ISC/25/ALBWG-01/05

Update on the age and growth of North Pacific albacore tuna (*Thunnus alalunga*) from the central and eastern Pacific Ocean

Owyn Snodgrass¹, Kelsey James¹, Chiee-Young Chen², and Brad Erisman¹

¹Southwest Fisheries Science Center, NOAA NMFS, La Jolla, CA, USA

²Dept. Marine Environmental Engineering, National Kaohsiung University of Science and Technology, Kaohsiung, Taiwan

Email: owyn.snodgrass@noaa.gov; kelsey.james@noaa.gov; brad.erisman@noaa.gov



This working paper was submitted to the ISC Albacore Working Group Intercessional Workshop, 10-14 March 2025, held at the National Taiwan University, Institute of Oceanography in Taipei, Taiwan.

Abstract

Regional and sex-specific, length-at-age data are important for stock assessments for North Pacific albacore tuna. We generated updated length-at-age data and modeled sex-specific growth for albacore sampled from recreational and commercial fisheries in the eastern and central Pacific Ocean from 2013 through 2023. The von Bertalanffy growth model was selected to estimate growth parameters, which were then compared to previous parameter estimates from both sex-specific and non-sex-specific models. The sex-specific model produced by this study overlapped with the sex-specific model presented by James et al. (2020a) until age 6, with small differences in length-at-age between males and females observed among older age classes. Results of this study were consistent with previous studies showing that females may grow slower than males, and a sex-specific growth model fit the data best according to a bias-corrected Akaike Information Criteria (AICc). However, a combined sexes growth model was selected using Bayesian Information Criterion (BIC) indicating the difference in sex-specific growth was slight and inconclusive. The sex-specific growth models from this study were associated with higher L_{∞} values and correspondingly lower K values compared to previous studies. This pattern was likely driven by the inclusion of older, larger males and females in the current dataset. These data are presented for consideration and use in future management evaluations of the North Pacific albacore stock.

Introduction

The Pacific albacore tuna (*Thunnus alalunga*) is a highly migratory, pelagic fish that is targeted internationally by both commercial and recreational fisheries across the North Pacific. Along the U.S. West coast, the albacore fishery generates the highest ex-vessel revenue of any fishery on highly migratory species (\$36 million USD in 2022), ranking it third in economic importance among all fisheries in the region (McCluney et al. 2019, Frawley et al. 2021, PacFIN 2023). According to the most recent stock assessments, the North Pacific stock is listed as not overfished and not subject to overfishing (ISC 2023).

Recent stock assessments for North Pacific albacore have consistently identified age and growth information as a key source of uncertainty. In response, Xu et al. (2014) used the data from Chen et al. (2012) and Wells et al. (2013) to calculate an updated and improved sex-specific growth model, and the stock assessment began utilizing an integrated length-based age and sex-structured stock synthesis model in 2020 (ISC 2023). Whilst the inclusion of sex-specific length-at-age data improved confidence in model results, gaps in sex-specific data on age and growth from certain regions and length bins remain (James et al. 2020a). Specifically, sampling design and insufficient sample sizes have limited efforts to resolve regional and sex-specific variations in growth observed in North Pacific albacore (James et al. 2020b).

Building upon James et al. (2020a,b), this study aimed to produce additional sex-specific, lengthat-age data for North Pacific albacore sampled from U.S. fisheries in the eastern Pacific Ocean (EPO) and central Pacific Ocean (CPO). These data were used to update the growth model and compare it with growth models from previous studies to determine whether growth in North Pacific albacore is best explained by a sex-specific or combined sexes model.

Material and Methods

Data sources and sample collections

North Pacific albacore were collected from fisheries operating in the CPO and EPO from 2013 through 2023 (Figure 1). In the EPO, fish were collected annually from June through October from two sources in the U.S. West coast: the recreational fishery (hook and line) in Southern California and the commercial troll fishery in Oregon and Washington. From 2013 through 2020, we requested that 120 albacore be sampled annually across the length range available to the commercial troll fishery. We received samples for all years except 2016, and the number of samples received was dependent on the available catch. From 2021 through 2023, we requested 180 albacore across five specific length bins (0-59.9 cm, 60-69.9 cm, 70-79.9 cm, 80-89.9 cm, > 90 cm) for each year. We received samples for all years with most length bins represented.

In the CPO, fish were collected in 2022 and 2023 from September to January from the commercial deep-set longline fishery operating in the waters around Hawaii. We requested fish processors in Hawaii to collect albacore samples representative of the length range of fish landed by the deep-set longline fleet.

Each fish collected was measured to the nearest centimeter fork length (FL), and sagittal otoliths were extracted, dried, and stored for aging. Muscle tissue and fin clips were also taken from each fish to determine sex through genetic analyses (Craig et al. 2025).

Otolith Processing

Sagittal otoliths were excised from the heads of sampled fish, cleaned of organic tissue using deionized water, dried for 24 hours, and weighed to the nearest hundredth of a milligram. Otoliths were then embedded in clear epoxy resin following the methods described by Wells et al. (2013). Embedded otoliths were cut into 3-4 thin sections around the core using a Buehler IsoMet 1000 precision saw and a 4" diamond wafering blade (Proctor et al. 2021). Sections were cut at a low speed to a thickness of approximately 400 μ m to ensure the primordium and growth axis were retained (Wells et al. 2013). Otoliths were polished on each side with 30 μ m and 9 μ m grit paper to remove imperfections prior to being placed on a labeled microscope slide and covered in clear casting epoxy resin prior to aging (Proctor et al. 2021).

Aging

Albacore otoliths from the EPO were subsampled for aging. Sixty samples from each 10 cm length bin were selected accounting for temporal representation. All albacore otoliths from the CPO were selected for aging.

Sectioned otoliths were aged using a compound microscope at 4-63x magnification with transmitted light (Wells et al. 2013). Specifically, otoliths were aged by identifying opaque

(dark) and translucent (light) zones, reading from the core to the outer edge. The combination of consecutive opaque and translucent zones corresponded to the assignment of a single annuli. A confidence rating from 1 to 5 (1= low confidence; 5= high confidence) based on the clarity and distinction of annuli was assigned to each otolith (Wells et al, 2013).

All otoliths (n = 412) were aged independently two times by a single reader without reference to prior readings or knowledge of fish length, location of capture, or other collection data. Ages were determined to be final if the first and second age readings were in agreement. When the first and second age readings did not align, a third reading was conducted by the same reader with conditional awareness of the prior two readings to decide on a final age (Farley and Clear 2008). A random subset (n = 100) of sampled fish were then aged independently by a second reader to further evaluate aging precision and bias (see below).

Previous studies (Chen et al. 2012; Wells et al. 2013) calculated a decimal age based on collection date, birth date (May 1st), and whole age. For this study, fit of growth models to the decimal ages performed worse than the fit to the whole ages based on AICc and BIC (K. James unpublished data). To best compare this study and previous work (Chen et al. 2012, Wells et al. 2013, Xu et al. 2014, James et al. 2020a) we adjusted our ages to the peak collection month (September). All aged fish were assigned a collection date of September 1st, and a decimal age was calculated (i.e., 0.337 added to each age). This adjustment did not change the L^{∞} and K parameters of the von Bertlanffy growth model, but it did change the t_0 .

Aging Precision and Bias

Within and among reader precision was assessed using percent agreement, average percent error (APE; Beamish and Fournier 1981), and average coefficient of variation (ACV; Chang 1982). Precision and bias metrics were calculated in the R package 'FSA' (Ogle et al. 2023, R Core Team 2024). Within and among reader bias were evaluated with three tests of symmetry: McNemar's, Evans-Hoenig, and Bowker's (Hoenig et al. 1995; Evans and Hoenig 1998) using the 'FSA' package in R (Ogle et al. 2023, R Core Team 2024).

Growth Modelling

Age data from Reader 1 were used to model growth in North Pacific albacore sampled from the EPO and CPO (see Results). The von Bertalanffy, Gompertz, and Logistic growth models were each fit to the length-at-age data using the 'FSA' package in R (Ogle et al. 2023, R Core Team 2024). The best fitting model was used to examine whether sexes should be modeled together or separately. The bias-corrected Akaike's Information Criterion (AICc) and Bayesian Information Criterion (BIC) were used to evaluate model fit in R (R Core Team 2024) for all growth models (i.e., sex-specific and combined sexes) generated for this study. We compared mean length-at-ages between males and females at each age class with two-sample t-tests in R when the sample size had more than 3 observations and were normally distributed (R core Team 2024).

We compared the results of the growth models produced by this study with those from previous studies to evaluate potential differences and assess the degree to which the addition of larger, older fish impacted model selection and estimated growth in North Pacific albacore. The von

Bertalanffy growth model was used in all subsequent analyses and growth comparisons, as it was selected as the best fit for the full data set of all aged fish using both AICc and BIC (see Results). First, we compared the overall (combined sexes) growth curve from the full data set to the curve produced by Wells et al. (2013) since the aging methods, collection regions, and fish sizes were most similar. Second, we compared the sex-specific growth models (i.e., separate growth curves for males and females) and growth parameters from this study to those presented at the ISC Albacore Working Group in 2020 by James et al. (2020a). The data from James et al. (2020a) was a compilation (by Xu et al. 2014) of sex-specific length-at-age data from Chen et al. (2012) and Wells et al. (2013).

Results

Length and Age Distributions

Length distributions by region are shown in Figure 2. North Pacific albacore sampled from the EPO (n = 233) ranged from 48.6 cm FL to 102.0 cm FL with a mean length of 69.0 cm FL \pm 0.74 SE. Albacore sampled from the CPO (n = 179) ranged in length from 66.8 cm FL to 124.3 cm FL with a mean length of 100.5 cm FL \pm 0.82 SE. The mean length of albacore for the combined dataset (n = 412) was 82.6 cm FL \pm 0.95 SE.

Age distributions by region are shown in Figure 3. North Pacific albacore sampled from the EPO ranged in age from 1 to 10 years with a mean age of 2.53 years ± 0.09 SE. Conversely, fish sampled from the CPO ranged in age from 2 to 15 years with a mean age of 7.91 years ± 0.21 SE. The mean age of albacore for the combined data set was 4.86 years ± 0.17 .

Of the 412 aged albacore, 312 were sexed using genetics:109 females and 203 males (Figure 4). The estimated age of sexed fish ranged from 1 to 13 years for females (mean = 4.58 years ± 0.29 SE) and from 1 to 15 years for males (mean = 5.83 years ± 0.26 SE) (Figure 5).

Aging Precision and Bias

Precision of age estimates within and among readers is summarized in Table 1. Percent agreement within readers was high, with ACV and APE values generally below 5%. Percent agreement among readers was very high and correspondingly very low ACV and APE.

Comparison	n	РА	APE	ACV
Reader 1 x Reader 1	412	72.09	3.121	4.413
Reader 2 x Reader 2	100	65.00	4.094	5.79
Reader 1 x Reader 2	100	90.00	0.593	0.839

Table 1. Precision results within and among age readers. PA = percent agreement; APE = average percent error; ACV = average coefficient of variation.

There was no bias within or among readers, as the results of all three tests of symmetry showed no differences (Table 2). It is important to note here again that results for Reader 2 were only generated to estimate and assess precision and bias among readers, and all age data used for growth modeling were from Reader 1.

		McNe	mar]	Evans-Hoe	nig		Bowker'	S
Comparison	df	χ2	р	df	χ2	р	df	χ2	р
Reader 1 x Reader 1	1	0.22	0.641	3	0.66	0.882	17	24.11	0.116
Reader 2 x Reader 2	1	0.71	0.398	2	2.06	0.357	11	12.49	0.328
Reader 1 x Reader 2	1	0.40	0.527	1	0.40	0.527	3	3.33	0.343

Table 2. Tests of symmetry results. df = degrees of freedom, $\chi 2$ = chi-squared test statistic, and p = p-value.

Growth Modelling

For the combined data set using all aged albacore (n=412), a von Bertalanffy growth model fit the length-at-age data the best based on both AICc and BIC values (Supplemental Table 1). The von Bertalanffy model produced the following parameter estimates: $L_{\infty} = 123.5$, K = 0.172 year⁻¹, and $t_0 = -2.07$. These parameter estimates were nearly identical to those produced by Wells et al. (2013). When the length-at-age data and modeled growth curve of this study are plotted against those produced by Wells et al. (2013), the results are nearly identical, including a complete overlap of the curves and the 95% confidence intervals (Figure 6).

The von Bertalanffy model was used to determine whether a sex-specific or a non-sex-specific growth model best fit the length-at-age data generated by this study. A sex-specific model was favored using AICc, but BIC favored combining data for both sexes into a single model (Table 3). The sex-specific and combined sexes growth models overlapped (visually) completely until age 7, with small differences in length-at-age between males and females observed for older age classes (Figure 7). Pairwise comparisons of mean length-at-age between males and females with t-tests were possible for ages 1, 3-4, 6-9. Other age classes had fewer than 3 samples or the data were not normally distributed. Only ages 6, 8, and 9 had different mean length-at-age between sexes (Table 4) with males larger than females.

Table 3. Model fit for sexes combined and sexes separate from this study. K = number of parameters; AICc = bias-corrected Akaike's Information Criterion; BIC = Bayesian Information Criterion. AICc and BIC values are indicators of model fit.

Model	Κ	AICc	BIC
Sexes Combined	4	1721.43	1736.28

Sexes Separate	7	1715.91	1741.74

Table 4. Mean length-at-age, standard error (SE), and number (n) for females and males for each age class. Pairwise comparisons were significant (*) or not significant (ns); blanks indicate no pairwise test was performed due to low sample size (n < 3) or the data were not normally distributed.

	Females		Males				
Age	Mean length- at-age	SE	n	Mean length- at-age	SE	n	Pairwise comparisons
Age 1	56.0	0.555	15	55.1	0.390	22	ns
Age 2	64.1	0.607	21	64.7	0.536	26	
Age 3	72.4	1.279	15	73.1	0.948	29	ns
Age 4	84.5	1.684	11	81.2	0.677	16	ns
Age 5	92.7	0.837	11	94.1	0.551	10	
Age 6	93.9	0.353	7	95.3	0.400	18	*
Age 7	98.7	1.086	6	96.4	0.764	9	ns
Age 8	99.8	0.413	4	102.9	0.744	12	*
Age 9	102.9	0.921	15	107.3	0.769	18	*
Age 10	101	I	1	106.7	0.809	18	
Age 11	107.1	-	1	112.6	0.576	12	
Age 12	-	-	-	114.4	1.742	5	
Age 13	114.9	5.400	2	115.2	1.940	5	
Age 14	-	-	-	122.6	0.150	2	
Age 15	-	_	-	124.3	-	1	

The growth curves of the sex-specific models presented here strongly overlapped with the sexspecific models presented by James et al. (2020a), particularly for ages 2 through 6 (Figure 8). The current dataset contained both older and larger individuals of both sexes than the previous report, which resulted in correspondingly higher L_{∞} values and lower K values (Table 5). Notably, the 95% confidence intervals of both parameters did not overlap for males or females between this study and James et al. (2020a) (Table 5).

Table 5. Growth model parameters for sexes combined and sexes separate from this study and the sex-specific model presented at the ISC Albacore Working Group in 2020 (James et al. 2020a). L_{∞} , K, and t₀ are von Bertalanffy model parameters. 95% confidence intervals are in parentheses following the parameter estimates.

Model	L∞	К	to
Sexes Combined	123.5 (121.0 - 126.5)	0.172 (0.158 - 0.186)	-2.07 (-2.321.83)
Females	116.3 (111.7 - 122.1)	0.203 (0.168 - 0.240)	-1.75 (-2.301.33)
Males	126.6 (123.1 - 131.1)	0.159 (0.141 - 0.177)	-2.19 (-2.561.88)
James et al. 2020a Females	106.6 (103.7 - 109.7)	0.298 (0.262 - 0.338)	-0.76 (-1.070.49)
James et al. 2020a Males	119.1 (116.8 - 121.8)	0.208 (0.187 - 0.229)	-1.45 (-1.791.15)

Discussion

We engaged in a coordinated effort to collect albacore from fisheries operating out of Hawaii, Oregon, and Washington to assist in efforts to generate more robust growth models with adequate representation of samples across all age classes for both male and female albacore in the North Pacific. Based on analyses for fleet-specific collection from James et al. (2020b) we collected an adequate sample size of fish from the EPO. For the CPO, effort to increase representative samples was identified by James et al. (2020b) as a significant priority and regional data gap. Consequently, we aged all samples collected from the CPO, resulting in ~60 aged fish per length bin, except for fish larger than 110 cm FL that were rare (Figure 1).

Age and growth of albacore was identified as a continued data gap by the ISC in 2011, with sexspecific growth highlighted as a key uncertainty in 2014. Similar to the results generated from previous reports and studies of somatic growth in North Pacific albacore (e.g., Wells et al. 2013, James et al. 2020a), the von Bertalanffy growth model continued to have the best goodness of fit. Moreover, the parameter estimates for the growth model that used all aged fish (i.e., both sexed and unsexed fish) were nearly identical to those produced by Wells et al. (2013). Assuming both studies contained sample sizes and distributions representative of the stock, this result would suggest growth patterns in North Pacific albacore have remained stable in the EPO and CPO over the last 10 years. Previous studies concluded that growth in North Pacific albacore differed by sex, with females thought to grow slower than males (Williams et al. 2012, Chen et al. 2012, Wells et al. 2013, Xu et al. 2014). Wells et al. (2013) explored sex-specific growth rates of albacore from the CPO and EPO, but the results were somewhat biased due to the small sample size of females in the data set. The data set in this current study contains samples of larger and older individuals for both sexes compared to Chen et al. (2012) and Wells et al. (2013), although Wells et al. (2013) did have one age-15 fish of unknown sex. In comparison to previous studies, the larger sample size and broader sample distribution with respect to both age and length present in this current study resulted in a higher L_{∞} value and a lower K value for both sexes and less pronounced differences in the modeled growth patterns of males and females.

The use of AICc and BIC for model selection produced contradictory results, such that the former supported a sex-specific growth curve and the latter supported a single growth curve. The two criteria hold different assumptions. AICc will select the best approximating model while there is no 'true model'. Conversely, BIC will select the 'true model' assuming the 'true model' is among the models provided (Burnham and Anderson 2002, Bolser et al. 2018). BIC assumes that the number of parameters within the 'true model' is low and therefore penalizes models with more parameters than AICc (Burnham and Anderson 2002, Bolser et al. 2018). In this instance, taking into account the continued efforts to obtain large, sex-specific samples, it seems unreasonable to assume that the 'true model' is among the models tested. Following this rationale, we recommend the growth model selected by AICc, which in this case would be sex-specific. However, as we have shown, whether growth in North Pacific albacore is best described by sex-specific growth remains uncertain.

Continued effort to collect and produce sex-specific length-at-age data for fish over 110 cm FL from the CPO is an ongoing priority. Results presented here provide an important update on length-at-age data for albacore in the CPO, and EPO, and support the findings of James et al. (2020a) that the current model from Xu et al. (2014) used in stock assessments of North Pacific albacore remains as the best approach. However, combining and modeling the dataset presented here with updated sex-specific length-at-age datasets from additional regions could better inform stock assessment scientists on the best path forward.

References

- Bolser DG, Grüss A, Lopez MA, Reed EM, Mascareñas-Osorio I, Erisman BE. 2018. The influence of sample distribution on growth model output for a highly-exploited marine fish, the Gulf Corvina (*Cynoscion othonopterus*) PeerJ 6:e5582.
- Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer. 488 p.
- Chen KS, Shimose T, Tanabe T, Chen CY, Hsu CC. 2012. Age and growth of albacore *Thunnus alalunga* in the North Pacific Ocean. Journal of Fish Biology 80:2328-2344.

- Craig MT, Andrew M, Tsuda Y, Chen CY, O'Malley J, Hyde JR. 2025. Estimating sex ratio in North Pacific Albacore (*Thunnus alalunga*) Using Genetic Methods. Work. Pap. Submitted to ISC Albacore Work. Gr. Taipei, Taiwan.
- Evans GT, Hoenig JM. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. Biometrics 54:620-629.
- Farley J, Clear N. 2008. Preliminary study of age, growth, and spawning activity of albacore in Australia's eastern tuna & billfish fishery. Scientific Committee Fourth Regular Session. 11-22 August 2008 Port Moresby, Papua New Guinea. WCPFC-SC4-2008/BI-IP-1.
- Frawley T, Muhling B, Brodie S, Fisher M, Tommasi D, Le Fol G, Hazen E, Stohs S, Finbeiner E, Jacox M. 2021. Changes to the structure and function of an albacore fishery reveal shifting social-ecological realities for Pacific Northwest fishermen. Fish and Fisheries 22:280–297.
- Hoenig J, Morgan MJ, Brown CA. 1995. Analysing differences between two age determination methods by tests of symmetry. Canadian Journal of Fisheries and Aquatic Sciences 52:364-368.

ISC. 2023 Annex 08. Stock assessment of albacore tuna in the North Pacific Ocean in 2023. Report of the Albacore Working Group. International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean. 12-17 July 2023 Kanazawa, Japan.

- James K, Dewar H, Teo S. 2020a. Review of current status of North Pacific albacore (*Thunnus alalunga*) age and growth. ISC/20/ALBWG-01/07 Work. Pap. Submitt. to the ISC Albacore Work. Gr. 6-15 April, 2020.
- James K, Dewar H, Teo S. 2020b. Ideas for future sampling programs of North Pacific albacore (*Thunnus alalunga*). ISC/20/ALBWG-01/09 Work. Pap. Submitt. to the ISC Albacore Work. Gr. 6-15 April, 2020.
- McCluney JK, Anderson CM, Anderson JL. 2019. The fishery performance indicators for global tuna fisheries. Nature Communications 10:1–9.
- Ogle DH, Doll JC, Wheeler AP, Dinno A. 2023. FSA: Simple Fisheries Stock Assessment Methods. R package version 0.9.5. <u>https://www.CRAN.R-project.org/package=FSA</u>.
- PacFIN. 2023. Pacific Fisheries Information Network, Highly Migratory Species SAFE Portal. Pacific Fisheries Management Council, West Coast Fisheries for Highly Migratory Species Landings and Revenue Data. <u>https://apex.psmfc.org/pacfin/f?p=501:2001</u>.

Proctor C, Robertson S, Jatmiko I, Clear N. 2021. An introductory manual to fish ageing using otoliths. CSIRO Oceans and Atmosphere, Fish Ageing Services, Research Institute for Tuna Fisheries, 41 pp. ISBN 978-0-646-83421-4.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <u>https://www.R-project.org</u>.

- Wells RJD, Kohin S, Teo SLH, Snodgrass OE, Uosaki K. 2013. Age and growth of North Pacific albacore (*Thunnus alalunga*): Implications for stock assessment. Fisheries Research 147:55-62.
- Williams AJ, Farley JH, Hoyle SD, Davies CR, Nicol SJ. 2012. Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. PLoS ONE 7(6):e39318.
- Xu Y, Sippel T, Teo SLH, Piner K, Chen KS, Wells RJ. 2014. A comparison study of North Pacific albacore (*Thunnus alalunga*) age and growth among various sources. ISC/14/ALBWG/04 Work. Pap. Submitt. to ISC Albacore Work. Gr. 14-28 April, 2014.



Figure 1. Sample count by year and collection region. CPO = central Pacific Ocean, EPO = eastern Pacific Ocean.



Figure 2. Sample count by fork length (FL) and collection region binned by 10 cm length increments. CPO = central Pacific Ocean, EPO = eastern Pacific Ocean.



Figure 3. Age frequency distributions by collection region. CPO = central Pacific Ocean, EPO = eastern Pacific Ocean.



Figure 4. Sample count by sex and fork length (FL) binned by 10 cm length increments separated by collection region. CPO = central Pacific Ocean, EPO = eastern Pacific Ocean.



Figure 5. Sample count by sex and age separated by collection region. CPO = central Pacific Ocean, EPO = eastern Pacific Ocean.



Figure 6. von Bertalanffy growth model of current dataset compared to Wells et al. (2013) with sexes combined.



Figure 7: von Bertalanffy growth models of current dataset comparing growth patterns when sexes are combined versus treated separately.



Figure 8. Sex-specific growth models of the current dataset (This Study) compared to the sex-specific growth models used in the North Pacific albacore stock assessment (James et al. 2020a).

Supplemental Table 1. Model fit for three growth models fit to sexes combined data (n=412). K = number of parameters; AICc = bias-corrected Akaike's Information Criterion; BIC = Bayesian Information Criterion. AICc and BIC values are indicators of model fit.

Model	К	AICc	BIC
von Bertalanffy	4	2252.99	2269.08
Gompertz	4	2256.46	2272.53
Logistic	4	2269.17	2285.25