



Journal of Fish Biology (2012) **80**, 2328–2344

doi:10.1111/j.1095-8649.2012.03292.x, available online at wileyonlinelibrary.com

Age and growth of albacore *Thunnus alalunga* in the North Pacific Ocean

K.-S. CHEN*†, T. SHIMOSE‡, T. TANABE§, C.-Y. CHEN|| AND C.-C. HSU*¶

**Institute of Oceanography, College of Science, National Taiwan University, Taipei 10617, Taiwan, R.O.C.*, ‡*Research Center for Subtropical Fisheries, Seikai National Fisheries Research Institute, Fisheries Research Agency, 148-446, Fukai-Ohta, Ishigaki, Okinawa 907-0451, Japan*, §*National Research Institute of Far Seas Fisheries, Fisheries Research Agency, 5-7-1, Orido, Shimizu, Shizuoka 424-8633, Japan* and ||*Department of Environmental Engineering, National Kaohsiung Marine University, Kaohsiung 81143, Taiwan, R.O.C.*

(Received 20 April 2011, Accepted 28 February 2012)

The age and growth of North Pacific albacore *Thunnus alalunga* were investigated using obliquely sectioned sagittal otoliths from samples of 126 females and 148 males. Otolith edge analysis indicated that the identified annulus in a sagittal otolith is primarily formed during the period from September to February. The assessments of the fish age at first annulus formation indicated that the first annulus represents an age of <1 year. This study presents an age estimate (0.75 years) for the formation of the first annulus. The oldest fish ages observed in this study were 10 years for females and 14 years for males. The von Bertalanffy growth parameters of females estimated were $L_{\infty} = 103.5$ cm in fork length (L_F), $K = 0.340 \text{ year}^{-1}$ and $t_0 = -0.53$ years, and the parameters of males were $L_{\infty} = 114.0$ cm, $K = 0.253 \text{ year}^{-1}$ and $t_0 = -1.01$ years. Sexual size dimorphism between males and females seemed to occur after reaching sexual maturity. The coefficients of the power function for expressing the L_F –mass relationship obtained from sex-pooled data were $a = 2.964 \times 10^{-5}$ and $b = 2.928$.

© 2012 The Authors

Journal of Fish Biology © 2012 The Fisheries Society of the British Isles

Key words: age validation; growth parameter; length and mass relationship; otolith microstructure.

INTRODUCTION

Albacore *Thunnus alalunga* (Bonnaterre 1788) is a cosmopolitan species and an important exploited resource for many nations. For stock-assessment and fisheries-management purposes, at least six *T. alalunga* stocks have been distinguished or used, *i.e.* North Pacific, South Pacific, North Atlantic, South Atlantic, Mediterranean and Indian stocks (Murray, 1994; ICCAT, 1996; Huang *et al.*, 2003). Young *T. alalunga* tend to inhabit temperate waters, whereas mature fish are likely to stay in subtropical waters for protracted periods (Kimura *et al.*, 1997; Chen *et al.*, 2005). The distribution of North Pacific *T. alalunga* ranges from the equator to 45° N in the west and from the waters off Mexico (*c.* 20° N) to the Gulf of Alaska (*c.* 60° N)

¶Author to whom correspondence should be addressed. Tel.: +886 2 33661393; email: hsucc@ntu.edu.tw

†Present address: Department of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung 80424, Taiwan, R.O.C.

in the east (Foreman, 1980). The annual fisheries production of North Pacific *T. alalunga* reported for the period of 2000 to 2008 ranges from c. 63 000 to 105 000 t (ISC, 2010).

Age and growth studies of fish stocks can provide essential biological parameters for modelling population dynamics of the stocks. In conducting stock assessment of an exploited fish stock, growth parameters are frequently estimated and used to determine the mean length at age, age composition and mortality rates of the stock (Ricker, 1975; King, 2007). Using less accurate and precise biological parameters in inputs of stock assessment models can increase uncertainty in model outputs (Hilborn & Walters, 1992). The growth parameters used in the current stock assessment of North Pacific *T. alalunga* (ISC, 2006) were based on the studies conducted four decades ago (Suda, 1966). To improve assessment outputs of this stock, biological parameters must be updated regularly to provide recent information on the life-history traits of the stock in question.

As reviewed by Foreman (1980), both hard parts (*e.g.* scales and vertebrae) and tag–recapture methods have been used to investigate the age and growth of North Pacific *T. alalunga*. Little information is available, however, on the sex-specific growth functions of this stock. Because *T. alalunga* exhibit the sexual size dimorphism that adult males attain a larger size than females (Otsu & Uchida, 1959; Otsu & Sumida, 1968; Yoshida, 1975), knowing whether male and female North Pacific *T. alalunga* have different growth functions is important for accurately modelling the population dynamics of this stock.

Sagittal otoliths are frequently used in age determination studies of tunas and many other teleosts (Campana & Neilson, 1982; Tzeng, 1990; Neilson & Campana, 2008). Transversely sectioned otolith slices are commonly used to assess the fish age in tunas. Nevertheless, the otolith slices produced by oblique sections are longer and wider in appearance than the transversely sectioned slices. Longer and wider otolith slices are helpful for clarifying annuli. In tunas, obliquely sectioned otoliths have been used previously for age-and-growth studies (Stéqueret *et al.*, 1996; Clear *et al.*, 2000; Schaefer & Fuller, 2006) and were produced and used for the age determination of North Pacific *T. alalunga* in this study.

The first goal of this study was to determine the sex-specific growth parameters of North Pacific *T. alalunga*. Length and age were recorded and age of each collected fish specimen was determined by examining annuli in obliquely sectioned otolith slices. The goodness of fit of the von Bertalanffy growth model was evaluated using both the coefficient of determination (R^2) and an *F*-test for lack of fit. The likelihood ratio test was used to compare sex-specific growth and length and mass functions. Bootstrapping was conducted to assess uncertainty in the estimates of the biological parameters.

MATERIALS AND METHODS

COLLECTION OF SPECIMENS

Thunnus alalunga specimens [112 females, straight fork length (L_F) of 59–101 cm; 132 males, L_F of 58–118 cm] were sampled from the catches of Taiwanese longline vessels operated in the central and western North Pacific Ocean during the period from October 2001 to April 2006 (Fig. 1, A1 to A5). These specimens were landed at the fishing ports

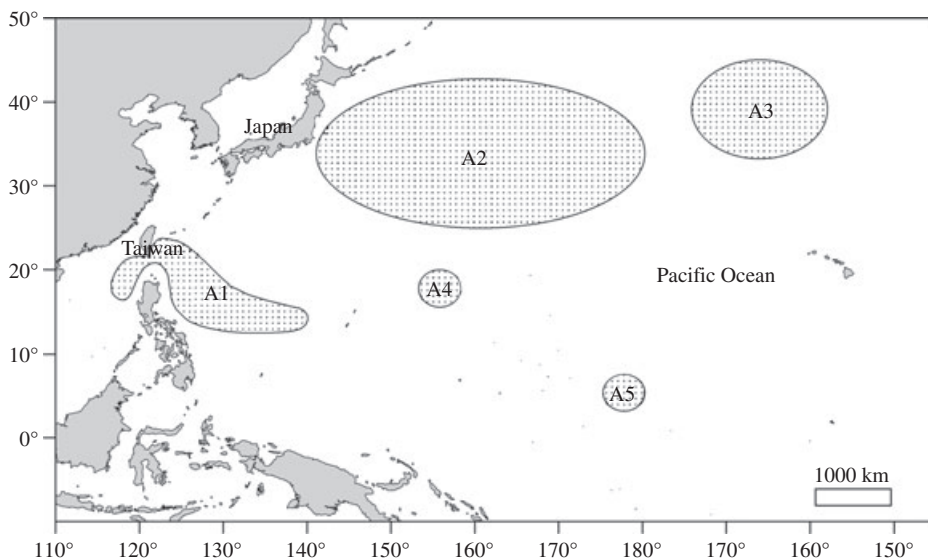


FIG. 1. Fishing operation areas (▨, A1–A5) of the North Pacific *Thunnus alalunga* specimens collected during the period from October 2001 to January 2008. The number of fish collected in each area was: 136 in A1, 120 in A2, 30 in A3, 6 in A4 and 1 in A5.

of Tungkang and Kaohsiung in Taiwan. In addition, specimens of smaller *T. alalunga* (21 females, L_F of 46–73 cm; 28 males, L_F of 45–74 cm), from A2 in Fig. 1 were collected by colleagues of the National Research Institute of Far Sea Fisheries, Japan, from the catches of Japanese pole-and-line vessels during the period from June 2006 to January 2008. These specimens were landed at the fishing port of Kesennuma in Japan. The numbers of fish collected by year were: 33 in 2001, 79 in 2002, 38 in 2003, 30 in 2004, 40 in 2005, 43 in 2006 and 30 between 2007 and 2008; total 293. For each fish, the straight L_F (from the tip of the upper jaw to the end of the caudal fork) and body mass (M_B) were recorded. In the laboratory, sagittal otoliths were removed from 288 fish (157 males, L_F of 45–118 cm, M_B of 2.0–32.2 kg; 131 females, L_F of 46–101 cm, M_B of 2.2–23.0 kg) and stored in labelled plastic capsules.

PREPARING OTOLITH SLICES

For each fish, an obliquely sectioned slice of the right or left sagittal otolith was obtained using a low-speed diamond saw. First, each otolith was embedded in slow-drying resin (Mark V Laboratory Inc., resin RR32 and hardener RH-4 in a 10:1 mass ratio; www.markvlab.com). The posterior-dorsal part of the otolith close to the dashed line in Fig. 2(a) was then cut off. The surface of the sectioned side of the remnant resin block was sequentially ground close to the primordium using sandpapers (800, 1200 and 2000 in grit size). The ground surface was then polished using aluminium powder (1.00 and 0.05 μm , sequentially). After polishing, the resin block was cut again to obtain a thin slice (c. 1–2 mm thick) through the primordium. The polished side of the thin slice was stuck to a glass slide using clear acrylic glue. The rough side of the slice was then ground and polished to obtain a slice of c. 0.2–0.6 mm in thickness [Fig. 2(b)]. Finally, annuli in each prepared otolith slice were examined by one reader using a light microscope (magnification up to $\times 400$) with transmitted or reflected light. For each slice, the length of the postrostral axis (L_P ; from the primordium to the posterior-ventral edge) was measured as $L_P = L_1 + L_2$ [Fig. 2(b)] using a micrometer mounted on one eyepiece of the microscope. Images of otolith slices were obtained using a digital camera attached to the microscope.

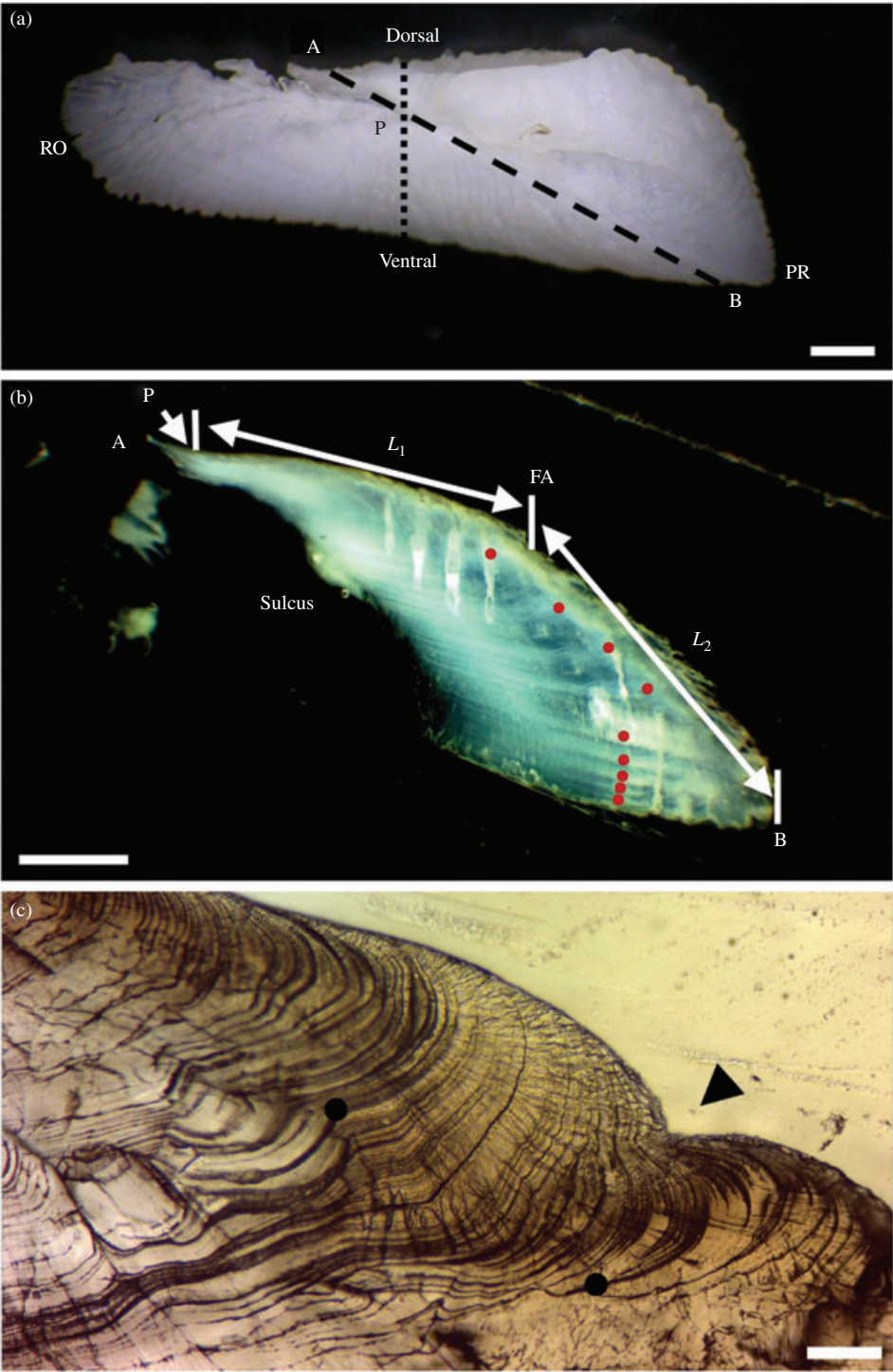


FIG. 2. Legend on next page.

AGE ESTIMATION

Annuli in each otolith slice were examined as the zones composed of relatively compact (higher density) micro-increments [Fig. 2(c)]. The annuli examined were assumed to represent slow-growth phases of the fish. In this study, opaque or translucent zones were not used to represent annuli because several factors (*e.g.* light source, background colour, magnification and thickness of the otolith slice) may affect the appearance of opaque and translucent zones in an otolith under a light microscope. Each annulus identified in the prepared otolith slice frequently accompanied the crenulation (Gambell & Messtorff, 1964; Anon., 2002), which occurred on the outer margin of the slice [Fig. 2(c)].

For each otolith slice, the annuli in the slice were examined. The condition of the posterior-ventral otolith edge was also assessed and classified based on whether or not it was undergoing the formation of an annulus. When an annulus occurred on the posterior-ventral edge, the annulus on the edge was included in the calculation of the annuli in the otolith slice, and the fish age was determined to be the number of annuli counted. When no annulus was formed on the posterior-ventral edge, the fish age was assigned to be the number of annuli plus 0.5. To check if an annulus is formed once a year, otolith edge analysis (Gambell & Messtorff, 1964; Campana, 2001; Shimose *et al.*, 2009) was conducted. In the edge analysis, the proportion of fish that had an annulus on the posterior-ventral edge was calculated for each month to verify the period of annulus formation. Additionally, the age at the formation of the first annulus was investigated for 55 fish (L_F of 71–105 cm) that had clearer micro-increments (assumed to be daily growth increments) in their otolith slices (Fig. 3). For each fish, two counts of the micro-increments from the primordium to the end of the first annulus were conducted, and the time interval between the two counts was at least 1 week.

Five age readings were conducted for each otolith slice to determine the fish age. To avoid bias in the age estimates resulting from a reader recalling previous age estimates, a time interval of at least 1 week between two age readings was used. To obtain a more precise age estimate from the five readings, each fish with at least three identical age estimates among the five age readings was selected for further growth investigations. The age of the fish was then determined to be the value observed in the majority of the five age estimates. In addition, to include more samples for growth investigations, an additional age reading was conducted for those fish that had only two identical estimates among five readings. Subsequently, fish that had three identical age estimates among six readings were also included for growth investigations. The index of the average per cent error (I_A) was used to assess precision in the age estimates for both males and females using the following equation (Beamish & Fournier, 1981):

$$I_A = (100N_A^{-1}) \sum_{j=1}^{N_A} \left[(N_R^{-1}) \sum_{i=1}^{N_R} |X_{ij} - X_j| X_j^{-1} \right] \quad (1)$$

where N_A is the number of aged fish, N_R is the number of age readings, X_{ij} is the i th age estimate of the j th fish and X_j is the mean age estimate calculated for the j th fish.

FIG. 2. Images [(a), (b), using reflected light] showing (a) a right sagittal otolith (outer view) and (b) an obliquely sectioned slice [indicated by --- in (a)] of the otolith from a female North Pacific *Thunnus alalunga* (101 cm fork length). The annuli ($n = 9$) identified in (b) are shown by ●. The image (c) (using transmitted light) shows the microstructure of an annulus, indicated by two ●, and a crenulation, indicated by ◀. For comparison, the transversely sectioned slice is indicated by in (a). PR, postrostrum; P, primordium; RO, rostrum; A, the dorsal edge of --- in (a); B, the posterior-ventral edge of --- in (a); FA, the first annulus; L_1 , the distance from P to the outer-ventral margin of FA; L_2 , the distance from the outer-ventral margin of FA to B. In (a) and (b), bar = 1 mm; in (c), bar = 0.1 mm.



FIG. 3. A transmitted light photograph showing the microstructure close to the primordium in an obliquely sectioned sagittal otolith slice from a female North Pacific *Thunnus alalunga* (100 cm in fork length). \rightarrow , the primordium. \bullet , some of the micro-increments identified. Bar = 0.1 mm.

MODELLING FISH GROWTH

The von Bertalanffy growth function (VBGF) was used to model fish growth, as described in the equation (von Bertalanffy, 1938) $L_t = L_\infty[1 - e^{l-K(t-t_0)}]$, where L_t is L_F at age t , L_∞ is the theoretical asymptotic L_F , K is a growth coefficient, t is the fish age (in years) and t_0 is the hypothetical age (in years) at a L_F of zero. The VBGF was, respectively, fitted to male and female age and L_F data to obtain sex-specific growth parameters (L_∞ , K and t_0) using non-linear least-squares method. To fit the VBGF, individual age and L_F data were used to incorporate individual variability into the growth analyses. Because of limited samples, interannual variability in growth rates was assumed to be less important than age-class variability in the growth analyses. Moreover, bootstrapping was used to estimate the s.e. of each growth parameter and to construct bias-corrected and accelerated (BCa) 95% c.i. of each parameter (Efron & Tibshirani, 1993). In the bootstrapping procedure, sampling with replacement from age and L_F data was conducted (5000 bootstrap replicates including the original data as one sample). Jackknifing was used to calculate the acceleration in computing BCa 95% c.i. (Efron & Tibshirani, 1993). To compare the growth parameters obtained in this study with those reported for *T. alalunga* stocks in previous studies, the phi prime, $\phi' = \ln K + 2 \ln L_\infty$ (Sparre & Venema, 1998; Megalofonou *et al.*, 2003), was calculated for each sex and used for such comparisons.

GOODNESS OF FIT FOR THE GROWTH MODEL

Goodness of fit of the VBGF was evaluated by both R^2 (Motulsky & Christopoulos, 2004) and by an F -test for lack of fit (Neill, 1988). The R^2 values for males and females can be calculated as $R^2 = 1 - (S_E S_T^{-1})$, where S_E is the residual sum of squares and S_T is the total sum of squares. To conduct the F -test for lack of fit, the sum of squares caused by pure error (S_P) is calculated as $S_P = \sum_{i=1}^{N_C} \sum_{j=1}^{n_i} (L_{ij} - \bar{L}_i)^2$, where N_C is the number of age classes, n_i is the number of samples in each age class, L_{ij} is the individual L_F for each age class and \bar{L}_i is the mean L_F of age class i . The sum of squares caused by lack of fit (S_L) is calculated as $S_L = S_E - S_P$, where the d.f. of S_E is calculated as the total data points (N) minus the number of parameters (N_P) fitted by regression, the d.f. of S_P is N minus N_C and the d.f. of S_L is N_C minus N_P . Ultimately, the test statistic of the F -test for lack of fit is calculated as $F = [S_L(N_C - N_P)^{-1}][S_P(N - N_C)^{-1}]^{-1}$.

COMPARING SEX-SPECIFIC GROWTH FUNCTIONS

Likelihood ratio tests can be used to compare sex-specific functions of the non-linear VBGF (Haddon, 2001). In this study, the three parameters (L_∞ , K and t_0) of the VBGF were compared simultaneously using the likelihood ratio test instead of comparing one or two parameters. Haddon (2001) found that the test statistic of the likelihood ratio test is empirically a χ^2 distribution and can be simplified as $\chi_r^2 = -N \ln(S_S S_C^{-1})$, where N is the total number of samples, r is the d.f. of the assumed χ^2 distribution, S_S is the total sum of squares derived from fitting the VBGF by setting all parameters as being different between sexes and S_C is the total sum of squares obtained from fitting the VBGF using the hypothesized constraints of parameters (*i.e.* an equal value for each parameter between sexes). To avoid comparing the size distributions of males and females, restricted age and L_F data (*i.e.* age classes of 1.25–10.25 years for both sexes) were used in the test.

LENGTH AND MASS RELATIONSHIP

The allometric equation for the L_F – M_B relationship can be expressed as a power function, $M_B = aL_F^b$, where a and b are the coefficients to be estimated (Hsu, 1999). Non-linear least-squares method was used to obtain estimates. Bootstrapping (5000 replicates) was also used to estimate the S.E. of each coefficient of the L_F and M_B function. The sex-specific L_F and M_B functions were compared using a similar approach to that used in comparing sex-specific growth functions, as presented above.

The statistical analyses (including curve fitting, likelihood ratio test and bootstrapping) used in this study were performed using MATLAB (version 7.2, MathWorks Inc.; www.mathworks.com).

RESULTS

AGE VALIDATION

The annuli found in sectioned otoliths were primarily formed during the period from autumn and through winter, *i.e.* from September to February (Fig. 4). High proportions of fish in which an annulus was formed on the posterior-ventral otolith edge occurred in December (74%) and January (64%). Moreover, no fish had an annulus on the posterior-ventral otolith edge during July and August. In the investigation on the age evaluation of first annulus formation, for the 55 fish examined, no significant differences were found between two counts of micro-increments (paired t -test, d.f. = 54, $P > 0.05$). Descriptive statistics for the mean values of the two counts were as follows: the mean \pm S.E. value was 257 (± 6), the median value was 266, the minimum value was 136 and the maximum value was 337. The results indicated that the suggested age estimate of the first annulus for the stock was close to 0.75 years. Therefore, for each fish, an adjustment in the age estimates for the first annulus was conducted. In the adjustment, 0.25 years was subtracted from all age estimates, which is an estimate of the time interval between birth and annulus formation, *i.e.* the birth date was assumed to be 30 April (Chen *et al.*, 2010), and the annulus was assumed to form on 31 January.

AGE ESTIMATION

Most of the otolith slices examined had clear annuli, and only four fish (1.4%) had no visual annuli in their otolith slices. In summary, 257 fish (89.2%) had at least

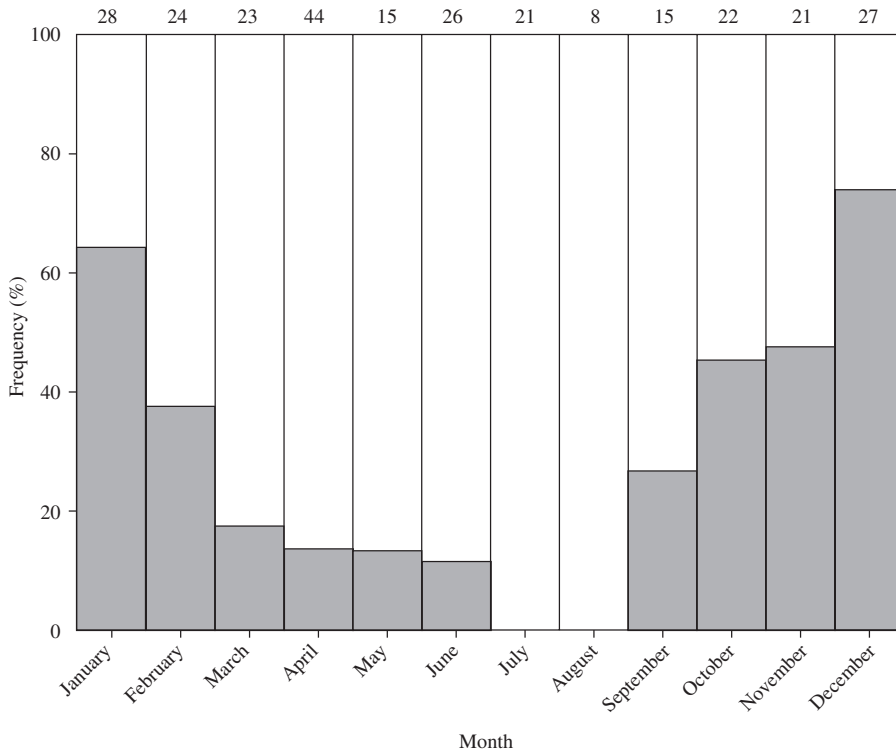


FIG. 4. The frequency distribution (■) of North Pacific *Thunnus alalunga* that had an annulus on the posterior-ventral otolith edge. The number on the top of each bar indicates the sample size.

three identical readings of the five age readings. Ten fish (3.5%) that had inconsistent age estimates (less than three identical readings) were excluded to allow for further growth investigations. Ageing older fish appeared to be more difficult than ageing younger fish. The I_A values of the aged fish were 7.4% for 126 females and 8.6% for 148 males. The assessed ages of females ranged from 1.25 to 10.25 years, and those of males ranged from 1.25 to 14.25 years.

GROWTH AND LENGTH AND MASS FUNCTIONS

Sex-specific growth curves (Fig. 5) differed significantly (likelihood ratio test, d.f. = 3, $P < 0.001$). Both male and female age-length data were properly fitted to the VBGF, as indicated by the R^2 and F -test values (Table I). As shown in the bootstrap estimates obtained for growth parameters (Fig. 6), all distributions (indicated by histograms) appeared to be normal, and there were correlations between the parameters of the VBGF (indicated by scatter plots). For each sex, simple linear regression seemed to delineate the relationship between the ln-transformed data of the determined fish age and L_P (Fig. 7). In the regression, females and males had different regression functions (*i.e.* two parallel lines), as evaluated using the t -test (Zar, 1999) on the regression coefficients (d.f. = 270, $P > 0.05$) and elevations (d.f. = 271, $P < 0.01$). For both sexes, the ϕ' values do not deviate greatly

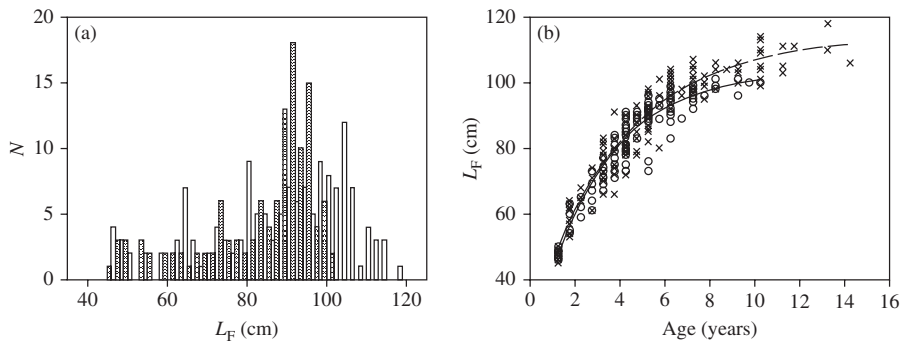


FIG. 5. Fork length (L_F) and age data of the aged North Pacific *Thunnus alalunga* (148 males and 126 females). (a) Frequency (N , in number) distribution by L_F for males (\square) and females (\blacksquare). (b) Scatter plot of age and L_F data for males (\times) and females (\circ). The fitted von Bertalanffy growth curves are shown as --- for males and — for females, and the parameters for plotting these curves are presented in Table I.

from those of previous studies (Table II). Sex-specific L_F and M_B curves did not differ significantly (likelihood ratio test, d.f. = 2, $P > 0.05$). An allometric equation was then obtained using sex-pooled data: $M_B = 2.964 \times 10^{-5} L_F^{2.928}$ ($R^2 = 0.98$, $n = 293$). The predicted mean L_F and M_B values for 5 year-old females were 88 cm and 14.5 kg, and the values for 5 year-old males were 89 cm and 15.2 kg.

DISCUSSION

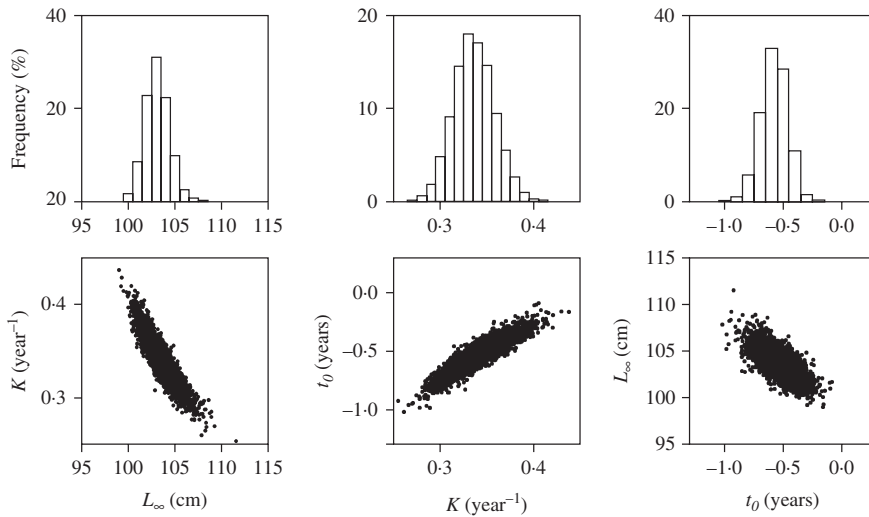
Sex-specific growth of North Pacific *T. alalunga* was determined in this study, and an updated L_F and M_B function for the stock was also presented. Obliquely sectioned otolith slices can be useful in assessing the age of North Pacific *T. alalunga*. The I_A values of males (8.6%) and females (7.4%) are $<10\%$, indicating that the precision in the age estimates of the aged fish is acceptable (Powers, 1983). The results of the

TABLE I. Estimated growth coefficients [L_∞ (cm), K (year^{-1}), t_0 (years)] of the von Bertalanffy growth function and their associated bootstrap (5000 replicates) s.e. and 95% c.i. for North Pacific *Thunnus alalunga*. The goodness of fit of the model was evaluated using the coefficient of determination (R^2) and an F -test for lack of fit

Sex	Coefficient	Estimated value \pm s.e.	95% c.i. (2.5%, 97.5%)	R^2	F -test (d.f.1, d.f.2)
Female	L_∞	103.5 \pm 1.3	(101.1, 106.2)	0.92	$P > 0.05$ (15, 108)
	K	0.340 \pm 0.022	(0.298, 0.384)		
	t_0	-0.53 \pm 0.12	(-0.79, -0.33)		
Male	L_∞	114.0 \pm 1.8	(110.8, 117.9)	0.93	$P > 0.05$ (19, 126)
	K	0.253 \pm 0.017	(0.218, 0.287)		
	t_0	-1.01 \pm 0.16	(-1.37, -0.75)		

d.f.1, d.f. for the sum of squares caused by lack of fit; d.f.2, d.f. for the sum of squares caused by pure error.

(a) Females



(b) Males

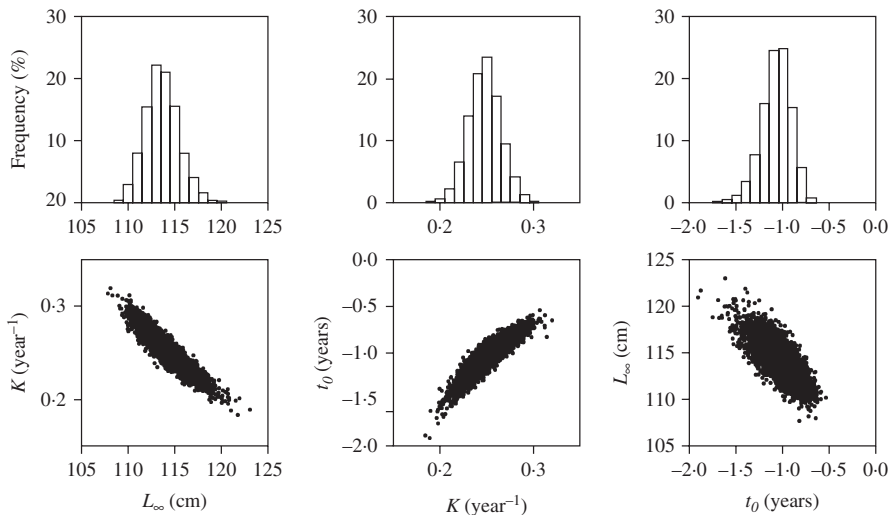


FIG. 6. Results of the bootstrapping (5000 replicates) of age and fork length (L_F) data for (a) female and (b) male North Pacific *Thunnus alalunga* produced by fitting the von Bertalanffy growth function. Histograms represent the frequency distributions of the bootstrap estimates of growth coefficients (L_{∞} , K and t_0), and scatter plots illustrate correlations between the coefficients.

otolith edge analysis suggest that the annuli in the sectioned otoliths of North Pacific *T. alalunga* are autumn-to-winter growth marks. In most cases, the first annuli found in sectioned otoliths represent the growth of <1 year.

Because the I_A and coefficient of variation (Chang, 1982) are functionally equivalent, as reported by Campana (2001), only the I_A value was used to quantify the precision of the age estimates obtained. Although this study attempted to obtain

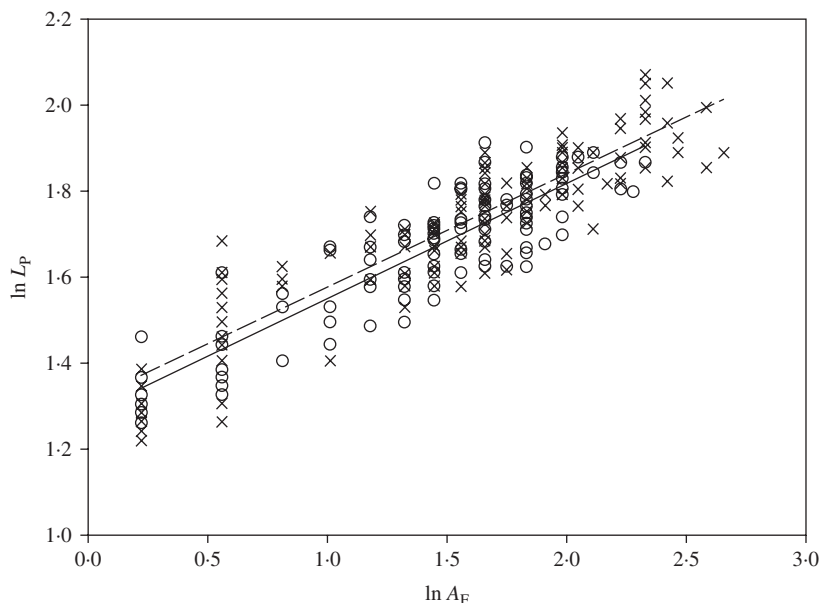


FIG. 7. The relationship between the ln-transformed postrostral otolith length (L_P , mm) and determined age (A_F , years) for North Pacific *Thunnus alalunga*. For males (\times , $n = 148$), the coefficients of the fitted simple linear function [$\ln L_P = a + b \ln A_F$, ---] and bootstrap s.e. of the coefficients were $a = 1.311$ (± 0.023) and $b = 0.264$ (± 0.013) and $r^2 = 0.805$. For females (\circ , $n = 126$), the coefficients of the fitted function — were $a = 1.278 \pm 0.021$ and $b = 0.270 \pm 0.013$ and $r^2 = 0.779$.

more accurate and precise age estimates using specific methodologies, biases in age estimates may exist as a result of individual variability at the times of birth and annulus formation, as a result of the misidentification of annuli, or from both of these factors. Also, biases in fish sampling may exist but are difficult to verify. As *T. alalunga* is a highly migratory species with a wide distribution in the North Pacific Ocean, collecting more representative samples from the entire stock distribution for biological investigations is difficult and time-consuming.

Micro-increments in North Pacific *T. alalunga* sagittae have been shown to be daily growth marks (Laurs *et al.*, 1985) but they suggested that counts of micro-increments need to be adjusted upward by 5%. In this study, the adjustment of 5% in the counts of micro-increments was ignored because only minor differences in age estimates were obtained. Moreover, the micro-increments deposited at ages of >2 years were compact and could not be precisely counted. Only the age estimates of first annulus formation were obtained by counting micro-increments. Because it was difficult to precisely define the margins of latterly formed annuli for older fish, no analyses in marginal increment widths were conducted in this study. In the otolith edge analysis, the micro-increments formed on the posterior-ventral edge during the spring and summer were broader than those formed during the autumn and winter (Fig. 4), indicating that North Pacific *T. alalunga* tend to grow faster in the spring and summer than in the autumn and winter. Furthermore, as indicated by L_∞ (Table I), mature male North Pacific *T. alalunga* are expected to attain a greater size than mature females. As reviewed by Quinn & Deriso (1999), several factors (*e.g.* depth,

TABLE II. A list of von Bertalanffy growth coefficients reported for *Thunnus alalunga*

Study	Area	Method	L_{∞} (cm)	K (year ⁻¹)	t_0 (years)	ϕ'
Clemens (1961)	North Pacific	Tagging	135.6	0.17	-1.87	8.047
Yabuta & Yukinawa (1963) ^a	North Pacific	Scales	146.3	0.150	-0.40	8.074
Beardsley (1971)	North Atlantic	Length data	140.0	0.141	-1.63	7.924
Labelle <i>et al.</i> (1993)	South Pacific	Vertebrae	121.0	0.134	-1.92	7.582
Megalofonou (2000)	Mediterranean	Spines	94.7	0.258	-1.35	7.747
Megalofonou <i>et al.</i> (2003)	Mediterranean	Scales	86.0	0.37	-0.76	7.908 ^b
Santiago & Arrizabalaga (2005)	North Atlantic	Spines and tagging	122.2	0.209	-1.34	8.046
Present study (females)	North Pacific	Otoliths	103.5	0.340	-0.53	8.200
Present study (males)	North Pacific	Otoliths	114.0	0.253	-1.01	8.098

$$\phi' = \ln K + 2 \ln L_{\infty}.$$

^aCoefficients calculated by Shomura (1966).

^bValue adapted from the original paper.

sex, habitat, weather, locality, genetics, year-class and density-dependence) may affect fish growth. Juvenile North Pacific *T. alalunga* have been shown to exhibit diverse behaviour in horizontal and vertical movements according to the habitats they inhabit (Childers *et al.*, 2011). Growth disparities are likely to be large among individuals, resulting from different habitats and food supply. It is difficult to verify this effect in this study because of the limited fish specimens obtained. In this study, the larger disparity in the growth curves between males and females seemed to occur at *c.* 85–90 cm L_F (Fig. 5), which coincides with the suggested size at which sexual maturity is reached (Chen *et al.*, 2010). Thus, reproduction seems to be an important factor affecting fish growth in mature North Pacific *T. alalunga*.

Because strong correlations existed among the three coefficients of the VBGF (Fig. 6), in the likelihood ratio test of this study, the three growth coefficients were compared simultaneously rather than comparing one or two coefficients. A disadvantage of the likelihood ratio test is that the size ranges of both sexes should be identical to avoid comparing size distributions of the two data sets (Haddon, 2001). Bootstrap tests can be also used for hypothesis testing, although this method may be less accurate (Efron & Tibshirani, 1993). Also, the 95% bootstrap c.i. of the coefficients L_{∞} and K between males and females did not overlap (Table I).

The VBGF was well-fitted to male and female age and L_F data, as indicated by both R^2 and F -test values, and thus, alternative growth models were not used or compared with the results of the VBGF in this study. In addition, the coefficients obtained for the VBGF are easier to compare with the results of previous studies regardless of whether the VBGF is the best-fitted model to age and length data among several growth models. For both sexes, the normality of the bootstrap estimates was obvious for each coefficients of the VBGF. All scatter plots between parameters seemed to have linear mean functions (Fig. 6). These results indicate that large sample inference is adequate for bootstrapping (Weisberg, 2005). The estimated coefficient t_0 in this study may have less biological meaning as a result of model fit.

Many studies have reported coefficient estimates of the VBGF not only for North Pacific *T. alalunga* but also for other *T. alalunga* stocks (Table II). Other than the study by Megalofonou (2000), the present study presented lower values of L_{∞} and higher values of K (Table II). One possible explanation for this effect is that only small differences in the mean L_F values (by age) of older fish were obtained in the present study (*i.e.* slow growth rate for adult fish). Moreover, reasons for the differences in growth coefficients among *T. alalunga* studies are likely to be different stocks and the methods used for age determination. For example, Mediterranean *T. alalunga* of older ages tend to exhibit smaller mean sizes than other *T. alalunga* stocks of older ages (Table II); results of tagging experiments have also shown the growth differences between North Atlantic and Mediterranean stocks (Ortiz de Zárate *et al.*, 1996; De Metrio *et al.*, 1997) as well as between North Pacific and Mediterranean stocks (Clemens, 1961). As calculated by the growth coefficient estimates obtained in this study, the expected mean L_F values for fish that are 1–6 years of age are close to the tagging results of North Atlantic *T. alalunga* presented by Santiago & Arrizabalaga (2005). In this study, the predicted mean L_F values of 1 year-old fish (at the beginning of May) were 42 cm L_F for females and 45 L_F cm for males. These two estimates are close to the estimate (a standard length of 38 cm) reported by Yoshida (1968). Moreover, the predicted mean L_F values (females = 60 cm; males = 61 cm) of 2 year-old fish are close to the estimate (59.9 cm) reported by K. A. Bigelow, R. N. Nishimoto, R. M. Laurs & J. A. Weatherall, unpubl. data. Because many age and growth studies only used a small number of old fish to obtain the von Bertalanffy growth coefficients of *T. alalunga*, the use of the growth predictions of old fish by calculating growth coefficients in stock assessment models should be done with caution.

The length–mass curve obtained in this study is close to that reported by Clemens (1961) for North Pacific *T. alalunga* as well as that reported by Beardsley (1971) for the North Atlantic stock, but the curve apparently differs from those reported for Mediterranean and Indian stocks (Megalofonou, 1990; Hsu, 1999; Megalofonou, 2000). Many factors may affect the estimation of length and mass coefficients, for example, different stocks, sampling seasons (or years or locations), measurement methods (*e.g.* curved or straight L_F , the tip of upper or lower jaw used as the measurement base, round or dressed mass), sexes, size ranges, storage conditions and regression methods. To find out the potential factors resulting in the differences of length and mass coefficients between two studies, at least detailed information needs to be known on the fish sampling and fish measurement of the two studies. Because many factors may affect the estimation of length and mass coefficients and that limited information is available on the fish sampling and fish measurement in previous studies, here trying to verify which factors result in the differences in length and mass coefficients among *T. alalunga* studies was avoided.

The coefficients of the VBGF have been used to estimate fish longevity (Taylor, 1958). When applying the growth coefficients obtained to estimate the longevity of North Pacific *T. alalunga*, the mean L_F values of older fish are similar as shown by growth curves (Fig. 5). If a smaller proportion of L_{∞} (*e.g.* 0.95 L_{∞} instead of 0.99 L_{∞}) is used to estimate the longevity of North Pacific *T. alalunga*, the longevity will be underestimated for the oldest fish. In this case, estimates of longevity may be better interpreted as the age at which the mean fish length tends to increase slowly towards L_{∞} with increasing age. The longevity of a fish species may be better estimated

TABLE III. The maximum age estimates reported for *Thunnus* species based on the analyses of sagittal otolith annuli

Species	Study	Maximum age estimate (years)
<i>Thunnus alalunga</i>	This study	14
<i>Thunnus obesus</i>	Farley <i>et al.</i> (2006)	16
<i>Thunnus tonggol</i>	Griffiths <i>et al.</i> (2010)	18
<i>Thunnus orientalis</i>	Shimose <i>et al.</i> (2009)	26
<i>Thunnus thynnus</i>	Secor <i>et al.</i> (2009)	33
<i>Thunnus maccoyii</i>	Gunn <i>et al.</i> (2008)	41

by ageing mature fish with a large sample size than by growth coefficients. The maximum age determined in this study was 14.25 years for a male (106 cm L_F). Both males and females had age estimates that were >10 years old. In comparing the maximum fish age estimate obtained in this study with that reported for other *Thunnus* species (Table III), North Pacific *T. alalunga* are relatively short-lived. *Thunnus alalunga* are a small *Thunnus* species, and the common size of *T. alalunga* in catches is <110 cm L_F (Otsu & Sumida, 1968; Yoshida, 1975). Fish size is an important factor that affects the longevity of pelagic fish species. That is, as a result of predation, small pelagic fish species are believed to have higher natural mortality rates than large species. Moreover, according to the Pauly (1980) and Hoenig (1983) equations, female North Pacific *T. alalunga* would have higher natural mortality estimates than males based on the growth coefficients obtained in this study.

Because North Pacific *T. alalunga* exhibit sex-specific growth, the use of an identical growth function for both sexes in stock assessment models may be controversial. Modelling the population dynamics of the stock using sex-specific growth coefficients may, however, be difficult at present because of the lack of sex-specific size or age compositions. In addition, it is difficult to precisely split up mature fish into many age classes using growth coefficients and size-frequency data because the mean fish lengths of older age classes may be similar. More simplified groups are recommended to represent the stock in stock assessment models, such as in immature fish (recruited or not recruited) and mature fish (representing the spawning stock, all recruited). Because of increasing concern regarding the sustainability of the stock, constructing sex-specific age compositions of the stock is urgently needed to advance current stock assessment.

Funding for this study was provided to C.-C. Hsu by the National Science Council of Taiwan (NSC90-2313-B-002-314; NSC91-2313-B-002-290; NSC92-2313-B-002-060). We would like to thank C.-L. Chen, K. Uosaki and anonymous boat captains for their help in collecting fish samples.

References

- Beamish, R. J. & Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–983.
- von Bertalanffy, L. (1938). A quantitative theory of organic growth (Inquiries on growth laws. II). *Human Biology* **10**, 181–213.
- Beardsley, G. L. (1971). Contribution to population dynamics of Atlantic albacore with comments on potential yields. *Fishery Bulletin* **69**, 845–857.

- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197–242. doi: 10.1006/jfbi.2001.1668
- Campana, S. E. & Neilson, J. D. (1982). Daily growth increments in otoliths of starry flounder (*Platichthys stellatus*) and the influence of some environmental variables in their production. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 937–942.
- Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1208–1210.
- Chen, I. C., Lee, P. F. & Tzeng, W. N. (2005). Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography* **14**, 71–80. doi: 10.1111/j.1365-2419.2004.00322.x
- Chen, K. S., Crone, P. R. & Hsu, C. C. (2010). Reproductive biology of albacore *Thunnus alalunga*. *Journal of Fish Biology* **77**, 119–136. doi: 10.1111/j.1095-8649.2010.02662.x
- Childers, J., Snyder, S. & Kohin, S. (2011). Migration and behavior of juvenile North Pacific albacore (*Thunnus alalunga*). *Fisheries Oceanography* **20**, 157–173. doi: 10.1111/j.1365-2419.2011.00575.x
- Clear, N. P., Gunn, J. S. & Rees, A. J. (2000). Direct validation of annual increments in the otoliths of juvenile southern bluefin tuna, *Thunnus maccoyii*, by means of a large-scale mark-recapture experiment with strontium chloride. *Fishery Bulletin* **98**, 25–40.
- Clemens, H. B. (1961). The migration, age, and growth of Pacific albacore (*Thunnus germon*), 1951–1958. *California Department of Fish and Game, Fish Bulletin* **115**, 1–128.
- De Metrio, G., Megalofonou, P., Caccucci, M., Sion, L., Ortiz de Zárate, V. & Acone, F. (1997). Results of tagging experiments on albacore (*Thunnus alalunga*) in the Northern Ionian and Southern Adriatic Seas from 1990 to 1995. *ICCAT Collective Volume of Scientific Papers* **46**, 148–151.
- Efron, B. & Tibshirani, R. J. (1993). *An Introduction to the Bootstrap*. New York, NY: Chapman & Hall.
- 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. *Marine and Freshwater Research* **57**, 713–724.
- Foreman, T. J. (1980). Synopsis of biological data on the albacore tuna, *Thunnus alalunga* (Bonnaterre, 1788), in the Pacific Ocean. In *Synopses of Biological Data on Eight Species of Scombrids* (Bayliff, W. H., ed.), pp. 17–70. San Diego, CA: Inter-American Tropical Tuna Commission.
- Gambell, R. & Messtorff, J. (1964). Age determination in the whiting (*Merlangius merlangus* L.) by means of the otoliths. *Journal du Conseil international pour l'Exploration de la Mer* **28**, 393–404.
- Griffiths, S. P., Fry, G. C., Manson, F. J. & Lou, D. C. (2010). Age and growth of longtail tuna (*Thunnus tonggol*) in tropical and temperate waters of the central Indo-Pacific. *ICES Journal of Marine Science* **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. *Fisheries Research* **92**, 207–220.
- Haddon, M. (2001). *Modelling and Quantitative Methods in Fisheries*. New York, NY: Chapman & Hall.
- Hilborn, R. & Walters, C. J. (1992). *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. New York, NY: Chapman & Hall.
- Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **81**, 898–903.
- Hsu, C. C. (1999). The length–weight relationship of albacore, *Thunnus alalunga*, from the Indian Ocean. *Fisheries Research* **41**, 87–92.
- Huang, H. W., Hsu, C. C., Lee, H. H. & Yeh, Y. M. (2003). Stock assessment of albacore, *Thunnus alalunga*, in the Indian Ocean by surplus production models with a new relative abundance index. *Terrestrial, Atmospheric and Oceanic Sciences* **14**, 201–220.
- ICCAT (1996). Report of the final meeting of the ICCAT Albacore Research Program. *ICCAT Collective Volume of Scientific Papers* **43**, 1–140.

- Kimura, S., Nakai, M. & Sugimoto, T. (1997). Migration of albacore, *Thunnus alalunga*, in the North Pacific Ocean in relation to large oceanic phenomena. *Fisheries Oceanography* **6**, 51–57. doi: 10.1046/j.1365-2419.1997.00029.x
- King, M. (2007). *Fisheries Biology, Assessment and Management*. Oxford: Fishing News Books.
- 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. *Fishery Bulletin* **91**, 649–663.
- Laurs, R. M., Nishimoto, R. & Wetherall, J. A. (1985). Frequency of increment formation on sagittae of North Pacific albacore (*Thunnus alalunga*). *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1552–1555.
- Megalofonou, P. (1990). Size distribution, length–weight relationships, age and sex of albacore, *Thunnus alalunga* Bonn., in the Aegean Sea. *ICCAT Collective Volume of Scientific Papers* **33**, 154–162.
- Megalofonou, P. (2000). Age and growth of Mediterranean albacore. *Journal of Fish Biology* **57**, 700–715. doi: 10.1006/jfbi.2000.1345
- Megalofonou, P., Yannopoulos, C. & Dean, J. M. (2003). The potential use of scales for estimating age and growth of Mediterranean albacore (*Thunnus alalunga*). *Journal of Applied Ichthyology* **19**, 189–194. doi: 10.1046/j.1439-0426.2003.00450.x
- Motulsky, H. J. & Christopoulos, A. (2004). *Fitting Models to Biological Data Using Linear and Nonlinear Regression*. New York, NY: Oxford University Press.
- Murray, T. 1994. A review of the biology and fisheries for albacore, *Thunnus alalunga*, in the South Pacific Ocean. *FAO Fisheries Technical Paper* **336/2**, 188–206.
- Neill, J. W. (1988). Testing for lack of fit in nonlinear regression. *The Annals of Statistics* **16**, 733–740.
- Neilson, J. D. & Campana, S. E. (2008). A validated description of age and growth of western Atlantic bluefin tuna (*Thunnus thynnus*). *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1523–1527.
- Ortiz de Zárate, V., Megalofonou, P., De Metrio, G. & Rodriguez-Cabello, C. (1996). Preliminary age validation results from tagged–recaptured fluorochrome label albacore in North East Atlantic. *ICCAT Collective Volume of Scientific Papers* **43**, 331–338.
- Otsu, T. & Sumida, R. (1968). Distribution, apparent abundance, and size composition of albacore (*Thunnus alalunga*) taken in the longline fishery based in American Samoa, 1954–65. *Fishery Bulletin of the Fish and Wildlife Service* **67**, 47–69.
- Otsu, T. & Uchida, R. N. (1959). Study of age determination by hard parts of albacore from central north Pacific and Hawaiian waters. *Fishery Bulletin of the Fish and Wildlife Service* **59**, 353–363.
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil international pour l'Exploration de la Mer* **39**, 175–192.
- Powers, J. E. (1983). Some statistical characteristics of ageing data and their ramifications in population analysis of oceanic pelagic fishes. *NOAA Technical Report NMFS* **8**, 19–24.
- Quinn, T. J. & Deriso, R. B. (1999). *Quantitative Fish Dynamics*. New York, NY: Oxford University Press.
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**.
- Santiago, J. & Arrizabalaga, H. (2005). An integrated growth study for North Atlantic albacore (*Thunnus alalunga* Bonn. 1788). *ICES Journal Marine Science* **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-American Tropical Tuna Commission, Bulletin* **23**, 33–76.
- Secor, D. H., Wingate, R. L., Neilson, J. D., Rooker, J. R. & Campana, S. E. (2009). Growth of Atlantic bluefin tuna: direct age estimates. *ICCAT Collective Volume of Scientific Papers* **64**, 405–416.
- 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. *Fisheries Research* **100**, 134–139.

- Shomura, R. S. (1966). Age and growth studies of four species of tunas in the Pacific Ocean. In *Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu – Hilo, February 28–March 12, 1966* (Manar, T. A., ed.), pp. 203–219. Honolulu, HI: State of Hawaii.
- Sparre, P. & Venema, S. C. (1998). Introduction to tropical fish stock assessment. Part 1: manual. *FAO Fisheries Technical Paper* **306/1**, 1–407.
- Stéquert, B., Panfili, J. & Dean, J. M. (1996). Age and growth of yellowfin tuna, *Thunnus albacares*, from the western Indian Ocean, based on otolith microstructure. *Fishery Bulletin* **94**, 124–134.
- Suda, A. (1966). Catch variations in the North Pacific albacore VI. The speculations about the influences of fisheries on the catch and abundance of the albacore in the North-west Pacific by use of some simplified mathematical models (continued paper - I). *Report of Nankai Regional Fisheries Research Laboratory* **24**, 1–14.
- Taylor, C. C. (1958). Cod growth and temperature. *Journal du Conseil international pour l'Exploration de la Mer* **23**, 366–370.
- Tzeng, W. N. (1990). Relationship between growth rate and age at recruitment of *Anguilla japonica* elvers in a Taiwan estuary as inferred from otolith growth increments. *Marine Biology* **107**, 75–81.
- Weisberg, S. (2005). *Applied Linear Regression*. Hoboken, NJ: John Wiley and Sons.
- Yabuta, Y. & Yukinawa, M. (1963). Growth and age of albacore. *Report of Nankai Regional Fisheries Research Laboratory* **17**, 111–120.
- Yoshida, H. O. (1968). Early life history and spawning of the albacore, *Thunnus alalunga*, in Hawaiian waters. *Fishery Bulletin of the Fish and Wildlife Service* **67**, 205–211.
- Yoshida, H. O. (1975). The American Samoa longline fishery, 1966–1971. *Fishery Bulletin* **73**, 747–765.
- Zar, J. H. (1999). *Biostatistical Analysis*, 4th edn. Upper Saddle River, NJ: Prentice Hall.

Electronic References

- Anon. (2002). A manual for age determination of southern bluefin tuna, *Thunnus maccoyii*: Otolith sampling, preparation and interpretation. *The Direct Age Estimation Workshop of the CCSBT, 11–14 June 2002, Queenscliff, Australia*. Available at http://www.ccsbt.org/userfiles/file/docs_english/operational_resolutions/age_determination_manual.pdf (last accessed 28 October 2011).
- ISC (2006). Report of the albacore working group workshop, Annex 5. *Proceedings of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, 28 November–5 December 2006, National Research Institute of Far Seas Fisheries, Orido, Japan*. Available at http://isc.ac.affrc.go.jp/pdf/ISC7pdf/Annex_5_ALBWG_Nov2Dec_06.pdf (last accessed 28 October 2011).
- ISC (2010). Report of the albacore working group workshop, Annex 9. *Proceedings of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, 12–13 July 2010, Victoria, British Columbia, Canada*. Available at http://isc.ac.affrc.go.jp/pdf/ISC10pdf/Annex_9_ISC10_ALBWG_Jul10.pdf (last accessed 28 October 2011).