ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/236964666

FR2013

Data · May 2013

CITATIONS
0

READS
160

5 authors, including:

R. J. David Wells
Texas A&M University - Galveston
59 PUBLICATIONS **609** CITATIONS

SEE PROFILE

Suzanne Kohin
NOAA Southwest Fisheries Science Center
53 PUBLICATIONS **1,095** CITATIONS

SEE PROFILE

Owyn E Snodgrass
Ocean Associates contractor for Southwest Fisheries Science Center
23 PUBLICATIONS **175** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project Common Oceans (ABNJ) Tuna Project View project

Project Pelagic Habitat Analysis Module View project

All content following this page was uploaded by R. J. David Wells on 01 June 2014.

The user has requested enhancement of the downloaded file.

Fisheries Research 147 (2013) 55–62

Contents lists available at SciVerse ScienceDirect

Fisheries Research

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

Age and growth of North Pacific albacore (*Thunnus alalunga*): Implications for stock assessment

R.J. David Wells[a,*], Suzanne Kohin[b], Steven L.H. Teo[b], Owyn E. Snodgrass[b], Koji Uosaki[c]

[a] *Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Road, Galveston, TX 77553, USA*
[b] *Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA*
[c] *National Research Institute of Far Seas Fisheries, 5-7-1 Orido, Shimizu-ku, Shizuoka 424-8633, Japan*

ARTICLE INFO

Article history:
Received 15 February 2013
Received in revised form 2 May 2013
Accepted 3 May 2013

Keywords:
Albacore
Thunnus alalunga
Otoliths
Fin spines
Length frequency

ABSTRACT

Accurate estimates of age and growth parameters are important for fisheries management because these values affect stock assessment models. Age and growth of North Pacific albacore (*Thunnus alalunga*) was assessed by examining annual growth increments in sagittal otoliths from 486 fish collected in different regions of the North Pacific Ocean. A wide size range of albacore (52–128 cm fork length, FL) was collected in an attempt to incorporate size-at-age information over juvenile, sub-adult, and adult life history stages. Overall, ages ranged from 1 to 15 years, with the majority of fish between 2 and 4 years of age. Growth models fit otolith-based size-at-age well, and Akaike's Information Criterion corrected for small sample size indicated that the specialized von Bertalanffy (VB) model provided the best fit. The estimated biological parameters of the specialized VB model were $L_\infty = 124.1$ cm FL, $K = 0.164$ year^{-1}, and $t_0 = -2.239$. Daily ages were also determined and verified correct age-1 assignments for fish 55–61 cm FL, with daily ages ranging from 378 to 505 days. In addition, dorsal fin spines and length frequency (LF) analysis were used to obtain estimates of size-at-age and corroborated results from otolith-based techniques. Modeling exercises resulted in nearly an order of magnitude difference in spawning stock biomass (SSB) when comparing growth parameters obtained from this study relative to previous stock assessment models of North Pacific albacore. Results suggest North Pacific albacore is a relatively long lived tuna species and provide updated biological parameters useful for future stock assessment models.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Albacore (*Thunnus alalunga*) is a highly migratory species (HMS) with a circumglobal distribution throughout the Atlantic, Indian, and Pacific Ocean basins. In the North Pacific, albacore spawn during the early spring and summer months throughout tropical and sub-tropical waters in the western and central Pacific Ocean (WCPO) (Yoshida, 1968; Ueyanagi, 1969; Sund et al., 1981). During the juvenile and sub-adult stages (ages 1–5), an unknown percentage of albacore migrate across the North Pacific Transition Zone (NPTZ), recruiting into the temperate waters of the eastern Pacific (Clemens, 1961; Ichinokawa et al., 2008). A suite of movement patterns have been documented throughout the eastern Pacific during juvenile and sub-adult stages (Laurs and Lynn, 1991; Childers et al., 2011), after which it is thought that sexually mature fish migrate west to tropical and sub-tropical spawning grounds in the WCPO. Given the highly migratory nature of North Pacific albacore, sustainability and management of this economically important species is a multi-national effort.

North Pacific albacore support one of the most lucrative and valuable tuna fisheries in the eastern Pacific along the U.S. West Coast and are currently managed as a single, well-mixed stock (ISC 2011). The most recent stock assessment estimated that spawning stock biomass (SSB) of albacore in the North Pacific has averaged around 300,000–500,000 metric tons (t) since 1966 (ISC 2011). Annual harvest of albacore in the North Pacific has averaged around 75,000 t since 1952, with Japanese fisheries historically harvesting the largest percentage at approximately 72% while U.S. fisheries annually harvest about 21% of the total catch (Childers and Betcher, 2010). Additional fisheries include Korean and Taiwanese longline, Mexican purse seine and pole-and-line, and Canadian troll fisheries. Current stock status of North Pacific albacore indicates the stock is currently not experiencing overfishing and is not overfished (ISC 2011). Information from age and growth studies is critical for fisheries management because stock assessment models rely on biological parameters including size-at-age and growth. In this study, in addition to generating

* Corresponding author. Tel.: +1 409 740 4989.
E-mail address: wellsr@tamug.edu (R.J.D. Wells).

0165-7836/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.fishres.2013.05.001

age and growth estimates, we demonstrate the difference in the stock assessment results for North Pacific albacore based on our estimates of growth parameters relative to results by Yabuta and Yukinawa (1963) used in previous stock assessments (ISC 2007).

A suite of studies examining age and growth of albacore have been conducted throughout their geographic range using a suite of techniques. These include direct aging of calcified hard parts such as scales, vertebrae, fin spines, and otoliths (Yabuta and Yukinawa, 1963; Labelle et al., 1993; Santiago and Arrizibalaga, 2005; Farley and Clear, 2008; Karakulak et al., 2011; Chen et al., 2012; Williams et al., 2012), tag-recapture estimates of growth (Laurs and Wetherall, 1981), and length frequency (LF) analysis from fishery catch data (Labelle et al., 1993; Santiago and Arrizibalaga, 2005). Using tetracycline tagging, Laurs et al. (1985) validated daily increment deposition in otoliths of North Pacific albacore up to three years of age. Otolith-based aging studies of *Thunnus* spp. have increased in recent years and are generally used for aging tuna species (Farley et al., 2006; Griffiths et al., 2009; Shimose et al., 2009), including albacore (Farley and Clear, 2008; Chen et al., 2012; Williams et al., 2012). Many tuna aging studies have not incorporated the full size range due to their highly migratory nature, and this is particularly true for North Pacific albacore, which spend portions of their life history stages throughout different regions of the ocean basin. Therefore, we used sagittal otoliths as the primary method to examine age and growth of North Pacific albacore collected throughout the western, central, and eastern Pacific Ocean in an attempt to incorporate size-at-age information over juvenile, sub-adult, and adult life history stages. In addition, we used both dorsal fin spines and length frequency (LF) analysis to integrate multiple approaches of determining size-at-age of albacore in the North Pacific Ocean.

2. Materials and methods

2.1. Sample collections and procedures

Albacore samples were collected in the western, central, and eastern Pacific Ocean to obtain a wide size range from recreational and commercial fishing operations. Regional boundaries were based on collections using the following coordinates: western Pacific (130°E to 150°E, 30°N to 15°N), central Pacific (165°E to 155°W, 30°N to 15°N), and eastern Pacific (145°W to 118°W, 50°N to 30°N) (Fig. 1). Samples from the western Pacific ($n = 49$) were obtained from Japanese longline vessels from 1997 to 2012, while central Pacific samples ($n = 142$) were obtained from both Japanese and U.S. commercial longline vessels from 1990 to 2012. Lastly, samples were collected from U.S. commercial (troll and pole-and-line) and recreational fisheries in the eastern Pacific (offshore U.S. west coast including Washington, Oregon, California, and northern Baja, Mexico) from 2007 to 2011. Fish were measured to the nearest cm straight fork length (FL) either directly on the boat or in the laboratory. Gonads were often missing after fish had been processed because samples were obtained opportunistically. Therefore, sex could be determined only for 26% of the total number of albacore used in this study.

Sagittal otoliths were extracted from albacore, cleaned, dried, and weighed to the nearest 0.0001 g. Left or right otoliths were haphazardly selected and mounted in epoxy resin (Spurr, 1969) and a Buehler isomet low-speed saw equipped with a diamond wafering blade was used to transversely cut embedded otoliths. A 400-μm transverse section was cut from each sample in order to expose the otolith core. Otolith sections were then attached to slides with Crystalbond thermoplastic cement, type A alumina powder (0.3 μm) was used on 30-μm and 9-μm grit paper to polish otoliths, and a polishing cloth was used for final preparations. Annual ages were

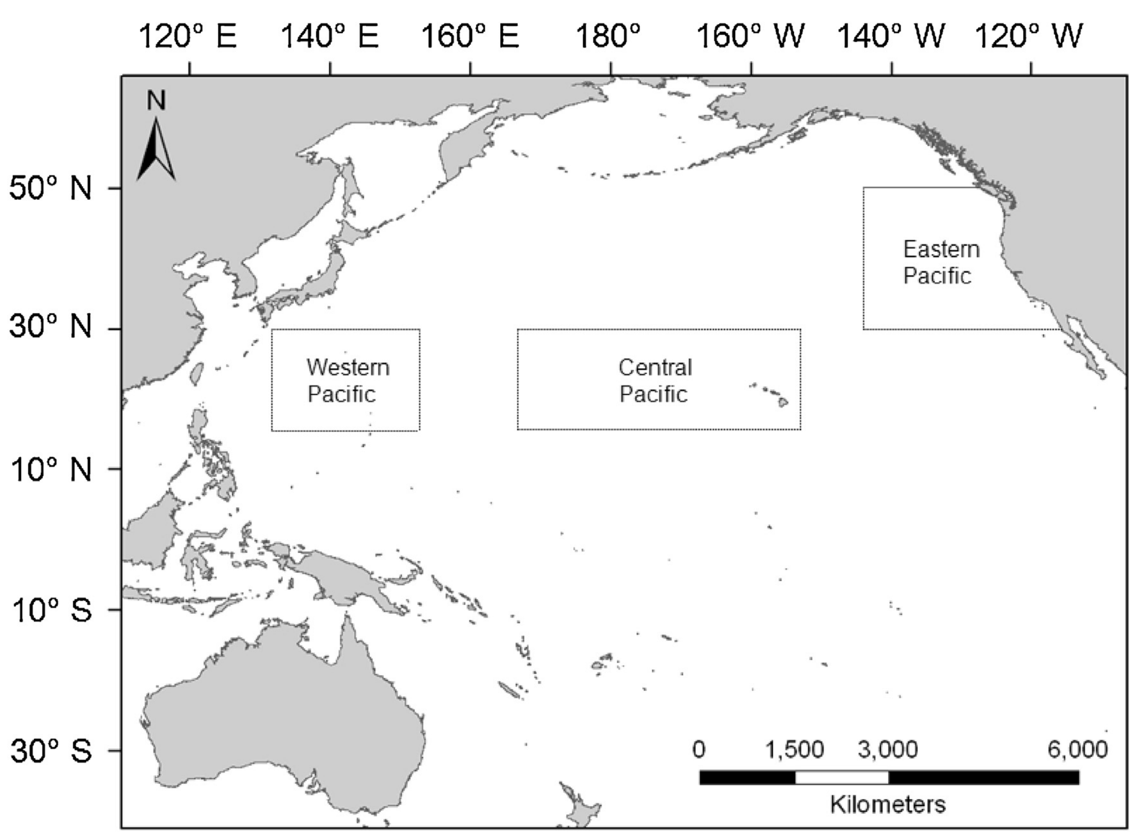

Fig. 1. Regional collection areas for North Pacific albacore.

determined by counting growth increments along the sulcus from the core to the outer margin using a light transmitted compound microscope at 4–63× magnification (Farley et al., in press). A single annual growth increment was defined as one translucent and one opaque zone and a confidence score from 1 (poor) to 5 (excellent) was assigned to each otolith. Age assignments were based on a May 1 birthdate, since this is the peak spawning time of North Pacific albacore (Otsu and Uchida, 1959a; Chen et al., 2010). An absolute decimal age was calculated as the number of annual rings plus the percentage of the year that had passed from May 1 to date of capture to avoid any bias in growth estimates due to collection dates (Hajjej et al., 2012). In addition to annual age estimates, otoliths of six albacore classified as age-1 were further processed and polished to read daily increments to verify correct annual age class assignment and obtain hatch-dates (birth dates). The first dorsal fin spine was also used to age a subset ($n = 265$) of albacore collected in the eastern Pacific. A 500 μm transverse section was cut above the condyle and attached to a slide with Crystalbond thermoplastic cement. Ages were determined using similar counting methodology as otoliths; however, double bands were sometimes present and counted as a single band if the distance between translucent double bands was less than the distance of the preceding and following translucent band (Megalofonou, 2000).

All otoliths were read two to three times by a single reader and a subset of otoliths (36%) were read by two independent readers without information such as size, collection date or location. For the single reader, if the first two independent readings matched then that age was deemed final; however, in some cases a third independent reading was required and was matched to a previous reading for a final age estimate. For subsamples with two readers, if the age readings matched from both readers, this age was used; however, if readings differed, a second or third (if needed) independent reading was taken and agreed upon for a final age estimate. In addition, two readers estimated ages of all albacore fin spines using the same protocol as the otolith subsamples. Differences in age estimates between readers (otoliths and fin spines) were evaluated by the average percent error (APE) (Beamish and Fournier, 1981) and coefficient of variation (CV) (Chang, 1982).

Albacore size data (cm FL) from the U.S. troll and longline fisheries were used for LF analysis. Albacore size data from 1994 to 2009 were partitioned into 2 cm size bins for LF analysis. The MULTIFAN model (Fournier et al., 1990) was used to analyze LF data and produce a von Bertalanffy (VB) growth model based on size distributions. This model simultaneously analyzes multiple LF distributions using a maximum likelihood method to estimate the number of age classes, proportions of fish at age, and VB growth parameters. Tests for statistical significance of the growth parameters were made using likelihood ratio tests. First, a systematic search was performed to estimate the number of age classes and the growth parameter, K, while keeping the standard deviations of length held constant across all age classes. Next, standard deviations of length were allowed to vary across age classes.

2.2. Growth models and analysis

Several growth models were used to fit length-at-age from otolith-based age estimates of albacore. These included the specialized VB growth model (von Bertalanffy, 1938):

$$L_t = L_\infty[1 - e^{-K(t-t_0)}]$$

where L_t is size (cm FL) at age t, L_∞ is the mean asymptotic length (cm FL), K is the Brody growth parameter (year^{-1}), and t_0 the theoretical age at zero length; the generalized VB growth model (Pauly, 1979):

$$L_t = L_\infty[1 - e^{-KD(t-t_0)}]^{1/D}$$

where D is the change in ratio of gill surface area to body weight with age and can be estimated from $D = 3(1 - d)$, where $d = 0.6742 + 0.03574$ ($\log W_{\max}$), and $W_{\max}$ is the maximum weight for the species (Griffiths et al., 2009; maximum weight for albacore is approximately 36.4 kg, thus $D = 0.81$); the Gompertz growth model (Gompertz, 1825):

$$L_t = L_\infty e^{(-(1/K)e^{-K(t-t_0)})}$$

and the logistic model (Ricker, 1975):

$$L_t = L_\infty[1 + e^{-K(t-t_0)}]^{-1}$$

Growth model parameters were estimated using non-linear least squares and the Marquardt's iterative algorithm with additive error structure. Growth model fit was compared using the Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Katsanevakis, 2006), with the smallest AIC_c value as the best fit model, and residuals were checked for homoscedasticity. To test the relative plausibility of each model, the difference in AIC_c values of the best fit model from others was calculated as Δ_i.

Sex ratio was examined for samples collected in the central and western Pacific using a Chi-squared test within each region. Sex-specific growth was compared using likelihood ratio tests using the methodology of Chen et al. (2012). A linear regression was used to examine the relationship between albacore age and otolith weight. Lastly, since the oldest aged fish estimated using otoliths likely underestimates the maximum age in a fished population, Fabens' (1965) method was used to estimate the life span of albacore based on 99% of L_∞: 99% $L_\infty = 5(\ln 2/K)$. Statistical analyses and growth models were performed with SAS version 9.2.

2.3. Assessment model comparison

To demonstrate the importance of these growth parameters for stock assessments, SSB estimates for North Pacific albacore were compared using growth parameters from two studies. First, we used growth estimates obtained from the most plausible model from this study. Second, we utilized estimates obtained by Yabuta and Yukinawa (1963) that were used in previous stock assessments (e.g., ISC 2007). We compared stock assessment outcomes with the two suites of growth parameters using the Stock Synthesis (v3.11b) modeling platform (Methot and Wetzel, 2013) that was used in 2011 by the Albacore Working Group (ALBWG) of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC) to assess the North Pacific albacore stock. The base case model of that assessment used conditional age-at-length data (which is included as part of the dataset in this study) and estimated growth within the model, which resulted in growth model parameters similar to ours. In this study, we used a slightly modified model structure to that used by the ALBWG for the 2011 assessment (ISC 2011). The modifications were: (1) elimination of the conditional age-at-length data and (2) use of fixed growth parameters instead of estimating growth within the model. No other changes were made to the assessment model. A jitter analysis was performed on each model to ensure that the SSB estimates were taken from the model at the global minima. Initial values for the parameters of each model were randomly jittered for 100 runs each and the run with the best negative log-likelihood was used to estimate the SSB for each model.

3. Results

A total of 486 albacore otoliths were examined for age and growth from fish ranging in size from 52 to 128 cm FL (Fig. 2) with estimated ages ranging from one to 15 years, respectively. Overall average fish size was 88.5 cm FL (±0.76 standard error, SE),

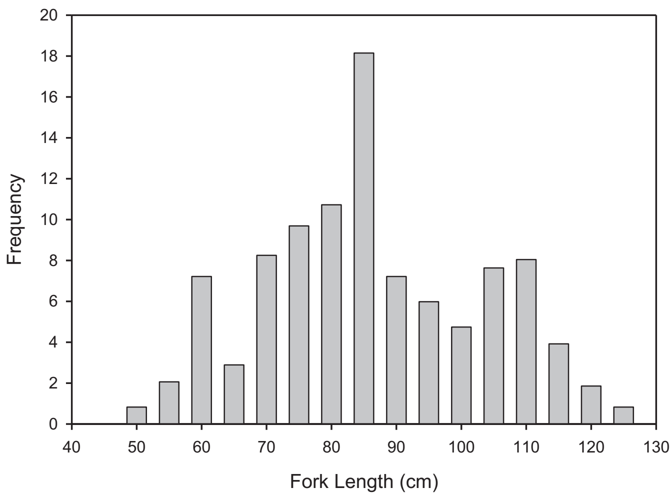

Fig. 2. Length frequency distribution of North Pacific albacore collected for age and growth. Histograms are binned by 5 cm length increments.

but size varied according to region. The largest albacore were collected in the central Pacific and averaged 108.3 cm FL (±0.74 SE, n = 142), followed by collections in the western Pacific that averaged 96.6 cm FL (±0.92 SE, n = 49), and those from the eastern Pacific averaged 77.6 cm FL (±0.58 SE, n = 295). Of the 26% of albacore for which sex was determined, 73% were males and 27% were females, with average sizes of 108.1 (±0.87 SE) and 97.8 cm FL (±1.23 SE), respectively. The remaining fish were either sexually immature or sex was not determined.

A positive relationship between estimated age and otolith weight was observed (r^2 = 0.846, P < 0.05) (Fig. 3), suggesting that albacore otoliths continue to increase in size with increasing age. Approximately half of the otoliths (53%) received a reading score of 3 (good), 14% scored 4 (very good), and 2% scored 5 (excellent). In addition, 25% were scored 2 (readable) and 6% were scored 1 (poor). Fig. 4 shows images of albacore otolith cross-sections under transmitted light with estimated ages of four and nine years (confidence scores of 4 out of 5). Otolith-based age comparisons from the two readers (36% of total samples) had an APE of 4.75 and CV of 6.72. Also, six fish with annual readings as age-1 were evaluated for daily ages, and these fish ranged in age from 378 to 505 days (55.5–61.5 cm FL). Subtracting the daily age from collection date provided an estimate of hatch-dates that ranged from May

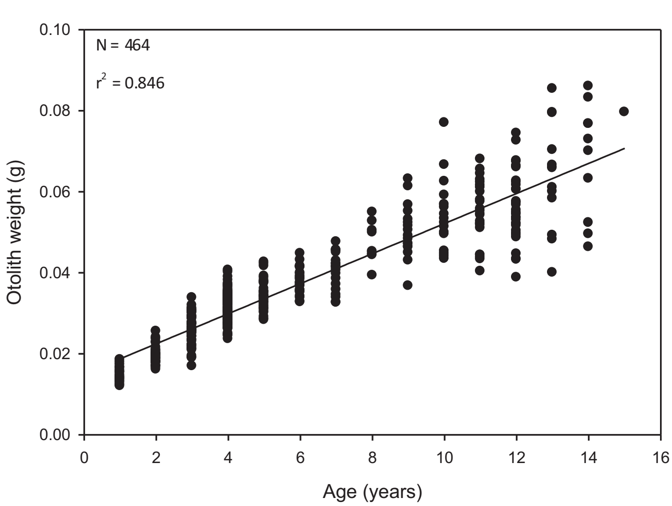

Fig. 3. Relationship between otolith weight (single otolith) and estimated age of North Pacific albacore.

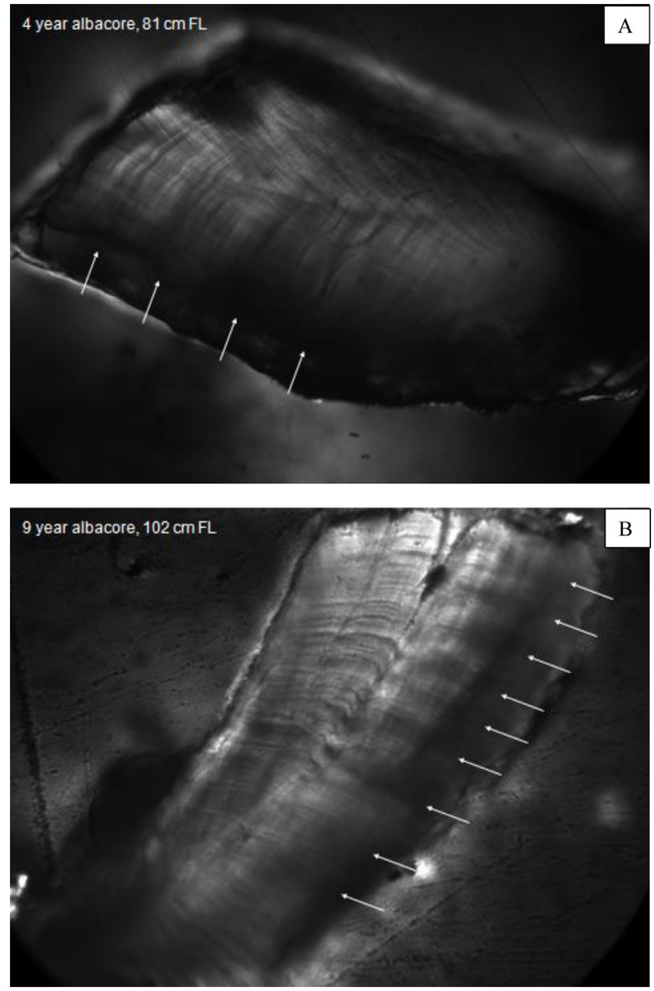

Fig. 4. Images of two North Pacific albacore sagittal otolith cross-sections estimated at (A) four years and (B) nine years of age.

to August. Lastly, 265 fin spines were aged from samples collected in the eastern Pacific. Estimated ages of the fin spines ranged from one to six years, which corroborated well with the otolith-based age estimates. Overall, 78.5% of the fin spine samples matched otolith-based age estimates, while 7.9% and 13.2% of the fin spine ages were one year above and below otolith ages, respectively, and only a single fin spine age estimate was two years below the otolith age estimate. For the two-reader fin spine age comparison, APE was 3.41 and CV was 4.83.

Otolith-based growth model fits obtained during this study were relatively similar to one another (Fig. 5 and Table 1). Growth model parameters ranged from 116.9 to 124.1 cm FL for L_∞, 0.164 to 0.296 year^{-1} for K, and 1.495 to −6.239 for t_0. All growth models resulted in similar fits; however, the specialized VB growth model had the lowest AIC$_c$ and was chosen as the best fit model with associated parameter estimates of L_∞ = 124.1 cm FL, K = 0.164 year^{-1}, and

Table 1
Growth model parameters and AIC$_c$ values of the five growth models for North Pacific albacore.

Model	L_∞ (cm FL)	K (year^{-1})	t_0 (year^{-1})	AIC$_c$	Δ_i
Specialized VB	124.1	0.164	−2.239	1.254	0
Generalized VB	124.1	0.203	−3.523	1.303	0.049
Gompertz	119.5	0.231	−6.239	1.272	0.018
Logistic	116.9	0.296	1.495	1.296	0.042
MULTIFAN VB	127.4	0.148			

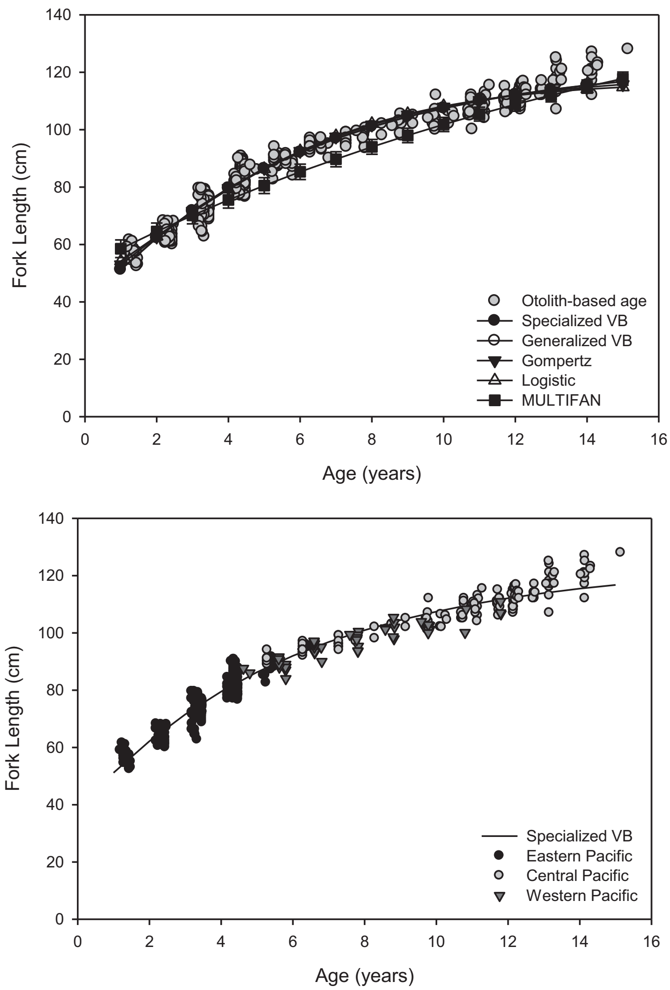

Fig. 5. Length-at-age of North Pacific albacore using otolith-based methods and associated growth model fits. Von Bertalanffy growth model fit from MULTIFAN length frequency analysis is also included. Second graph shows region of collection (eastern, central, western Pacific).

$t_0 = -2.239$. According to the specialized VB growth model, albacore reach approximately 51 cm FL by the end of their first year, and growth slows considerable therefore, with an estimated size of 62 cm FL by age-2. No sex-specific ratio difference was found from the expected ratio of 1:1 within central and western Pacific samples ($P > 0.05$) and no significant differences in growth parameters were found by sex ($P > 0.05$). Results of the MULTIFAN LF analysis provided growth parameter estimates of $L_\infty = 127.4$ cm FL and

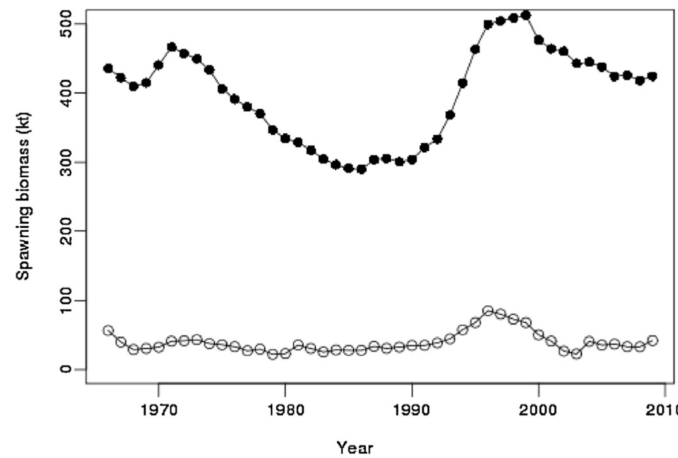

Fig. 6. Effect of different growth models on North Pacific albacore spawning stock biomass (SSB) estimates. Open circles represent the output when using the Yabuta and Yukinawa (1963) growth model and solid circles represent the output using the specialized VB growth model presented in this paper.

$K = 0.148$ year^{-1} (Table 1), which closely matched size-at-age of young (1–3 years) and old (>10 years) albacore, but fell slightly below otolith-based size-at-age from four to ten years (Fig. 5). Albacore longevity was estimated to approximately 21 years using the method of Fabens (1965).

Estimated SSB from the assessment model differed substantially depending upon growth model parameters used. The diagnostics of both models indicate that each converged and were at global minima: with gradients of $<10^{-5}$, positive definite Hessians, and jitter analysis failing to find model runs with improved likelihoods. The estimated SSB when using values from this study (~300,000–513,000 t) were approximately an order of magnitude larger than when the growth parameters from Yabuta and Yukinawa (1963) were used (~22,000–84,000 t) (Fig. 6).

4. Discussion

Results of this study provide updated biological parameters for North Pacific albacore growth within the range of values reported for albacore in other areas (Table 2). The range of previous estimates of L_∞ reported for North Pacific albacore has been reported from a low of 108.8 (Bell, 1962) to a high of 146.5 cm FL (Yabuta and Yukinawa, 1963), while South Pacific albacore range from 102.9 (Farley and Clear, 2008) to 121.0 cm FL (Labelle et al., 1993) (Table 2). L_∞ of 124.1 cm FL estimated in this study closely matches both North and South Pacific stocks. Similar patterns were found

Table 2
Growth model parameters from this study and other albacore studies in the North Pacific, South Pacific, and North Atlantic.

Location	Method	L_∞ (cm FL)	K (year^{-1})	t_0 (year)	Size range (cm FL)	Source
N. Pacific	Otoliths	124.1	0.164	−2.239	52–128	Current study
N. Pacific	Otoliths	114.0	0.253	−1.010	45–118	Chen et al. (2012) (males)
N. Pacific	Otoliths	103.5	0.340	−0.530	46–101	Chen et al. (2012) (females)
N. Pacific	Scales	146.5	0.149	−0.860	48–95	Yabuta and Yukinawa (1963)
N. Pacific	Scales	108.8	0.225	−2.273	51–94	Bell (1962)
N. Pacific	Scales	114.4	0.308	0.818	65–120	Nose et al. (1957)
N. Pacific	Tagging	125.0	0.199	na	47–92	Laurs and Wetherall (1981)
N. Pacific	Tagging	135.6	0.170	−1.870	54–77	Clemens (1961)
N. Pacific	Tagging	118.8	0.250	1.999	60–91	Otsu (1960)
S. Pacific	Otoliths	104.5	0.400	−0.490	43–116	Williams et al. (2012)
S. Pacific	Otoliths	102.9	0.321	−1.107	48–108	Farley and Clear (2008)
S. Pacific	Vertebrae	121.0	0.134	−1.922	44–110	Labelle et al., 1993
N. Atlantic	Spines	127.1	0.180	−1.620	40–119	Santiago and Arrizibalaga (2005)

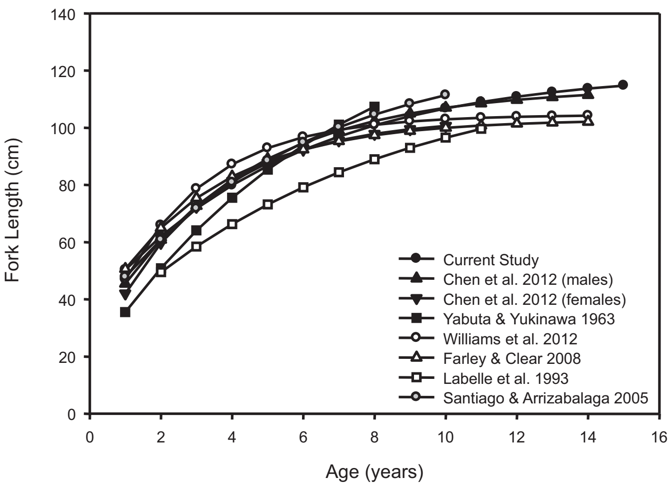

Fig. 7. Length-at-age estimates of the specialized VB growth model generated from this study and VB models from other albacore studies in the North Pacific (black), South Pacific (white), and North Atlantic (gray).

for K obtained here (0.164 year^{-1}), compared to prior estimates for North Pacific albacore ranging from 0.149 (Yabuta and Yukinawa, 1963) to 0.308 (Nose et al., 1957) and South Pacific albacore from 0.134 (Labelle et al., 1993) to 0.40 year^{-1} (Williams et al., 2012). Parameters obtained from an albacore age and growth study in the North Atlantic also had similar values of L_∞ = 127.1 cm FL and K = 0.18 year^{-1} (Santiago and Arrizibalaga, 2005). In addition, the specialized VB growth model was the best fit in this study, as well as for North Atlantic albacore (Santiago and Arrizibalaga, 2005) and other *Thunnus* species (bigeye tuna, Farley et al., 2006; yellowfin tuna, Lessa and Duarte-Neto, 2004).

Size-at-age estimates were similar to otolith-based aging results produced by other studies for both North and South Pacific albacore (Fig. 7) (Farley and Clear, 2008; Chen et al., 2012). Specifically, size-at-age of albacore here closely matched estimates from male albacore by Chen et al. (2012) throughout the entire size range examined and was similar to that of females up to age 8. Similar trends were seen when comparing South Pacific albacore, with closely matching size-at-age up to age 8, after which South Pacific albacore appear to have slower growth (Farley and Clear, 2008; Williams et al., 2012). North Pacific albacore appear to obtain larger sizes than South Pacific albacore beyond this age. Similar size at age-1 of albacore was previously reported with estimated sizes ranging from 48 to 56 cm FL and 62 to 67 cm FL by age-2 (Clemens, 1961; Bell, 1962; Santiago and Arrizibalaga, 2005). Our results also coincide with those of other studies examining mean size at age-1 of *Thunnus* species throughout the Pacific Ocean: bigeye tuna (*Thunnus obesus*, 56 cm) (Schaefer and Fuller, 2006), Pacific bluefin tuna (*Thunnus orientalis*, 50 cm) (Foreman, 1996; Shimose et al., 2009), longtail tuna (*Thunnus tonggol*, 45 cm) (Griffiths et al., 2009), and yellowfin tuna (*Thunnus albacares*, 52 cm) (Uchiyama and Struhsaker, 1981).

Age estimates were in general agreement using multiple methods. Fin spine and otolith-based age estimates compared very well with 78.5% of all samples having matching ages; however, our results are limited to albacore ranging from one to six years of age. Unfortunately, fin spines from larger fish were not available so comparisons were not made. Farley et al. (in press) found albacore age estimates from spines to be positively biased for ages 2–7 and negatively biased for ages greater than 11 years, compared to otolith-based age estimates. Underestimated age estimates using fin spines may occur because the inner translucent zones of fin spine cross-sections are difficult to see due to resorption or extra vascularization. Estimated size-at-age from LF also matched otolith-based age estimates at the younger (<4 years) and older (>10 years) ages, but underestimated size-at-age for fish between these age ranges. One explanation may be the lack of flexibility for MULTIFAN LF to properly adjust around the inflexion point of the growth curve, as seen by Ortiz de Zarate and Restrepo (2001) when estimating VB based size-at-age of albacore in the North Atlantic. A pattern of similar size-at-age between LF (using MULTIFAN) and vertebrae aging methods was also found by Labelle et al. (1993) for South Pacific albacore up until approximately 5–6 years of age followed by slower LF based growth thereafter. Length frequency analysis therefore appears useful when accompanied by direct aging methods (i.e., otoliths, fin spines, scales).

Age validation is needed to ensure that the periodicity of band formation is consistent with the counting methodology used by the reader. Laurs et al. (1985) validated daily growth ring deposition for North Pacific albacore up to three years of age and showed a slight divergence from one daily ring per day; their adjusted relationship was 0.954 ring per day. Taking this into account, our daily ages ranging from 378 to 505 days would range from 396 to 529 days, still confirming that albacore 55.5–61.5 cm FL are age-1. For purposes of this study, older fish were not processed for daily ring counts primarily because of ring compression and the associated difficulty in obtaining counts. This problem of increased daily increment compression resulted in the underestimation of longtail tuna age estimates beyond age-2 (Griffiths et al., 2009). Subtracting the daily age from collection date therefore provided an estimate of hatch-dates that ranged from May to August, consistent with previous studies examining spawning seasonality of North Pacific albacore (Otsu and Uchida, 1959a; Chen et al., 2010). Bigelow et al. (1993) also used daily ring counts to estimate peak hatch-dates of albacore that ranged from March to August.

North Pacific albacore appear to be relatively long-lived as the oldest aged fish of 15 years (128 cm FL) was slightly older than estimates obtained from other albacore age and growth studies. North Pacific albacore were aged out to only 9 years of age by Yabuta and Yukinawa (1963) using scales. Using otoliths, several studies have reported 14-year-old North and South Pacific albacore, with VB based mean sizes ranging from 102 to 111 cm FL (Farley and Clear, 2008; Chen et al., 2012; Williams et al., 2012) and Labelle et al. (1993) reported 13 years (107 cm FL) for South Pacific albacore. The estimated longevity of 21 years (based on 99% of L_∞) reported here is reasonable for *Thunnus* species, both bigeye and longtail tuna can live for at least 18 years (Farley et al., 2006; Griffiths et al., 2009) and southern bluefin (*Thunnus maccoyii*) for at least 31 years (Gunn et al., 2008).

Sex-specific differences in growth parameters were not found, but this may be due to the limited sample size of sexually mature albacore (ages 5 years and older) for which sex was determined. Male albacore have been shown to attain larger sizes than females in the North Atlantic (Santiago and Arrizibalaga, 2005), Mediterranean (Megalofonou, 2000; Karakulak et al., 2011), South Pacific (Farley and Clear, 2008; Williams et al., 2012), and North Pacific (Otsu and Uchida, 1959b, Chen et al., 2012). Mean size of male albacore (98.7 cm FL, n = 30) was larger than that of females (93.2 cm FL, n = 19) collected in the western region. Similarly, in the central region, mean male size was larger (112.7 cm FL, n = 62) than mean female size (103.7 cm FL, n = 15); however, sample sizes were likely too small to make any meaningful inferences and should be explored in further detail in the North Pacific. In addition, spatial variation in growth, as has been shown for South Pacific albacore across different longitudes (Williams et al., 2012), warrants further consideration in the North Pacific.

The sensitivity of stock assessment results to the growth parameters used illustrates the importance of developing accurate aging data and representative growth models (e.g., ISC 2011; Aires-da-Silva and Maunder, 2011). Of particular importance is the L_∞ parameter, which can be thought of as representing the average size of the oldest fish in the population. A larger L_∞ implies that fish of a larger size should be present in the population, but since these large fish were not present in the data, the assessment model results showed that the stock experienced high fishing mortality such that the fish did not survive long enough to reach these large sizes. However, as was shown in this study, if the true L_∞ is actually smaller, then estimates of fishing mortality will be reduced and reflective of the sizes of fish obtained from the fisheries. Otoliths and other hard parts can be difficult to age when the fish is relatively old, which makes it challenging to estimate an accurate L_∞. A likely explanation for differences between this study and that of Yabuta and Yukinawa (1963) was their inability to identify annuli for older albacore above 9 years of age using scales (resulting in an inflated L_∞) and counting two annuli for albacore ~50 cm FL that have a single annuli using otolith-based methods. One promising method to improve L_∞ estimates is to integrate tag-recapture, length-frequency and direct aging data (Eveson et al., 2004). Many managed fish stocks are without updated growth models and this exercise shows the importance of integrating size-at-age throughout the full life history for the most effective assessments to occur.

Acknowledgements

This project was in part funded through the NOAA Fisheries National Cooperative Research Program. We thank the American Albacore Fishing Association (AAFA) and American Fishermen's Research Foundation (AFRF) and all the captains and crew for providing samples necessary for this project. In addition, support from the Sportfishing Association of California and the Honolulu Fish Auction allowed personnel to acquire samples. Central Pacific samples were acquired with the assistance of N. Aberilla, K. Bigelow, B. Humphreys, D. Itano, J. Rooker, B. Takenaka and K. Underkoffler. Lastly, we thank R. Barabe for assistance with the processing of fin spines.

References

Aires-da-Silva, A., Maunder, M.N., 2011. Status of Bigeye Tuna in the eastern Pacific Ocean in 2009 and outlook for the future. Inter-Am. Trop. Tuna Comm. 11, 17–156, Stock Assessment Report.

Beamish, R.J., Fournier, D.A., 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38, 982–983.

Bell, R.R., 1962. Age determination of the Pacific albacore of the California coast. Calif. Fish Game 48, 39–48.

Bigelow, K.A., Jones, J.T., Sierra, M.M., 1993. Age variability within a length-frequency mode of the North Pacific albacore fishery as determined by otolith analysis. In: 13th North Pacific Albacore Workshop, NPALB13/20.

Chang, W.Y.B., 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39, 1208–1210.

Chen, K.S., Crone, P.R., Hsu, C.C., 2010. Reproductive biology of albacore tuna *Thunnus alalunga*. J. Fish Biol. 77, 119–136.

Chen, K.S., Shimose, T., Tanabe, T., Chen, C.Y., Hsu, C.C., 2012. Age and growth of albacore *Thunnus alalunga* in the North Pacific Ocean. J. Fish Biol. 80, 2328–2344.

Childers, J.F., Betcher, A.E., 2010. Summary of the 2008 U.S. North and South Pacific Albacore Troll Fisheries. Southwest Fisheries Science Center, administrative report LJ-01-10.

Childers, J., Snyder, S., Kohin, S., 2011. Migration and behavior of juvenile North Pacific albacore (*Thunnus alalunga*). Fish. Oceanogr. 20, 157–173.

Clemens, H.B., 1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951–1958. Calif. Dep. Fish Game, Fish. Bull. 115, 128.

Eveson, J.P., Laslett, G.M., Polacheck, T., 2004. An integrated model for growth incorporating tag-recapture, length-frequency, and direct aging data. Can. J. Fish. Aquat. Sci. 61, 292–306.

Fabens, A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29, 265–289.

Farley, J., Clear, N., 2008. Preliminary Study of Age, Growth, and Spawning Activity of Albacore in Australia's Eastern Tuna and Billfish Fishery. Western and Central Pacific Fisheries Commission, pp. 36, WCPFC-SC4-2008/BI-IP-1.

Farley, J.H., Williams, A.J., Clear, N.P., Davies, C.R., Nicol, S.J., 2013. Age estimation and validation for South Pacific albacore *Thunnus alalunga*. J. Fish Biol. (in press).

Farley, J.H., Clear, N.P., Leroy, B., Davis, T.L.O., McPherson, G., 2006. Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region. Mar. Freshwater Res. 57, 713–724.

Foreman, T., 1996. Estimates of age and growth, and an assessment of ageing techniques, for northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 21, 75–123.

Fournier, D.A., Sibert, J.R., Majkowski, J., Hampton, J., 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. 47, 301–317.

Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality and on a new mode of determining the value of life contingencies. Philos. Trans. Roy. Soc. Lond. 115, 515–585.

Griffiths, S.P., Fry, G.C., Manson, F.J., Lou, D.C., 2009. Age and growth of longtail tuna (*Thunnus tonggol*) in tropical and temperate waters of the central Indo-Pacific. ICES J. Mar. Sci. 67, 125–134.

Gunn, J.S., Clear, N.P., Carter, T.I., Rees, A.J., Stanley, C.A., Farley, J.H., Kalish, J.M., 2008. Age and growth in southern bluefin tuna, *Thunnus maccoyii* (Castelnau): direct estimation from otoliths, scales and vertebrae. Fish. Res. 92, 207–220.

Hajjej, G., Hattour, A., Hajjej, A., Cherif, M., Allaya, H., Jarboui, O., Bouain, A., 2012. Age and growth of little tuny, *Euthynnus alletteratus* (Rafinesque, 1810), from the Tunisian Mediterranean coasts. Cah. Biol. Mar. 53, 113–122.

Ichinokawa, M., Coan, A.L., Takeuchi, Y., 2008. Transoceanic migration rates of 544 young North Pacific albacore, *Thunnus alalunga*, from conventional tagging data. Can. J. Fish. Aquat. Sci. 65, 1681–1691.

International Scientific Committee (ISC), 2007. Report of the Albacore Working Group Workshop, November 28–December 5, 2006, Shimizu, Japan. In: ANNEX 5 of Report of the Seventh Meeting of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, July 25–30 Busan, Korea.

International Scientific Committee (ISC), 2011. Stock assessment of albacore tuna in the North Pacific Ocean in 2011. In: Report of the Albacore Working Group Stock Assessment Workshop. International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, Shizuoka, Japan, pp. 150.

Karakulak, F.S., Ozgur, E., Gokoglu, M., Emecan, I.T., Baskaya, A., 2011. Age and growth of albacore (*Thunnus alalunga* Bonnaterre, 1788) from the eastern Mediterranean. Turk. J. Zool. 35, 801–810.

Katsanevakis, S., 2006. Modelling fish growth: model selection, multi-model inference and model selection uncertainty. Fish. Res. 81, 229–235.

Labelle, M., Hampton, J., Bailey, K., Murray, T., Fournier, D.A., Sibert, J.R., 1993. Determination of age and growth of South Pacific albacore (*Thunnus alalunga*) using three methodologies. Fish. Bull. 91, 649–663.

Laurs, R.M., Wetherall, J.A., 1981. Growth rates of North Pacific albacore, *Thunnus alalunga*, based on tag return. Fish. Bull. 79, 293–302.

Laurs, R.M., Nishimoto, R., Wetherall, J.A., 1985. Frequency of increment formation on sagittae of North Pacific albacore (*Thunnus alalunga*). Can. J. Fish. Aquat. Sci. 42, 1552–1555.

Laurs, R.M., Lynn, R.J., 1991. North Pacific albacore ecology and oceanography. In: Wetherall, J.A. (Ed.), Biology, oceanography, and fisheries of the North Pacific transition zone and subarctic frontal zone. U.S. Dept. Commer., NOAA Tech. Memo., pp. 69–87, NOAA-TM-NMFS-SWFSC-105.

Lessa, R., Duarte-Neto, P., 2004. Age and growth of yellowfin tuna (*Thunnus albacares*) in the western equatorial Atlantic, using dorsal fin spines. Fish. Res. 69, 157–170.

Megalofonou, P., 2000. Age and growth of Mediterranean albacore. J. Fish Biol. 57, 700–715.

Methot Jr., R.D., Wetzel, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish. Res. 142, 86–99.

Nose, Y., Kawatsu, H., Hiyama, Y., 1957. In: Suisan Gaku Shusei (Ed.), Age and Growth of Pacific Tunas by Scale Reading. Tokyo University Press, Japan, pp. 701–716.

Ortiz de Zarate, V., Restrepo, V., 2001. Analysis of tagging data from North Atlantic albacore: von Bertalanffy growth estimates and catch-at-age. ICCAT Collect. Vol. Sci. Pap. 52, 1435–1446.

Otsu, T., 1960. Albacore migration and growth in the North Pacific Ocean as estimated from tag recoveries. Pac. Sci. 14, 257–266.

Otsu, T., Uchida, R.N., 1959a. Sexual maturity and spawning of albacore in the Pacific Ocean. Fish. Bull. 59, 287–304.

Otsu, T., Uchida, R.N., 1959b. Study of age determination by hard parts of albacore from central North Pacific and Hawaiian waters. Fish. Bull. 59, 353–363.

Pauly, D., 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Ber. Inst. Meeresk. 63, 156.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 91, pp. 382.

Santiago, J., Arrizibalaga, H., 2005. An integrated growth study for North Atlantic albacore (*Thunnus alalunga* Bonn. 1788). ICES J. Mar. Sci. 62, 740–749.

Schaefer, K.M., Fuller, D.W., 2006. Estimates of age and growth of bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean, based on otolith increments and tagging data. Inter-Am. Trop. Tuna Comm. Bull. 23, 35–76.

Shimose, T., Tanabe, T., Chen, K.S., Hsu, C.C., 2009. Age determination and growth of Pacific bluefin tuna, *Thunnus orientalis*, off Japan and Taiwan. Fish. Res. 100, 134–139.

Spurr, A.R., 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26, 31–43.
Sund, P.N., Blackburn, M., Williams, F., 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanogr. Mar. Biol. Ann. Rev. 19, 443–512.
Uchiyama, J.H., Struhsaker, P., 1981. Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. Fish. Bull. 79, 151–162.
Ueyanagi, S., 1969. Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. Bull. Far Seas Fish. Res. Lab. 2, 177–256.
von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10, 181–213.
Williams, A.J., Farley, J.H., Hoyle, S.D., Davies, C.R., Nicol, S.J., 2012. Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. PLoS ONE 7 (6), e39318, http://dx.doi.org/10.1371/journal.pone.0039318.
Yabuta, Y., Yukinawa, M., 1963. Growth and age of albacore. Rep. Nankai Reg. Fish. Res. Lab. 17, 111–120.
Yoshida, H.O., 1968. Early life history and spawning of the albacore, *Thunnus alalunga*, in Hawaiian waters. Fish. Bull. 67, 205–211.