02	2.12E-01	6.13E-01	1.71E-01	−5.22E-01	2.12E-01
1980	L_∞	8.81 E+01	9.88E-01	8.81 E+01	9.88E-01		
	k	1.04E-01	4.12E-03	1.04E-01	4.12E-03		
	t_0	7.01E-01	1.41E-01	7.01E-01	1.41E-01		

SE, standard error, L_∞, asymptotic length; k, growth coefficient; t_0, time 0.

Table A.7
Long Island 20-y cohort von Bertalanffy growth models.

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1700	L_∞	1.20 E+02	1.77 E+00			1.20 E+02	1.77 E+00
	k	5.32E-03	2.27E-04			5.32E-03	2.27E-04
	t_0	−6.16 E+01	2.76 E+00			−6.16 E+01	2.76 E+00
1740	L_∞	1.17 E+02	9.08E-01	1.17 E+02	8.41E-01	1.27 E+02	2.21 E+00
	k	7.05E-03	1.67E-04	7.60E-03	1.72E-04	4.76E-03	2.05E-04
	t_0	−4.31 E+01	1.23 E+00	−3.85 E+01	1.14 E+00	−6.60 E+01	2.44 E+00
1760	L_∞	1.13 E+02	8.58E-01	1.16 E+02	8.98E-01	9.51 E+01	1.05 E+00
	k	8.68E-03	2.15E-04	8.36E-03	2.04E-04	1.01E-02	4.32E-04
	t_0	−3.03 E+01	1.11 E+00	−3.10 E+01	1.08 E+00	−2.97 E+01	2.04 E+00
1780	L_∞	1.11 E+02	6.03E-01	1.14 E+02	6.46E-01	1.07 E+02	9.52E-01
	k	8.63E-03	1.42E-04	8.56E-03	1.46E-04	8.72E-03	2.38E-04
	t_0	−3.06 E+01	6.83E-01	−3.06 E+01	7.03E-01	−3.06 E+01	1.13 E+00
1800	L_∞	1.06 E+02	3.87E-01	1.10 E+02	6.50E-01	1.05 E+02	4.46E-01
	k	1.06E-02	1.29E-04	1.10E-02	2.15E-04	1.03E-02	1.48E-04
	t_0	−2.65 E+01	4.68E-01	−2.23 E+01	7.04E-01	−2.88 E+01	5.67E-01
1820	L_∞	1.03E+02	3.13E-01	1.05 E+02	4.00E-01	1.01 E+02	4.46E-01
	k	1.37E-02	1.61E-04	1.41E-02	2.09E-04	1.31E-02	2.18E-04
	t_0	−2.16 E+01	4.07E-01	−2.04 E+01	5.05E-01	−2.34 E+01	5.94E-01
1840	L_∞	9.98 E+01	2.83E-01	1.03 E+02	3.98E-01	9.64 E+01	3.66E-01
	k	1.75E-02	2.19E-04	1.73E-02	2.88E-04	1.78E-02	3.10E-04
	t_0	−1.86 E+01	3.93E-01	−1.78 E+01	5.12E-01	−1.96 E+01	5.60E-01
1860	L_∞	9.85 E+01	2.81E-01	1.02 E+02	3.59E-01	9.42 E+01	3.49E-01
	k	2.05E-02	2.66E-04	2.09E-02	3.32E-04	1.97E-02	3.29E-04
	t_0	−1.53 E+01	3.52E-01	−1.44 E+01	4.22E-01	−1.68 E+01	4.71E-01
1880	L_∞	9.41 E+01	2.21E-01	9.65 E+01	2.88E-01	9.14 E+01	3.00E-01
	k	2.77E-02	3.15E-04	2.80E-02	4.08E-04	2.73E-02	4.31E-04
	t_0	−9.40 E+00	2.35E-01	−9.08 E+00	2.97E-01	−9.77 E+00	3.30E-01
1900	L_∞	8.98 E+01	1.71E-01	9.23 E+01	2.55E-01	8.68 E+01	2.06E-01
	k	3.74E-02	3.71E-04	3.58E-02	5.01E-04	3.97E-02	5.06E-04
	t_0	−5.70 E+00	1.56E-01	−6.33 E+00	2.28E-01	−4.93 E+00	1.92E-01
1920	L_∞	8.38 E+01	1.25E-01	8.59 E+01	1.58E-01	8.12 E+01	1.82E-01
	k	5.52E-02	4.72E-04	5.46E-02	5.73E-04	5.65E-02	7.33E-04
	t_0	−2.87 E+00	9.47E-02	−2.92 E+00	1.17E-01	−2.75 E+00	1.41E-01
1940	L_∞	7.86 E+01	1.17E-01	8.18 E+01	1.71E-01	7.56 E+01	1.43E-01
	k	7.13E-02	6.15E-04	6.79E-02	8.11E-04	7.64E-02	8.66E-04
	t_0	−2.11 E+00	7.48E-02	−2.29 E+00	1.07E-01	−1.81 E+00	9.28E-02

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Table A.7 (*continued*)

Cohort	Parameter	Population		Female		Male	
		Estimate	*SE*	Estimate	*SE*	Estimate	*SE*
1960	L_∞	7.48 E+01	2.87E-01	7.93 E+01	4.24E-01	7.20 E+01	3.35E-01
	k	8.39E-02	1.47E-03	8.10E-02	1.96E-03	8.72E-02	1.88E-03
	t_0	−4.06E-01	1.03E-01	−4.79E-01	1.47E-01	−3.05E-01	1.22E-01
1980	L_∞	7.27 E+01	3.44E-01	7.50 E+01	5.53E-01	7.17 E+01	4.18E-01
	k	1.35E-01	2.59E-03	1.37E-01	4.02E-03	1.33E-01	3.12E-03
	t_0	7.03E-01	5.98E-02	5.81E-01	9.10E-02	7.57E-01	7.41E-02
2000	L_∞	7.88 E+01	8.56E-01	7.88 E+01	8.56E-01		
	k	2.18E-01	8.30E-03	2.18E-01	8.30E-03		
	t_0	9.96E-01	6.05E-02	9.96E-01	6.05E-02		

SE, standard error, L_∞, asymptotic length; k, growth coefficient; t_0, time 0.

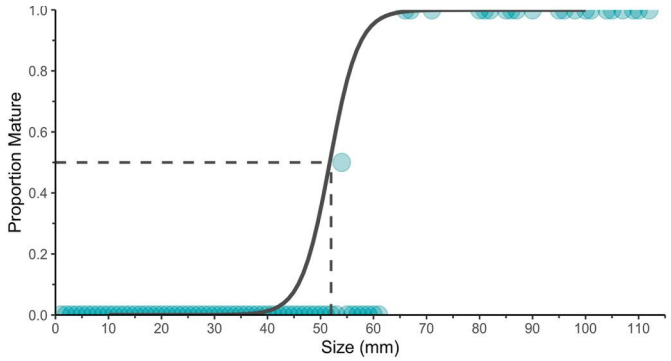

Figure A.1. Maturity by size. Combined proportion of *A. islandica* maturation data collected in 2017 from Georges Bank and Long Island (Mann, unpublished). Populations were 50% maturity at a mean size of 52 mm (dashed lines), with a 95% confidence interval of 50.4-53.0 mm using binomial logistic regression.

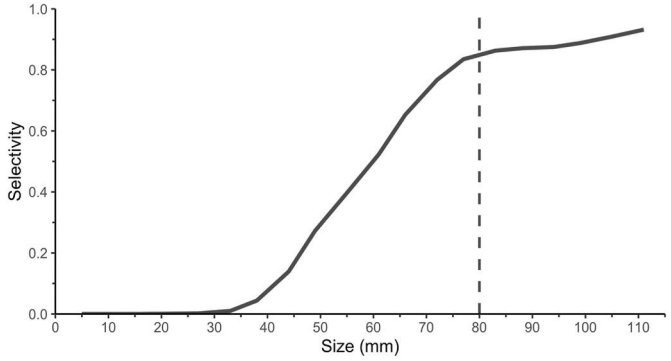

Figure A.2. Dredge selectivity by size. Dredge selectivity coefficient results from NEFSC (2017, Table 15) that demonstrated dredge selectivity as related to *A. islandica* shell length. Vertical dashed line indicated that at approximately 80-mm shell length, dredge selectivity stabilized.

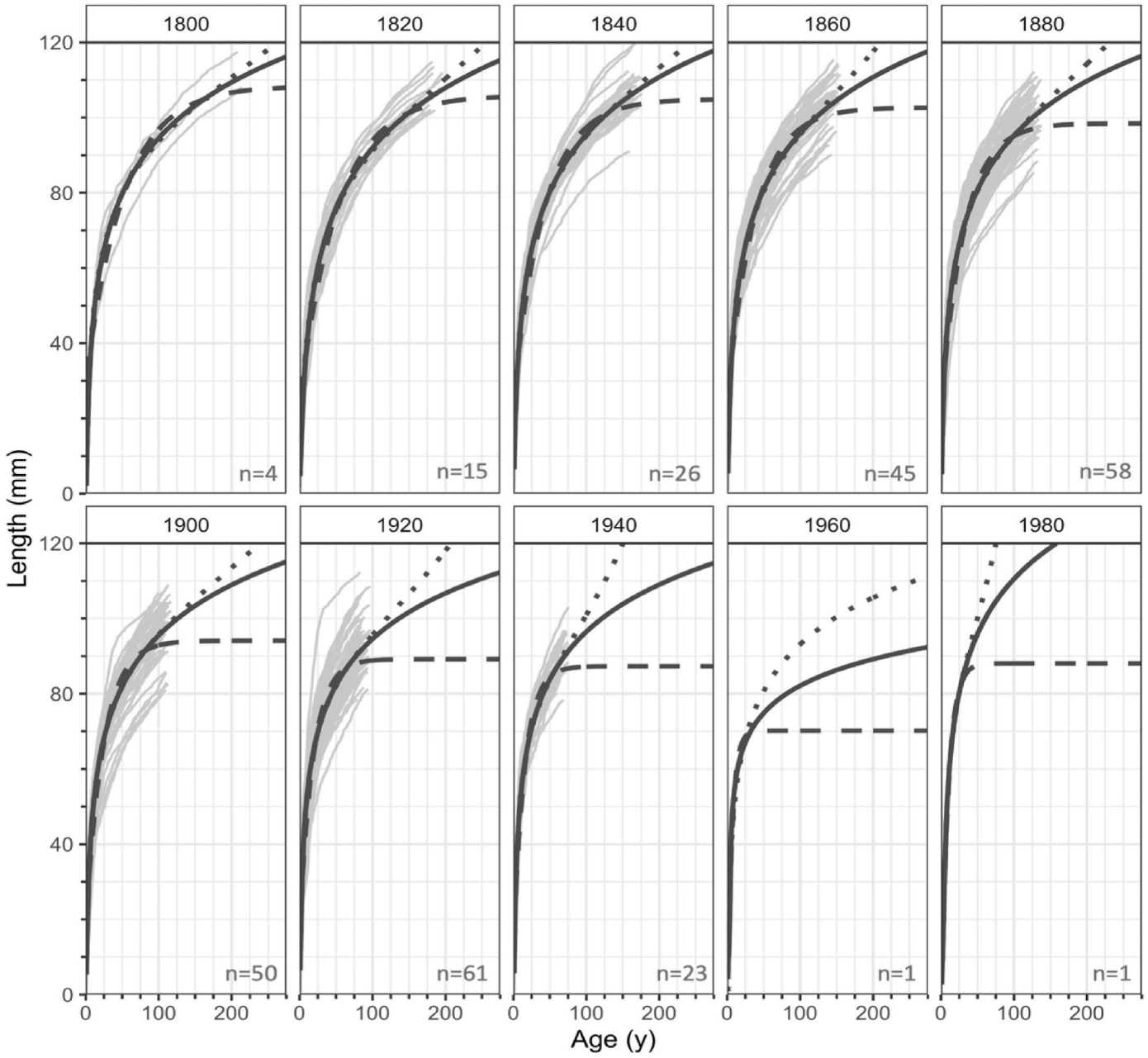

Figure A.3. Georges Bank female cohort models. Estimated Tanaka (solid line), modified Tanaka (dotted line), and von Bertalanffy (dashed line) models from individual age-length data (light grey) by 20-y birth-year cohorts.

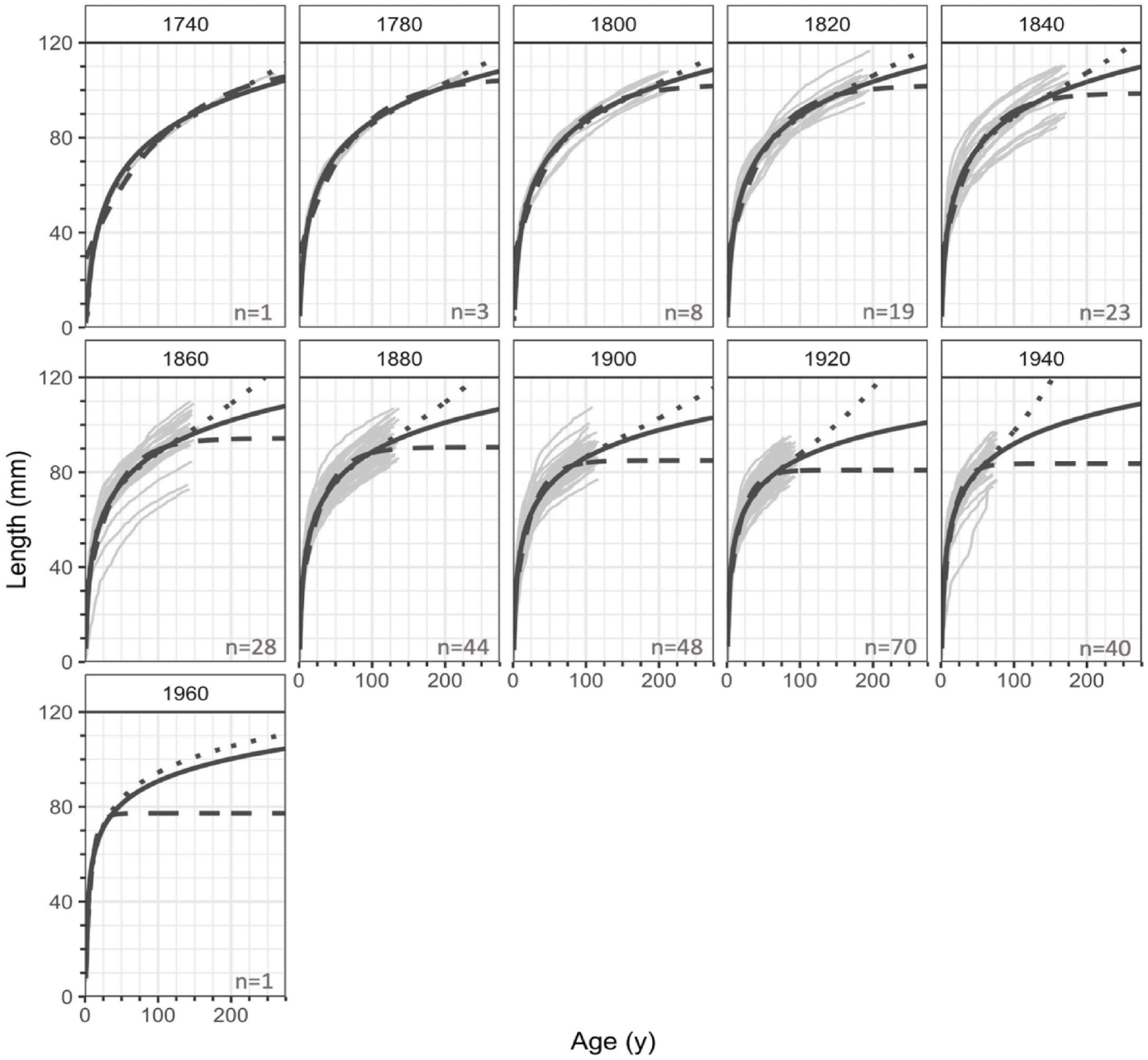

Figure A.4. Georges Bank male cohort models. Estimated Tanaka (solid line), modified Tanaka (dotted line), and von Bertalanffy (dashed line) models from individual age-length data (light grey) by 20-y birth-year cohorts.

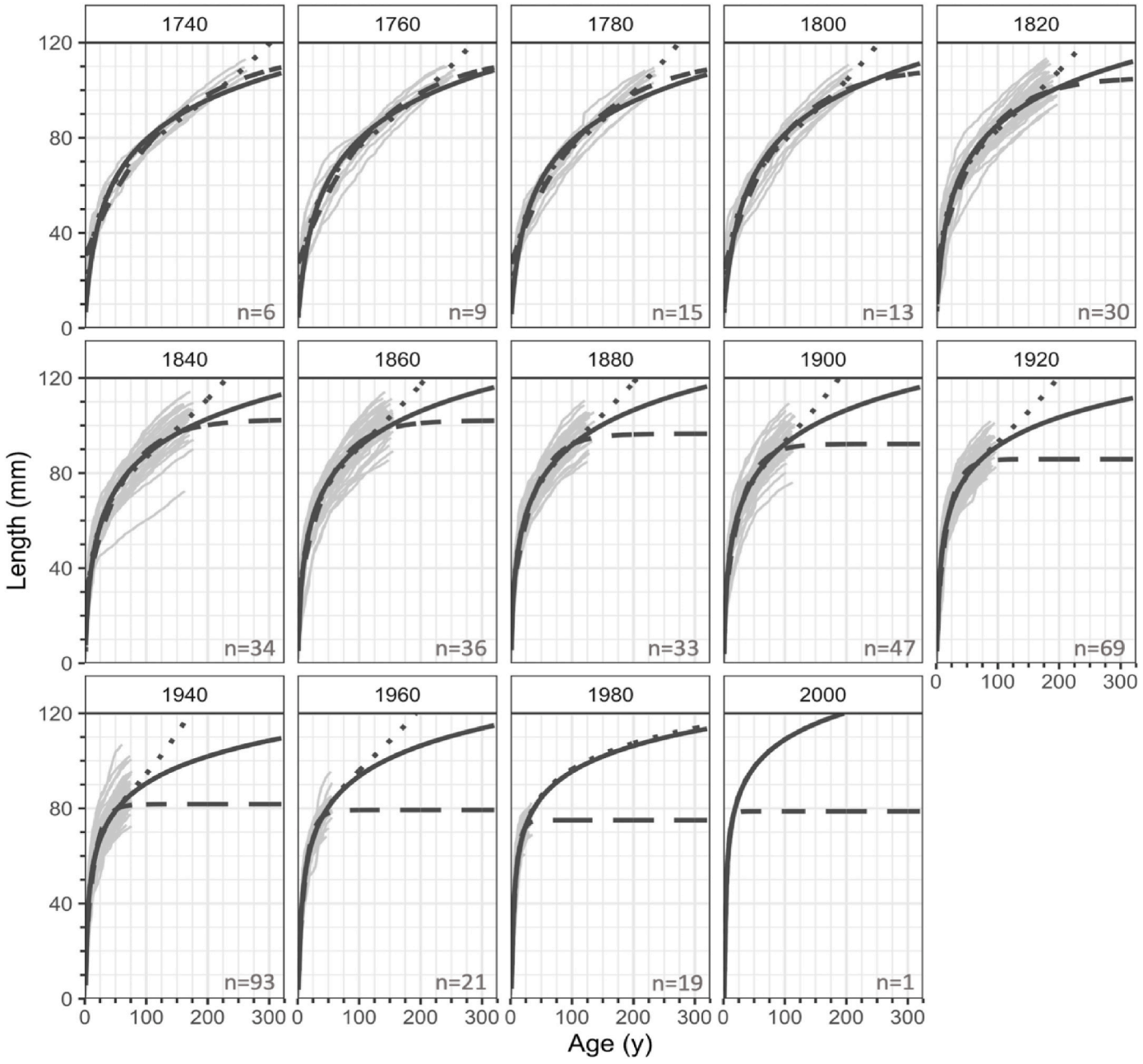

Figure A.5. Long Island female cohort models. Estimated Tanaka (solid line), modified Tanaka (dotted line), and von Bertalanffy (dashed line) models from individual age-length data (light grey) by 20-y birth-year cohorts.

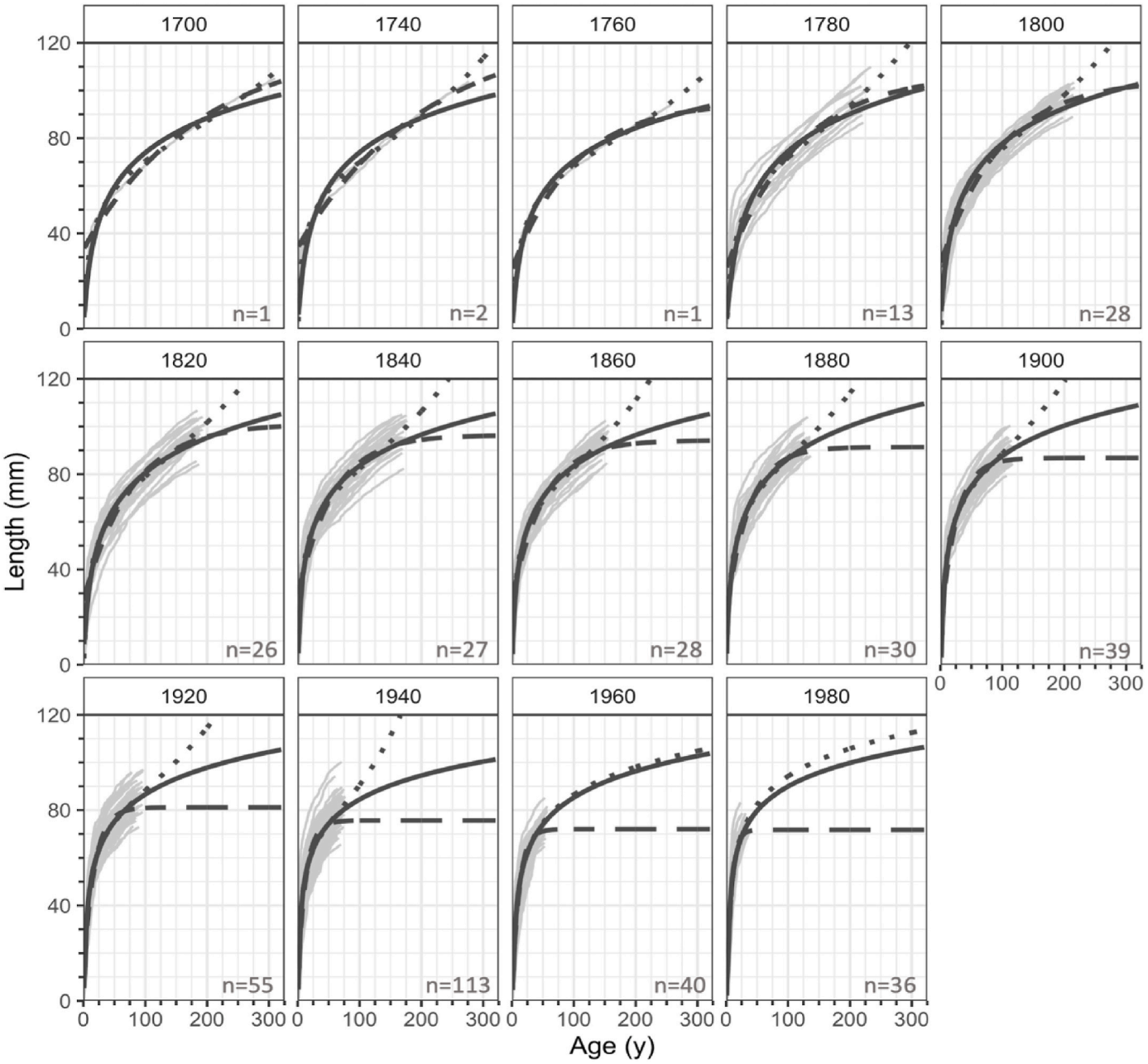

Figure A.6. Long Island male cohort models. Estimated Tanaka (solid line), modified Tanaka (dotted line), and von Bertalanffy (dashed line) models from individual age-length data (light grey) by 20-y birth-year cohorts.

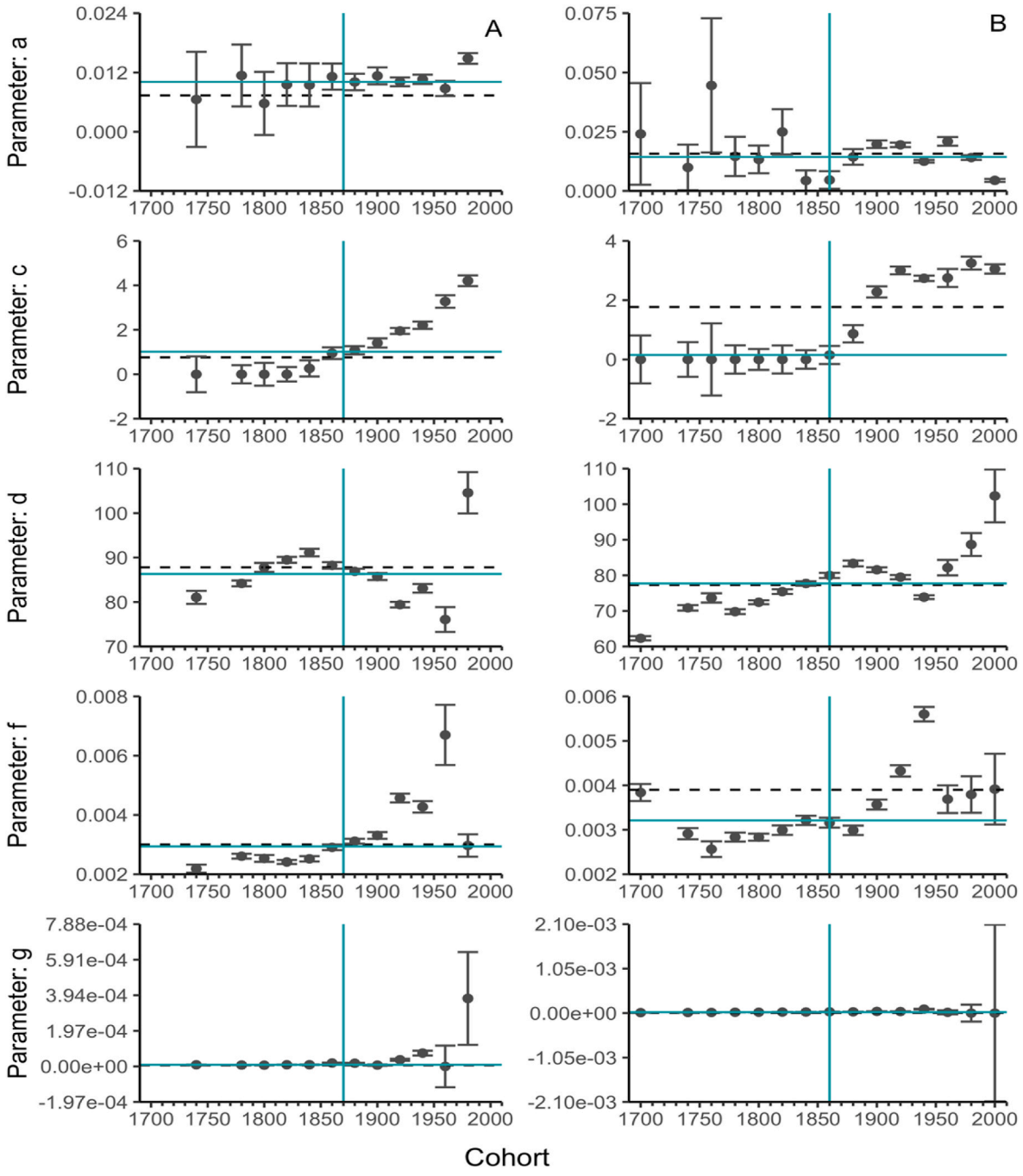

Figure A.7. Regional population modified Tanaka parameters. (A) Georges Bank (left), (B) Long Island (right) parameter values by 20-y birth-year cohorts. Quadrants delineated by solid vertical and horizontal lines mark the x and y median data values, horizontal dashed lines mark the respective site-specific population group parameter value (see Appendix Table A.1).

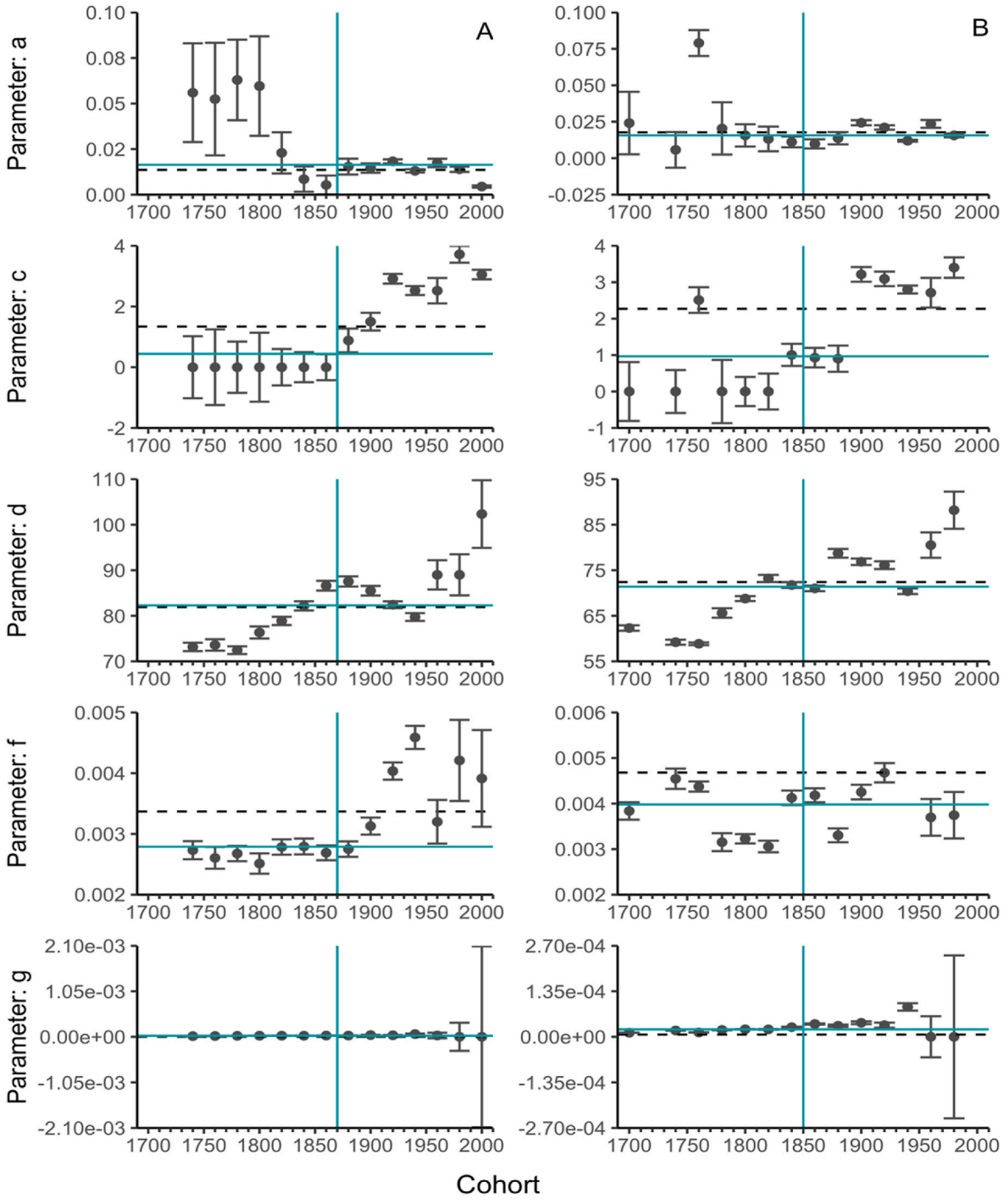

Figure A.8. Long Island modified Tanaka parameters by sex. (A) Female parameters, (B) male parameters. Green quadrants mark the x and y median data values, horizontal dashed line marks the population sex-specific group parameter value (see Table A.1).

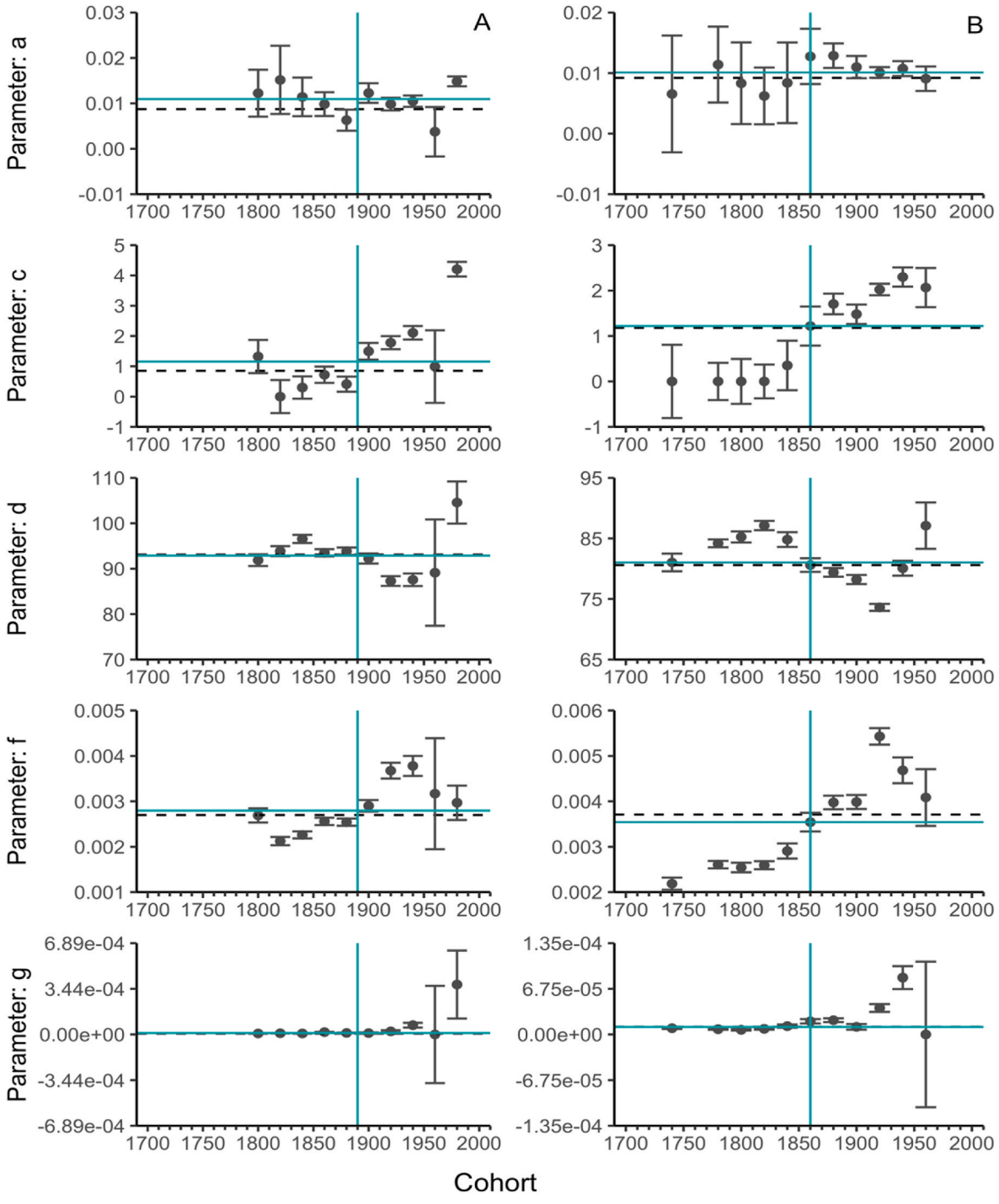

Figure A.9. Georges Bank modified Tanaka parameters by sex. (A) Female parameters, (B) male parameters. Green quadrants mark the x and y median data values, horizontal dashed line marks the population sex-specific group parameter value (see Table A.1).

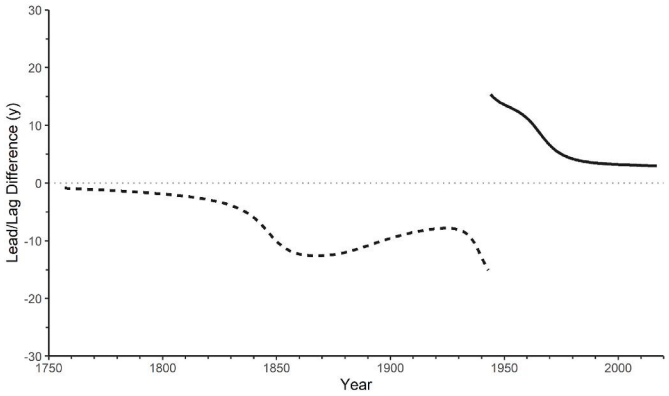

Figure A.10. Lead/lag of growth periodicities for the significant power 31-y period. Within-region comparison of Georges Bank to Long Island. Georges Bank "leads" Long Island in growth response when y values are positive (solid), and Long Island "leads" Georges Bank in growth response when y values are negative (dashed).

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