Availability: 15 October 2013
IOTC-2013-WPTT15-INF13

ICES Journal of
Marine Science

ICES
CIEM
International Council for
the Exploration of the Sea
Conseil International pour
l'Exploration de la Mer

ICES Journal of Marine Science (2013), 70(7), 1439–1450. doi:10.1093/icesjms/fst093

Comparison of daily- and annual- increment counts in otoliths of bigeye (*Thunnus obesus*), yellowfin (*T. albacares*), southern bluefin (*T. maccoyii*) and albacore (*T. alalunga*) tuna

Ashley J. Williams[1]*, Bruno M. Leroy[1], Simon J. Nicol[1], Jessica H. Farley[2], Naomi P. Clear[2], Kyne Krusic-Golub[3], and Campbell R. Davies[2]

[1]*Oceanic Fisheries Programme, Secretariat of the Pacific Community, BP D5, 98848 Noumea, New Caledonia*
[2]*Wealth from Oceans Flagship, CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, Tasmania 7001, Australia*
[3]*Fish Ageing Services, PO Box 396, Portarlington, Victoria 3223, Australia*

**Corresponding Author: tel: +687 262 000; fax: +687 263 818; e-mail: ashleyw@spc.int*

Williams, A. J., Leroy, B. M., Nicol, S. J., Farley, J. H., Clear, N. P., Krusic-Golub, K., and Davies, C. R. Comparison of daily- and annual-increment counts in otoliths of bigeye (*Thunnus obesus*), yellowfin (*T. albacares*), southern bluefin (*T. maccoyii*) and albacore (*T. alalunga*) tuna. – ICES Journal of Marine Science, 70: 1439–1450.

Received 25 March 2013; accepted 21 May 2013; advance access publication 6 August 2013.

Information on the age of individuals is often required for models assessing the status of stocks. Techniques used to estimate age of tuna have varied across species and agencies, precluding meta-analyses of age and growth. We compared age estimates obtained from commonly used ageing techniques for four important tuna species: bigeye tuna, yellowfin tuna, southern bluefin tuna, and albacore tuna. Estimates of age from counts of annual increments in transverse-sectioned otoliths were generally higher than those from counts of daily increments in transverse and longitudinal sections for all species, particularly for fish older than two years. However, annual counts produced younger estimates, on average, relative to daily counts for bigeye and yellowfin tuna younger than one year. Estimates derived from daily increments in longitudinal and transverse sections were generally similar, although longitudinal sections produced relatively older age estimates for individuals older than two years. A linear or non-linear increase in the magnitude of differences between ageing methods was the best-approximating model in all cases except when comparing daily-increment counts between transverse and longitudinal otolith sections for southern bluefin tuna. These observations are consistent with a narrowing of daily increments with increasing age, resulting in under-estimates of age relative to those derived from annual increments. We conclude that (i) daily increments are unsuitable for ageing individuals over two years, especially for southern bluefin and albacore, (ii) longitudinal sections are more precise and produce older age estimates than transverse sections for daily-age estimates, (iii) there are considerable differences in these trends between species, likely dependent on longevity, and (iv) parameter estimates and/or conclusions based on meta-analyses using age data derived from different ageing methods are likely confounded with methodological biases. This result demonstrates that greater effort is required to provide consistent, validated methods for routine age determination to support the assessment and management of these valuable populations.

Keywords: age estimation, annual increments, daily increments, Pacific Ocean, sectioned otoliths, tuna.

Introduction

Tuna are a globally significant resource, with annual catches from tuna fisheries approaching 10% of the total catch from global marine capture fisheries (Miyake *et al*., 2010; FAO, 2012). The sustainability of tuna fisheries is, therefore, a high priority in all of the world's oceans. In the Pacific Ocean, which yields around 70% of the world's tuna production, the primary commercial tuna species are skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), albacore tuna (*Thunnus alalunga*), southern bluefin tuna (*Thunnus maccoyii*) and Pacific bluefin tuna (*Thunnus orientalis*) (FAO, 2012). Routine stock assessments and the development of conservation and management measures for these species is the responsibility of Regional Fisheries Management Organisations (RFMOs). The most recent assessments indicate that skipjack, yellowfin, and albacore tuna stocks are not overfished, but overfishing of bigeye tuna continues in the South Pacific Ocean (Miyake *et al.*, 2010). Overfishing is occurring for Atlantic bluefin and Southern bluefin tuna, but only Atlantic bluefin are considered to be in an overfished state (Miyake *et al.*, 2010; Anon, 2011).

Biological data are regularly collected and analysed to assist with assessing the status of tuna stocks and the development of management measures aimed at achieving sustainable levels of harvest (Lewis, 1999; Langley *et al.*, 2009). Direct size-at-age data are generally an essential input into these assessments (Francis *et al.*, 2005). Age is most reliably estimated from the analysis and interpretation of mineral depositional layers observed in fish hard parts (e.g. otoliths, spines and vertebrae) (Campana, 2001). For tuna in the Pacific region, different approaches to estimating age from otoliths have evolved for the same species, most likely due to the geographic separation of ageing laboratories that provide age data for the assessments. The most notable difference is whether increments deposited in otoliths annually or daily are used to estimate age. Daily increments are exclusively used to estimate the age of skipjack and yellowfin tuna (Wild *et al.*, 1995), but both daily and annual increments have been used to estimate the age of adult bigeye (Farley *et al.*, 2006; Schaefer and Fuller, 2006), albacore (Laurs *et al.*, 1985; Farley *et al.*, 2013) and Pacific bluefin tuna (Foreman, 1996; Shimose *et al.*, 2009). Annual increments are predominantly used to estimate the age of adult southern bluefin tuna (Gunn *et al.*, 2008). A further divergence in age estimation methods between agencies is the sectioning plane used for preparing otoliths for daily-increment analysis. While the traditional transverse sections are commonly used for stocks in the western Pacific (Lehodey and Leroy, 1999), longitudinal (or frontal) sections are more frequently used for stocks in the eastern Pacific (Wild *et al.*, 1995; Schaefer and Fuller, 2006).

For some tuna species, counts of both annual and daily increments have been validated (e.g. Laurs *et al.*, 1985; Wild *et al.*, 1995; Kalish *et al.*, 1996; Clear *et al.*, 2000a, 2000b; Schaefer and Fuller, 2006; Neilson and Campana, 2008; Farley *et al.*, 2013). However, there are limitations with the use of both annual and daily increments in otoliths to estimate age. Estimating daily age from either transverse or longitudinal otolith sections is typically feasible only for short-lived species or juveniles because increments become indistinguishable in the outer regions of otolith sections from older individuals of longer-lived species (Campana, 1992; Jones, 1992). Conversely, counting annuli for older individuals is commonly practiced, but distinguishing annual increments and/or the first one or two annual increments from other substructures can sometimes be difficult. This can result in lower precision by one year or more and potential biases between readers (Campana, 2001).

Biases and imprecision in ageing data can result in biases in estimated stock status, productivity and projected catch levels from stock assessments (Powers, 1983; Barlow, 1984; Lai and Gunderson, 1987; Eklund *et al.*, 2000; Reeves, 2003). It is, therefore, important that the various sources of error associated with these age estimates are well characterized and included in the assessment process (Morton and Bravington, 2008). Although several studies of tuna species have compared age estimates from different structures from the same fish (e.g. Neilson *et al.*, 1994; Foreman, 1996; Gunn *et al.*, 2008; Filmalter *et al.*, 2009; Farley *et al.*, 2013), few studies (e.g. Stéquert *et al.*, 1996) have compared age estimates derived from alternative methods (i.e. counts of daily and annual increments), or age estimates derived from different sections of the same structure. Comparisons of this type are important for meta-analyses that compare age estimates through time and space where differing techniques have been applied and for the development of routine protocols for tuna ageing for monitoring and assessment purposes. For example, comparisons may reveal that it is most effective and efficient to count daily increments up to two years of age and then count annuli for all older fish.

Here, we compared age estimates based on daily- and annual-increment counts and between sectioning methods for four important tuna species: bigeye and yellowfin tuna from the Pacific Ocean, albacore tuna from the South Pacific Ocean, and southern bluefin tuna from the South Pacific and Eastern Indian Oceans. We then tested alternative hypotheses of how differences in age estimates might arise between annual and daily counts from longitudinal and transverse otolith sections. Our results demonstrate the need for further investment in validation studies and comprehensive comparisons of species and ageing methods to determine the most efficient and unbiased methods for routine ageing of these valuable stocks.

Material and methods

Sampling

Samples of sagittal otoliths from bigeye, yellowfin, southern bluefin and South Pacific albacore tuna were sourced from collections of otoliths archived by Australia's Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Secretariat of the Pacific Community (SPC). Southern bluefin tuna were sampled from the Indonesian spawning grounds and southern Australia, while individuals of all other species were sampled across a broad geographic range of the western and central Pacific Ocean. Otoliths were selected from 35 bigeye tuna and 30 individual yellowfin, southern bluefin and South Pacific albacore tuna across a wide size range to maximize the potential age range sampled (Table 1).

Otolith preparation and reading

Otoliths from each species were prepared using three techniques. One otolith from each pair was sectioned in the longitudinal

Table 1. Number of otoliths selected from four tuna species by length class.

	Species			
Fork length (cm)	**Albacore**	**Bigeye**	**Southern bluefin**	**Yellowfin**
40 – 49	3		2	3
50 – 59	4	3	2	3
60 – 69	4	3		3
70 – 79	4	3	3	3
80 – 89	4	3	2	3
90 – 99	4	4	3	3
100 – 109	4	3	3	3
110 – 119	3	5	3	3
120 – 129		5	3	3
130 – 139		3		3
140 – 149		1		
150 – 159		1	2	
160 – 169			2	
170 – 179		1	2	
180 – 189			2	
190 – 199			1	
Total	30	35	30	30

plane along the primordium to the postrostral axis and the other otolith was sectioned in the transverse plane. These two sections, which contained the primordium, were prepared for daily analysis (Figure 1). An additional single section from each transverse preparation was cut and prepared for annual-age reading (Figure 2).

For the longitudinal sections, silicon rubber moulds were partially filled with clear casting resin and allowed to cure for 15 min at 50°C. Four otoliths were placed in each mould and were then covered completely with additional resin. For the transverse sections, the other member of the pair of otoliths was embedded

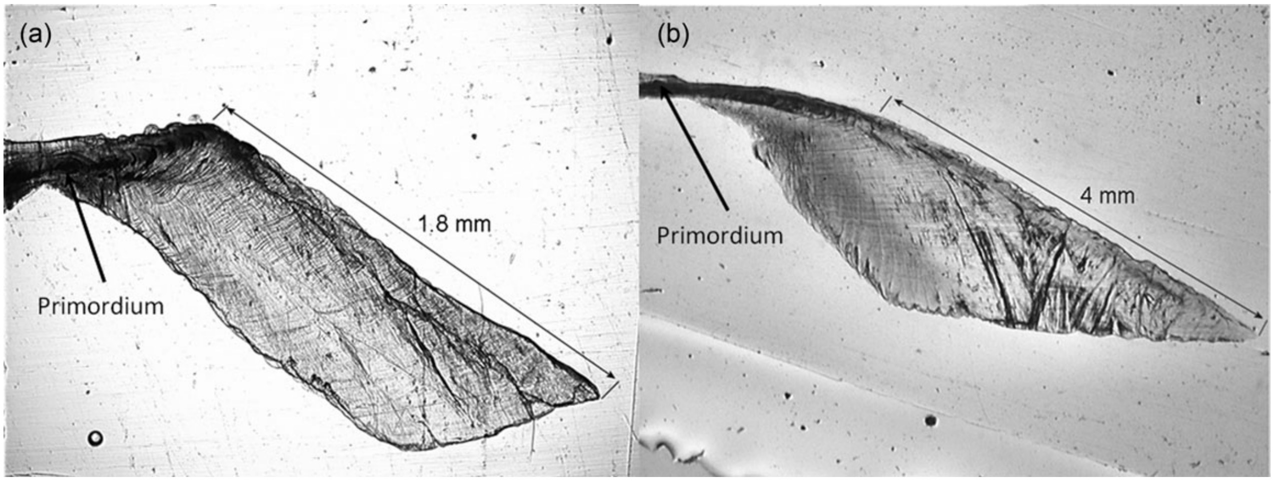

Figure 1. Transverse (**a**) and longitudinal (**b**) sections of the sagittae from a 97 cm FL bigeye tuna viewed under transmitted light showing the different length of the ventral arm in each section along which daily increments were counted.

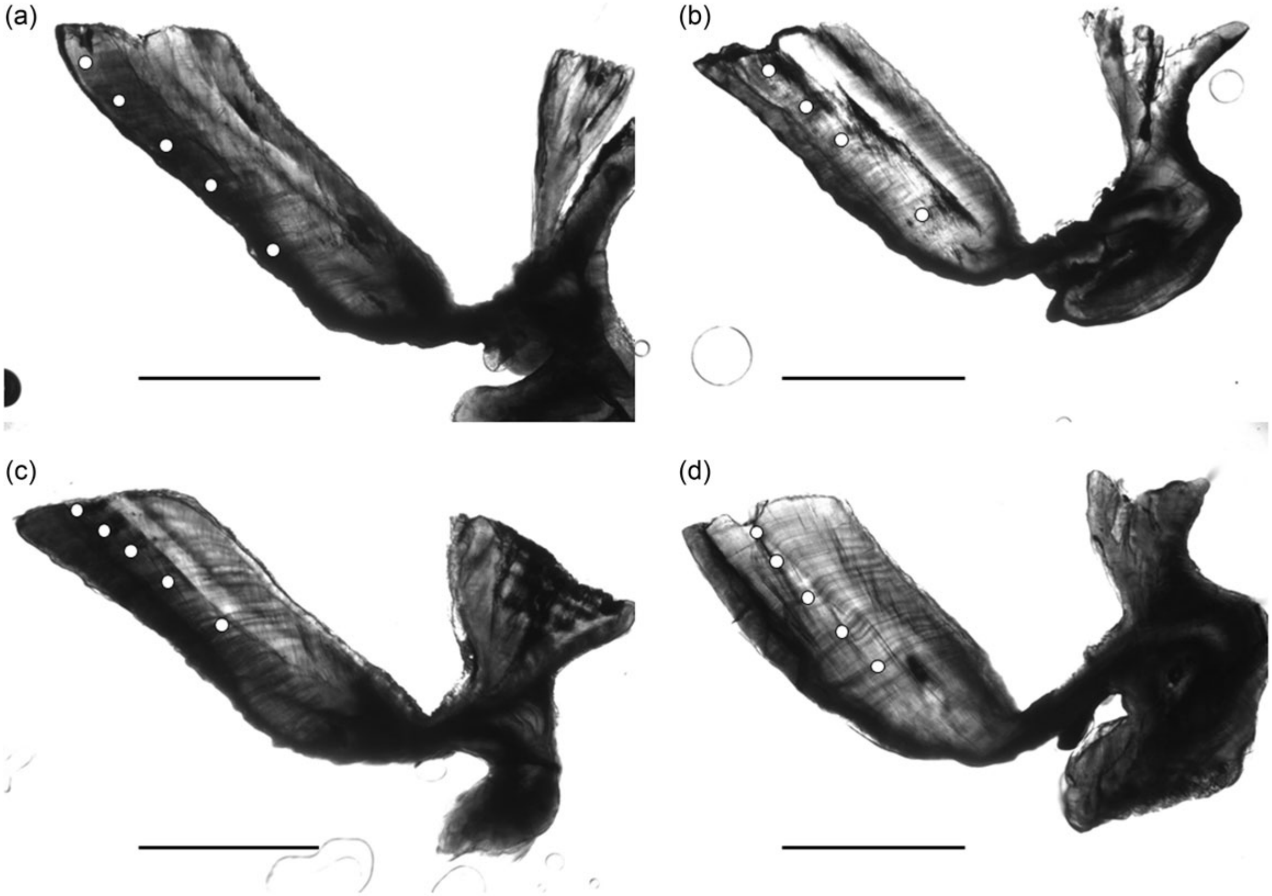

Figure 2. Transverse sections of sagittae from a 134 cm FL bigeye (**a**), 102 cm FL yellowfin (**b**), 115 cm FL southern bluefin (**c**), and 88 cm FL South Pacific albacore (**d**) viewed under transmitted light. Annual opaque increments were counted along the ventral arm and are marked with a circle on each section. Scale bars are 1 mm.

using the same methods. Once cured, the moulds were examined under a stereomicroscope and the sectioning plane (longitudinal or transverse) was marked for each otolith. Otoliths were sectioned using a modified high-speed gem-cutting saw with a 250-μm thick diamond impregnated blade. An initial section approximately 500 μm thick was taken along the marked transect that contained the primordium.

The otolith sections for daily-age estimation were fixed to glass slides with thermoplastic glue, ground with Norton waterproof sandpaper (800 and 1200 grit), and polished with aluminium powder (0.3 μm) until the primordium was reached. The slides were then placed on a hot plate to melt the thermoplastic glue and the sections were turned over, re-affixed and polished on the other side to obtain a thin section of 50–75 μm. The sections were continuously checked under a compound microscope to ensure that the sections were not over-polished. Identical methods were used for transverse and longitudinal sections. The surface of bigeye and yellowfin tuna otolith sections was partially decalcified with 5% EDTA (ethylene-diamine-tetra-acetic acid, pH 7.4) to emphasize the increments. This method was assessed for southern bluefin and albacore tuna otoliths but etching provided no improvement in the readability of increments for these two species.

An additional 300-μm section was taken from the transversely-sectioned otoliths and prepared for annual-age estimation. These sections were cleaned in water, dried and mounted on glass microscope slides with resin. Sections were then covered with further resin and a glass cover-slip. Prepared sections were placed in an oven at 35°C and allowed to cure for 3 h.

We used established protocols developed for estimating the age of different tuna species from daily (Wild *et al.*, 1995; Schaefer and Fuller, 2006) and annual (Clear *et al.*, 2000b; Anon, 2002; Farley *et al.*, 2006, 2013; Gunn *et al.*, 2008) increments in otoliths. For daily-age estimation, each otolith section was read at least twice by an experienced principal reader, and the average of the counts was used as the final age estimate. The principal reader varied between species and otolith preparation method (Table 2; R1 and R2). Five otoliths from each species and preparation method were read by a second experienced reader to examine between-reader variation. Otoliths were examined under a binocular microscope (LEICA DMLB 100) at ×400 and ×1000 magnification, depending of the microincrement spacing. Opaque microincrements were counted from the primordium to the edge of the otolith along the ventral "long" arm (Figure 1). A magnification of ×400 or less was used to count the first 150–200 microincrements and ×1000 was used to count the increments thereafter. If no clear pattern of alternating opaque and translucent increments could be seen in the otolith section, an age was not assigned.

Table 2. Design matrix for four otolith readers (R1–R4) using three methods to estimate age for four tuna species.

	Age estimation method		
Species	**DT**	**DL**	**AT**
Bigeye	R1 (R2)	R1 (R2)	R3, R4
Yellowfin	R1 (R2)	R1 (R2)	R3, R4
Southern bluefin	R2 (R1)	R2 (R1)	R3, R4
Albacore	R2 (R1)	R2 (R1)	R3, R4

Otolith reader in brackets read a subsample. AT = Annual counts from transverse sections, DL = daily counts from longitudinal sections, DT = daily counts from transverse sections.

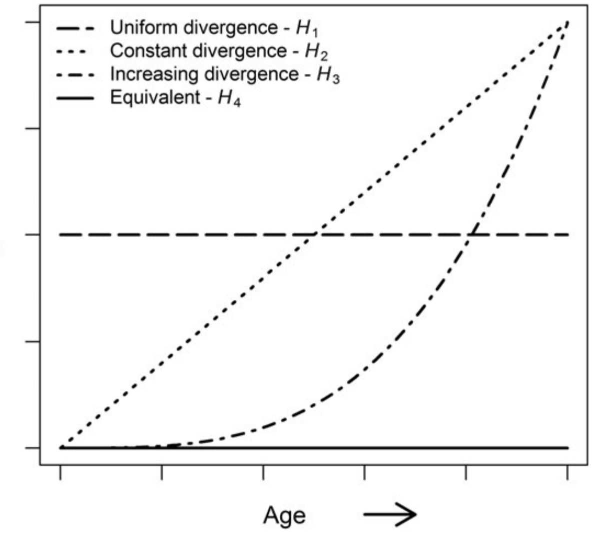

Figure 3. Expected patterns in the magnitude of differences in age estimates (d) with increasing nominal age for four alternative hypotheses.

For annual-age estimation, each transverse section was read twice by two experienced readers (R3 and R4). Otoliths were read using the methods described by Anon (2002), Farley *et al.* (2006) and Farley *et al.* (2013) for southern bluefin, bigeye and albacore tuna, respectively. Yellowfin tuna otoliths were read based on the experience gained from the other species. Otoliths were given a final count by each reader and, if the counts agreed between readers, that count was used as the final age. When counts differed, an agreed final age was assigned after a joint reading by both readers. If no pattern could be seen in the otolith section, the otolith was not aged. Otoliths for both daily and annual ageing were read without reference to size of fish or capture date. An initial readability score from 1 (poor) to 5 (excellent) was assigned by the principal otolith reader to each otolith section for both daily and annual ageing. For the purposes of the final analysis, these scores were used to assign the readability of each otolith as either poor (readability score ≤2) or good (readability score ≥3).

Age-bias plots (Campana *et al.*, 1995) were used to look for systematic differences and evaluate consistency of age estimates between readers for both daily- and annual-age estimates. The precision of age estimates was compared between readers using the index of average percent error (APE; Beamish and Fournier, 1981) and the coefficient of variation (CV; Chang, 1982).

Data analysis

Age estimates from daily-increment counts were standardized to fractional annual-age estimates, in years, for all comparisons between reading methods. Counts of annual increments were not converted into fractional annual ages given the difficulty in estimating a birth date and time of otolith increment formation for the tropical species (bigeye and yellowfin tuna) that spawn continuously throughout the year in equatorial waters. Implicitly this means we assumed that counts of annual increments were an estimate of age in whole years.

We tested four hypotheses about how differences in age estimates might arise from the different methods. These hypotheses were derived from those used to assess patterns in ageing errors from multiple reads of the same otolith (Marriott and Mapstone, 2006). The first hypothesis (H_1: uniform divergent) assumed a constant magnitude of differences between age estimates across all nominal ages, which may occur when ageing errors arise consistently with the same structure, such as when interpreting the first or last (marginal) increments. The second hypothesis (H_2: constant divergent) assumed that the magnitude of differences between age estimates increased linearly with nominal age because of such phenomena as reducing increment width with increasing age. The third hypothesis (H_3: increasing divergent) assumed that the magnitude of differences between age estimates increased non-linearly with nominal age for the same reasons as H_2. The final hypothesis (H_4: equivalent) assumed no difference in age estimates across all nominal ages. These hypotheses were tested for the three ageing methods: (i) daily and annual counts from transverse otolith sections, (ii) daily counts from longitudinal and transverse otolith sections, and (iii) daily counts from longitudinal otolith sections and annual counts from transverse otolith sections (Figure 3; Table 3).

The differences between age estimates, d, from each pair of readings of an otolith section was calculated for each nominal age, t. Nonlinear regression of d on t was used to fit the four models to the observed differences in age estimates for each species. The fit of each alternative model was compared for each processing method and species using Akaike's Information Criterion for small sample sizes (AIC_c: Burnham and Anderson, 2002) to infer which alternative hypothesis was best supported by the data. Models with an AIC_c value within two of that calculated for the best approximating model (lowest AIC_c) were considered to describe the data well (Burnham and Anderson, 2002).

Results

The precision of annual- and daily-age estimates, as indicated by the APE and CV, varied between species and reading methods (Table 4). For annual-age estimates, the APE and CV were lower for yellowfin, southern bluefin and albacore tuna than for bigeye tuna. The high APE and CV for bigeye was mostly due to Reader 2 overestimating the age of 0 and one-year-old bigeye tuna relative to Reader 1 (Figure 4). There was no clear evidence of bias between readers for the other three species, except for a positive bias for southern bluefin in age classes older than 9 years (Figure 4). For annual estimates, more than 80% of the ages assigned by the two readers for each species were within ± one year.

Table 3. Candidate models used to investigate the likelihood of hypotheses about differences in age estimates between readings of otoliths from four tuna species.

Hypothesis	Name	Model	Constraints
H_1	p uniform divergence	$d = c$	None
H_2	p constant divergence	$d = p(t - 1)+c$	$0 \le p \le 1$
H_3	p increasing divergence	$d = p(1+b)^{t-1}+c$	$0 \le p \le 1$; $b > 0$
H_4	equivalent	$d = 0$	None

d = differences between age estimates, p = probability of obtaining a different age estimate at each age (year), b = rate at which p changes, c = expected minimum difference between readings (Marriott and Mapstone, 2006).

For daily-age estimates, the APE and CV were lower for longitudinal sections in all species except albacore. Daily increments were often more difficult to interpret in transverse sections than in longitudinal sections, particularly for bigeye and yellowfin tuna, which might account for the higher APE and CV for transverse sections for these species. The APE was <10 for all species, and both reading methods, except for transverse sections of yellowfin otoliths and longitudinal sections of albacore otoliths, indicating reasonable precision between age readings. Interestingly, the APE for the complementary sections for yellowfin and albacore were <5. There was a bias between daily-age readings, with Reader 2 consistently underestimating ages >400 days compared with Reader 1 (Figure 5). However, the differences between age estimates from each reader were < 6 months for 75% of all transverse sections and 81% of all longitudinal sections. Due to poor readability, it was not possible to assign an age estimate to some otolith sections (Table 4).

Counting annuli in transverse-sectioned otoliths resulted in older age estimates, on average, than counting daily increments in transverse- and longitudinally-sectioned otoliths for southern bluefin and albacore tuna, particularly for the older age classes (Figure 6). The difference between annuli and daily-increment counts for bigeye and yellowfin tuna was less clear, but on average annual counts produced younger age estimates for individuals younger than one year, and older age estimates for individuals older than two years, compared with daily-increment counts (Figure 6). It is worth noting that the largest bigeye tuna (175 cm FL) was estimated to be 14 years of age based on annual-increment counts, yet it was not possible to count the number of daily increments from either transverse or longitudinal sections of the otoliths from this fish. Age estimates derived from daily increments in longitudinal and transverse sections were similar across most ages, but on average, longitudinal sections produced older age estimates for older individuals (Figure 6).

There was a similar distribution in the age estimates from otolith sections with good and poor readability for southern bluefin and albacore tuna (Figure 6), suggesting that readability of otolith sections did not bias the comparisons between processing methods for these species. However, for bigeye and yellowfin, all sections classified as having good readability were estimated to be younger than two years from all processing methods, suggesting difficulty in interpreting increments in individuals older than two years for these species.

Table 4. Precision of age estimates between readers for annual-age estimates from transverse sections (AT) and daily-age estimates from transverse (DT) and longitudinal (DL) otolith sections of four tuna species.

	APE			CV			Number not assigned an age		
Species	AT	DT	DL	AT	DT	DL	AT	DT	DL
Bigeye	22.54	9.24	6.64	31.87	13.07	9.39	0	3	4
Yellowfin	9.84	13.09	3.84	16.14	18.51	5.43	4	7	8
Southern bluefin	5.72	9.54	4.81	8.09	13.48	6.81	0	4	12
Albacore	6.01	3.59	16.06	8.50	5.08	22.71	0	2	2

APE = average percent error, CV = coefficient of variation. Number of sections not assigned an age estimate are indicated.

Examination of differences between age estimates derived from each reading method revealed distinct patterns (Figure 7). The H_2 model was the best-approximating model to describe the trends in age differences with nominal age for all comparisons between annuli and daily-age estimates, except for the comparison between annuli and daily-age estimates from transverse section for yellowfin tuna, for which the H_3 model provided the best fit, even when the oldest fish (6 years old, based on annual increments) was removed from the analysis (Table 5). The best-approximating models for comparisons between daily-age estimates from longitudinal and transverse sections were the H_3 model for bigeye and yellowfin tuna, the H_4 model for southern bluefin tuna and the H_2 model for albacore tuna (Table 5). However, the difference in daily-age estimates was substantially larger for a small number of bigeye and yellowfin tuna >3.5 years of age. Furthermore, the estimate of p for bigeye (0.002) and yellowfin (0.0001) tuna was very low, indicating a low probability of obtaining different age estimates between the two methods. Therefore, fish older than 3.5 years were removed from the analysis to examine the influence of these individuals on the predicted patterns in ageing errors. The best-approximating models following removal of these individuals were the H_1 model ($\text{AIC}_c = 1.91$) for bigeye and the H_4 model ($\text{AIC}_c = 5.75$) for yellowfin tuna (Figure 7). There was also substantial support ($\Delta\text{AIC}_c < 2$) for the H_4 model ($\text{AIC}_c = 3.22$) for bigeye and the H_1 model ($\text{AIC}_c = 6.13$) for yellowfin. The predicted difference between readings (d) for the H_1 model was small for both bigeye (-0.10 years) and yellowfin (0.10 years) tuna and suggested that longitudinal sections produce lower age estimates for bigeye tuna but higher age estimates for yellowfin tuna, compared with transverse sections.

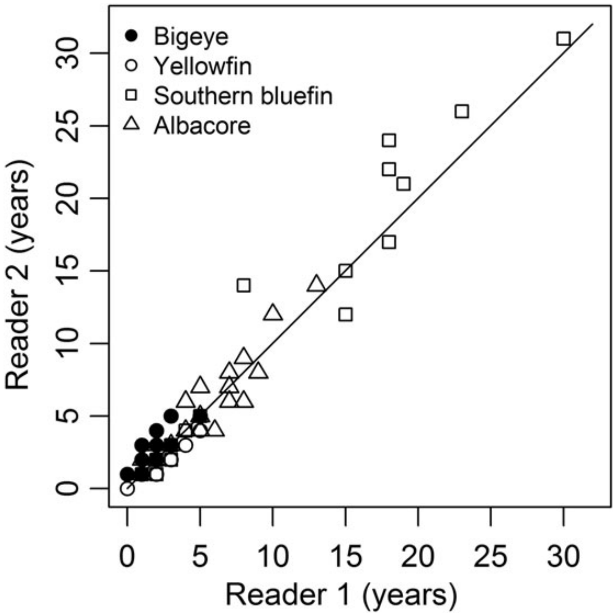

Figure 4. Age bias plots comparing annual-age estimates from two readers for four tuna species.

Discussion

Information on age of individuals has become increasingly important for stock assessments of tuna, either as an external data source for comparison with estimates of population parameters generated by the assessment models or as direct input data for these models. Oceanic tuna stocks are distributed across entire ocean basins, and age information is rarely collected in a single study at this scale (but see Williams *et al.*, 2012). Consequently, the synthesis of age information for a stock requires the interpretation of results from several studies undertaken at different times and locations, often using different ageing methods. Our study indicates that meta-analyses using data derived from different ageing methods are likely to be biased. We provide guidance on the development of standard approaches for the ageing of the major species of Pacific tuna.

We tested four hypotheses about how differences in age estimates might arise between annual and daily counts from longitudinal and

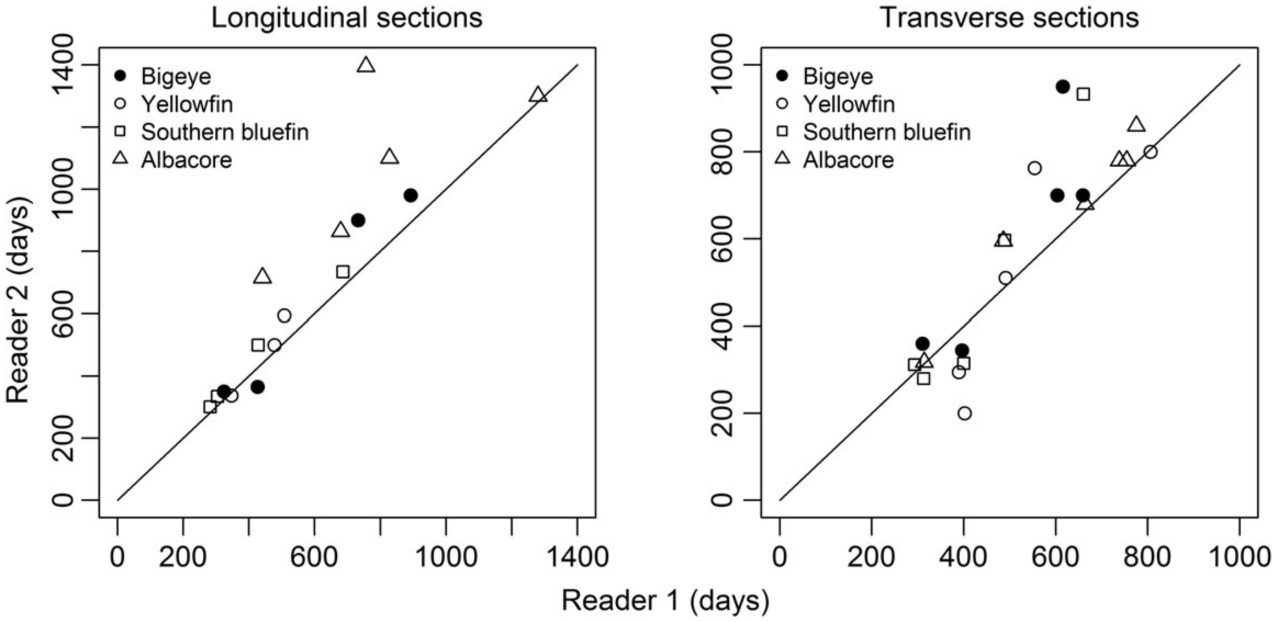

Figure 5. Age bias plots comparing daily-age estimates from two readers and two age estimation methods (longitudinal and transverse sections) for four tuna species.

Table 5. Parameter estimates and model fits to differences in age estimates between different age estimation methods for four tuna species.

Species	Comparison	Model	*c*	*b*	*p*	AIC_c
BET	AT vs. DL	H_1	−0.01	–	–	31.50
		H_2	**−0.21**	**–**	**0.26**	**19.19**
		H_3	−0.39	0.19	1.00	21.87
		H_4	–	–	–	29.10
	AT vs. DT	H_1	0.27	–	–	48.53
		H_2	**−0.13**	**–**	**0.40**	**12.98**
		H_3	−0.35	0.24	1.00	14.40
		H_4	–	–	–	50.98
	DL vs. DT	H_1	0.18	–	–	16.54
		H_2	0.005	–	0.18	7.92
		H_3	**0.06**	**2.82**	**0.002**	**4.81**
		H_4	–	–	–	20.06
YFT	AT vs. DL	H_1	0.61	–	–	46.14
		H_2	**0.05**	**–**	**0.51**	**20.36**
		H_3	−0.10	0.25	1.00	28.96
		H_4	–	–	–	51.18
	AT vs. DT	H_1	0.48	–	–	80.80
		H_2	−0.15	–	0.71	38.04
		H_3	**−0.44**	**0.35**	**1.00**	**25.81**
		H_4	–	–	–	83.33
	DL vs. DT	H_1	0.04	–	–	34.32
		H_2	−0.25	–	0.51	27.84
		H_3	**−0.12**	**12.90**	**0.00**	**11.49**
		H_4	–	–	–	31.75
SBT	AT vs. DL	H_1	5.07	–	–	194.83
		H_2	**−0.59**	**–**	**0.91**	**62.17**
		H_3	1.97	0.12	1.00	150.58
		H_4	–	–	–	203.66
	AT vs. DT	H_1	3.67	–	–	170.47
		H_2	**−0.36**	**–**	**0.84**	**49.78**
		H_3	1.11	0.14	1.00	108.97
		H_4	–	–	–	178.96
	DL vs. DT	H_1	0.02	–	–	42.17
		H_2	−0.01	–	0.02	44.72
		H_3	−0.01	2.00	0.00	47.13
		H_4	**–**	**–**	**–**	**39.82**
ALB	AT vs. DL	H_1	2.57	–	–	124.80
		H_2	**−0.22**	**–**	**0.79**	**27.02**
		H_3	0.73	0.20	1.00	78.01
		H_4	–	–	–	138.73
	AT vs. DT	H_1	3.67	–	–	123.81
		H_2	**−0.36**	**–**	**0.84**	**33.68**
		H_3	1.11	0.14	1.00	79.23
		H_4	–	–	–	134.67
	DL vs. DT	H_1	0.19	–	–	18.79
		H_2	**−0.07**	**–**	**0.27**	**7.36**
		H_3	−0.26	0.20	1.00	10.23
		H_4	–	–	–	23.09

Best-fit models, evaluated using AIC_c, are in bold. AT = Annual counts from transverse-sectioned otoliths, DL = daily counts from longitudinal-sectioned otoliths, DT = daily counts from transverse-sectioned otoliths. See Table 3 for details of models. *c*, *b* and *p* are model parameters.

transverse otolith sections. This provided statistical support for only two of these hypotheses: H_2 for all species, which predicted that the magnitude of differences between age estimates increased linearly with nominal age; and H_3 for yellowfin tuna when comparing annual- to daily-age estimates from transverse sections where the magnitude of differences between age estimates increased non-linearly with nominal age. These observations are consistent with a reduction in the width of daily increments with increasing age, corresponding to an increase in the magnitude of errors in correctly identifying and resolving daily increments. This relationship of decreasing daily-increment width with age is a common observation for many fish species (Campana and Neilson, 1985; Campana, 1992) and is generally the primary reason for restricting daily ageing methods to short-lived species, youngest age classes of long-lived species (Campana, 1992), or for identifying the position of the first annual increment in older individuals for annual ageing methods (Farley *et al.*, 2006; 2013).

With the exception of annual-age estimation for yellowfin tuna and daily-age estimation for southern bluefin tuna, both daily and annual ageing methods have been validated for these tuna species (Wild and Foreman, 1980; Laurs *et al.*, 1985; Clear *et al.*, 2000a, 2000b; Farley, *et al.*, 2003, 2006, 2013; Schaefer and Fuller, 2006), based on information obtained from chemical-based mark-recapture experiments and otolith increment analyses (Table 6). Our results, however, show a striking lack of correspondence between annual and daily ageing methods for yellowfin, southern bluefin and albacore tuna older than one year of age, and for bigeye tuna older than two years of age. Beyond these ages, the estimate of age from daily increments was consistently lower than that from annual increments. Schaefer and Fuller (2006) and Wild (1986) suggest that the age of bigeye and yellowfin tuna can be reliably estimated up to four or five years of age using daily increments. In contrast, Campana (1992) suggests that ageing of tuna beyond age three or four years using daily increments is not feasible because the increments become indistinguishable near the otolith margin. Our results demonstrate that it is probably not valid to assume that daily and annual ageing will result in equivalent estimates of age for tuna older than two years. Although the number of individuals aged with the different methods in this study was low, the consistency of the results within and across species indicates that the trend observed is likely to be real and warrants investment in large comparative studies.

The broader issue is that the available data for validation of ageing methods, particularly tagging experiments for which the sample size for individuals at liberty for periods longer than 12 months has been generally small and the individuals tagged have also generally been small/young (Table 6). For validation of daily increments, only one bigeye and two yellowfin were at liberty for 12 months or more after chemical marking of otoliths (Wild and Foreman, 1980; Wild *et al.*, 1995; Schaefer and Fuller, 2006). Furthermore, daily-age validation studies for bigeye, yellowfin and albacore have not reported information on the estimated age of individuals, from which the chemically marked otoliths were collected, making it difficult to assess the applicability of the results from daily-age validation studies to older individuals. For validation of annual increments, the sample sizes for albacore, bigeye and southern bluefin tuna ranged from 2–52, for fish at liberty for 12 months or more after chemical marking of otoliths (Clear *et al.*, 2000b; Farley *et al.*, 2003, 2013). Maximum age estimates were 8, 13 and 4 years for bigeye, southern bluefin and albacore, respectively (Table 6), indicating a greater potential longevity than that estimated from daily increments, at least for bigeye and southern bluefin tuna. Kalish *et al.* (1996) further extended the estimate of longevity for southern bluefin tuna to 34 years using radiocarbon dating to validate the age of 22 large individuals (Table 6). Further validation studies for both annual and daily methods, particularly for bigeye, yellowfin and albacore tuna, over more extended periods and size/age ranges are required to improve the comparison between daily- and annual-age estimation methods for tuna.

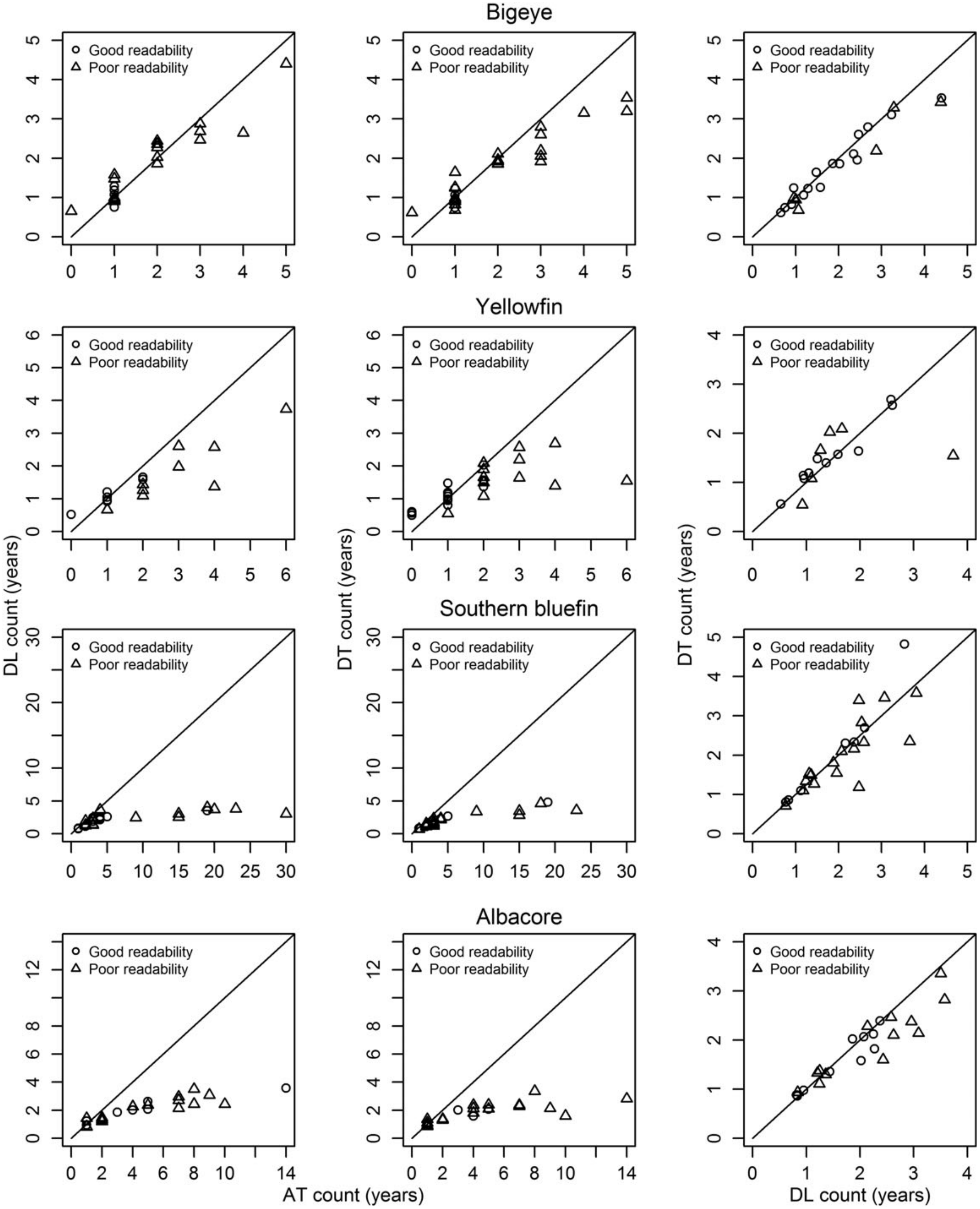

Figure 6. Age bias plots comparing age estimates from one reader for each of three age estimation methods (AT = Annual counts from transverse-sectioned otoliths, DL = daily counts from longitudinal-sectioned otoliths, DT = daily counts from transverse-sectioned otoliths) for four tuna species. The readability of otolith sections is indicated as good (readability score ≥3) or poor (readability score ≤2).

The reading of longitudinal sections rather than transverse sections has been used to extend the age to which individuals can be aged using daily increments. This is primarily because longitudinal sections are thought to provide a longer reading plane and wider increments than transverse sections (Wild and Foreman, 1980; Secor *et al.*, 1991; Schaefer and Fuller, 2006). Our observations

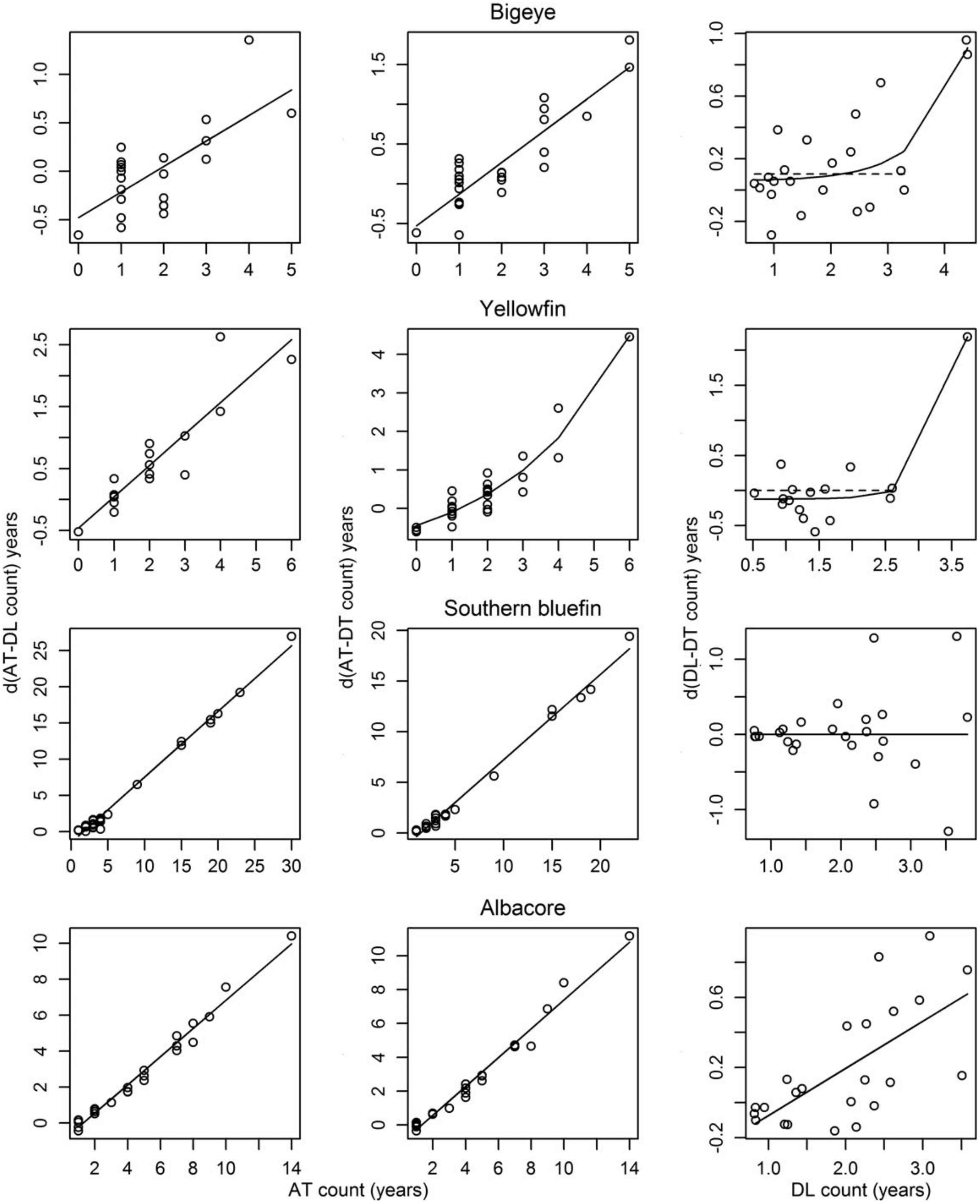

Figure 7. Best model fits to differences in age estimates (*d*) between readings of otoliths for each of three age estimation methods (AT = Annual counts from transverse-sectioned otoliths, DL = daily counts from longitudinal-sectioned otoliths, DT = daily counts from transverse-sectioned otoliths) for four tuna species. Dotted lines indicate additional model fits with fish older than 3.5 years removed for differences between longitudinal and transverse daily-age estimates for bigeye and yellowfin tuna.

Table 6. Summary of age validation studies for four species of tuna.

Species	Region	Sample size	Validation method	Structure	Increment type	Time at liberty (days)	Length range (cm)	Age range (years)	Source
Bigeye	East Pacific	70	OTC	otolith	daily	15–551	38–135	–	(Schaefer and Fuller, 2006)
	East Atlantic	83	OTC	otolith	daily	10–412	44–95	–	(Hallier *et al.*, 2005)
	West Pacific	10	SrCl	otolith	annual	207–2071	72–159	2–8	(Clear *et al.*, 2000a)
	West Pacific	1149	ETA	dorsal spine	annual	–	46–189	1–10	(Sun *et al.*, 2001)
	West Pacific & East Indian	1611	MIA & ETA	otolith	annual	–	39–178	1–16	(Farley *et al.*, 2006)
Yellowfin	East Pacific	53	OTC	otolith	daily	3–389	40–110	–	(Wild and Foreman, 1980)
	East Pacific	74	OTC	otolith	daily	<515	<148	–	(Wild *et al.*, 1995)
	West Pacific	12	OTC	otolith	daily	3–39	25–40	–	(Yamanaka, 1990)
	West Pacific	3	OTC	otolith	daily	49–175	42–91	–	(Lehodey and Leroy, 1999)
	West Atlantic	257	MIA	dorsal spine	annual	–	45–191	1–6	(Lessa and Duarte-Neto, 2004)
Southern bluefin	East Indian	5	Tagging	otolith	daily	292–975	40–110	1–3	(Tomoyuki and Sachiko, 1996)
	South Australia	59	SrCl	otolith	annual	8–1638	45–102	2–6	(Clear *et al.*, 2000b)
	South Australia	2	Tagging	–	annual	3500–3927	45–163	1–13	(Clear *et al.*, 2000b)
	South Australia & Indonesia	22	Radiocarbon	otolith	annual	–	55–201	1–34	(Kalish *et al.*, 1996)
	Indo-Pacific	61	MIA	otolith	annual	–	–	2	(Gunn *et al.*, 2008)
Albacore	North Pacific	116	OTC	otolith	daily	7–1142	51–97	–	(Laurs *et al.*, 1985)
	North Pacific	274	ETA	otolith	annual	–	58–118	1–14	(Chen *et al.*, 2012)
	South Pacific	3	OTC	otolith	annual	322–1104	51–83	2–4	(Farley *et al.*, 2013)
	South Pacific	1860	MIA	otolith	annual	–	54–133	2–14	(Farley *et al.*, 2013)
	East Atlantic	29	OTC	dorsal spine	annual	58–829	54–91	–	(Ortiz de Zárate *et al.*, 1996)
	Mediterranean	5	OTC	dorsal spine	annual	305–1157	66–77	–	(Megalofonou, 2000)

Validation methods included oxytetracycline mark-recapture experiments (OTC), Strontium Chloride ($SrCl_2$) mark-recapture experiments (SrCl), conventional tag-recapture experiments (Tagging), bomb-radiocarbon dating (Radiocarbon), marginal increment analysis (MIA) and edge type analysis (ETA).

were consistent with this assumption for albacore, for which the age estimated from longitudinal-sectioned otoliths were generally higher than that estimated from transverse sections from the other member of the pair of otoliths. For bigeye and yellowfin tuna, there was some evidence for higher age estimates from longitudinal sections, but there was no evidence for a difference in age estimates between transverse and longitudinal otolith sections for southern bluefin tuna. The predicted difference between readings from longitudinal and transverse sections for the uniform divergence hypothesis was approximately 37 days (0.1 years) for both bigeye and yellowfin tuna. We observed that the first 50 or so increments near the primordium were more difficult to interpret for transverse sections than for longitudinal sections for both species, which may explain the observed differences. Furthermore, the APE and CV for bigeye and yellowfin tuna were lower for longitudinal sections than for transverse sections, indicating greater precision in age estimates from longitudinal sections for these species. This indicates that longitudinal sections may be the preferable processing method for estimating daily ages of yellowfin and bigeye up to two years of age.

Two further areas of uncertainty in the annual-age estimates are associated with the number of transverse sections read per otolith and the determination of birth date and time of otolith increment formation for bigeye and yellowfin tuna. The common approach adopted for reading annuli from tuna otoliths is to prepare four or five transverse sections (Anon, 2002; Farley *et al.*, 2006, 2013). The reader is able to search for consistent patterns among the sections before selecting the most interpretable of these to read. This was not possible in this experiment as transverse sections were also cut for daily ageing from the same otolith. Consequently, some of the immediate departure observed between daily and annual estimates may be due to the compromised quality of some of the sections that were read. However, given that we observed a consistent bias in daily-age estimates being lower than annual estimates beyond age one or two years, rather than a random pattern, and a high level of agreement between readers, it is likely that the contribution of this was not substantial.

To assign each fish to its correct age class when using annual-ageing methods, an assumed birth date and time of annual-increment formation are required so that the final count can be adjusted according to the capture date of the fish. For species or locations with restricted spawning periods/seasons, assigning a nominal birth date that approximates the real birth date is relatively straightforward. Bigeye and yellowfin in equatorial waters, however, are known to spawn year-round when surface water temperatures are $>24^{\circ}C$ (Schaefer, 2001; Schaefer *et al.*, 2005) and, consequently, assigning a birth date is more difficult in these areas. To assign a formation date for the opaque increment requires marginal increment analysis or edge type analysis (Campana, 2001) to determine if increment formation occurs consistently within a particular time period or season in the year. No marginal-increment analysis or edge-type analysis for bigeye has been undertaken on otoliths collected from equatorial waters. Farley *et al.* (2006) observed that the timing of opaque increment formation in bigeye otoliths varies depending upon location, and detecting the cyclic pattern needed to assign an increment formation date can also vary between methods. Consequently, assigning a birth date and a date when the opaque growth increment forms is highly uncertain for species occupying equatorial waters. It is feasible that for bigeye and yellowfin in this study, the assignment of fish to an age class was incorrect and we have consistently overestimated the annual age. The collection of bigeye and yellowfin otoliths from equatorial waters with systematic temporal replication is required to determine if there is a seasonal pattern to increment deposition via marginal-increment and edge-type analyses.

The clarity of tuna otolith sections is typically highly variable (Anon, 2002; Farley *et al.*, 2006, 2013) and in this study we noted many cases for which we were not able to read all sections from the same species with similar confidence, and for some sections an age could not be assigned. Cutting multiple transverse sections from an otolith has the advantage of at least one section being clear enough to interpret, and allows the age to be estimated from the section(s) with the highest clarity (Farley *et al.*, 2006; Gunn *et al.*, 2008). Future ageing studies for tuna would benefit from taking multiple transverse sections from one otolith for annual-age estimation and, if required for some individuals, a single section from the other member of the pair of otoliths for daily-age estimation. This approach would maximize the accuracy of age estimates for individuals greater than two years of age and reduce costs, because the cost and time required to process and read otoliths for annual-age estimation is substantially less than that required for daily-age estimation. However, for species other than those examined here, we recommend testing the precision and bias of this approach compared with other routine techniques.

In the case of the four tuna species presented here, we conclude that (i) daily increments are unsuitable for ageing individuals over two years, especially for southern bluefin and albacore, (ii) longitudinal sections are more precise and produce older age estimates than transverse sections for daily-age estimates, (iii) there are considerable differences in these trends between species, likely dependent on longevity, and as a result (iv) parameter estimates and/or conclusions based on meta-analyses using age data derived from different ageing methods are likely confounded with methodological biases. We do not contend that the quantitative results for these four species will be applicable to populations of these species globally. We do, however, contend that the general qualitative conclusions from this work highlight the importance of improving the fundamentals of the age data available for monitoring and assessment. Much of the available age data for these species has been collected using a range of sampling regimes and ageing methods, which vary within and among species and stocks and over time. Our results demonstrate the need for systematic comparative studies to determine standard ageing procedures and improve the quality, consistency and efficiency of size-at-age monitoring programs for these globally significant fisheries.

Acknowledgements

SJN, AJW, BML, NPC, JHF and KK-G designed the study; BML, KK-G, JHF and NPC prepared and read the otoliths; AJW analysed the data; and all authors contributed to the writing of the paper. Additional assistance in preparation of the otoliths was provided by Andrew Brown of Fish Ageing Services. We thank Rik Buckworth and Shane Griffiths for useful comments on the manuscript.

Funding

This research is part of the 9th European Union Development Fund SCIFISH project. Additional funding was provided by the Commonwealth Scientific and Industrial Research Organisation's Wealth from Oceans Flagship.

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.

Anon. 2011. Report of the 16th meeting of the CCSBT Scientific Committee, 18–28 July 2011, Bali Indonesia.

Barlow, J. 1984. Mortality estimation: biased results from unbiased ages. Canadian Journal of Fisheries and Aquatic Sciences, 41: 1843–1847.

Beamish, R. J., and 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.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd edn. Springer-Verlag: New York.

Campana, S. E. 1992. Measurement and interpretation of the microstructure of fish otoliths. *In* Otolith Microstructure Examination and Analysis'. Ed. by D. K. Stevenson, and S. E. Campana. Canadian Special Publication of Fisheries and Aquatic Sciences, 117: 59–71.

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.

Campana, S. E., Annand, C. M., and McMillan, J. I. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society, 124: 131–138.

Campana, S. E., and Neilson, J. D. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences, 42: 1014–1032.

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

Clear, N., Davis, T., and Carter, T. 2000a. Developing techniques to estimate the age of bigeye and broadbill swordfish off eastern Australia: a pilot study. Final report No. 98/113 for the Fisheries Research Development Corporation Project, Australia.

Clear, N. P., Gunn, J. S., and Rees, A. J. 2000b. 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.

Eklund, J., Parmanne, R., and Aneer, G. 2000. Between-reader variation in herring otolith ages and effects on estimated population parameters. Fisheries Research, 46: 147–154.

FAO. 2012. The State of World Fisheries and Aquaculture 2012. FAO, Rome.

Farley, J., Clear, N., Leroy, B., Davis, T., and McPherson, G. 2003. Age and growth of bigeye tuna (*Thunnus obesus*) from the eastern and western AFZ. Final report No. 2000/100 for the Fisheries Research and Development Corporation, Australia.

Farley, J. H., Clear, N. P., Leroy, B., Davis, T. L. O., and 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.

Farley, J. H., Williams, A. J., Clear, N. P., Davies, C. R., and Nicol, S. J. 2013. Age determination and validation for South Pacific albacore *Thunnus alalunga*. Journal of Fish Biology, 82: 1523–1544.

Filmalter, J. D., Weyl, O. L. F., and Sauer, W. 2009. Otoliths and vertebrae as potential hard structures for ageing South African yellowfin tuna *Thunnus albacores*. African Journal of Marine Science, 31: 271–276.

Foreman, T. 1996. Estimates of age and growth, and an assessment of ageing techniques, for northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. Bulletin of the Inter-American Tropical Tuna Commission, 21: 75–123.

Francis, R. I. C. C., Harley, S. J., Campana, S. E., and Doering-Arjes, P. 2005. Use of otolith weight in length-mediated estimation of proportions at age. Marine and Freshwater Research, 56: 735–743.

Gunn, J. S., Clear, N. P., Carter, T. I., Rees, A. J., Stanley, C. A., Farley, J. H., and 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.

Hallier, J., Stequert, B., Maury, O., and Bard, F. 2005. Growth of bigeye tuna (*Thunnus obesus*) in the eastern Atlantic Ocean from tagging recapture data and otolith readings. ICATT Collective Volume of Scientific papers, 57: 181–194.

Jones, C. M. 1992. Development and application of the otolith increment technique. *In* Otolith Microstructure Examination and Analysis, pp. 1–11. Ed. by D. K. Stevenson, and S. E. Campana. Canadian Special Publication of Fisheries and Aquatic Sciences, 117.

Kalish, J. M., Johnston, J. M., Gunn, J. S., and Clear, N. P. 1996. Use of the bomb radiocarbon chronometer to determine age of southern bluefin tuna *Thunnus maccoyii*. Marine Ecology Progress Series, 143: 1–8.

Lai, H. L., and Gunderson, D. R. 1987. Effects of ageing errors on estimates of growth, mortality and yield per recruit for walleye pollock (*Theragra chalcogramma*). Fisheries Research, 5: 287–302.

Langley, A., Wright, A., Hurry, G., Hampton, J., Aqorua, T., and Rodwell, L. 2009. Slow steps towards management of the world's largest tuna fishery. Marine Policy, 33: 271–279.

Laurs, R. M., Nishimoto, R., and 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.

Lehodey, P., and Leroy, B. 1999. Age and growth of yellowfin tuna (*Thunnus albacares*) from the western and central Pacific Ocean as indicated by daily growth increments and tagging data. Working Paper YFT–2, 12th Meeting of the Standing Committee on Tuna and Billfish, Tahiti.

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

Lewis, A. 1999. Monitoring tuna fisheries in the western Pacific. *In* Proceedings of the International Conference on Integrated Fisheries Monitoring. Ed. by C. P. Nolan. FAO, Rome. 378pp.

Marriott, R. J., and Mapstone, B. D. 2006. Consequences of inappropriate criteria for accepting age estimates from otoliths, with a case study for a long-lived tropical reef fish. Canadian Journal of Fisheries and Aquatic Sciences, 63: 1–16.

Megalofonou, P. 2000. Age and growth of Mediterranean albacore. Journal of Fish Biology, 57: 700–715.

Miyake, M. P., Guillotreau, P., Sun, C. H., and Ishimura, G. 2010. Recent developments in the tuna industry: stocks, fisheries, management, processing, trade and markets. FAO Fisheries and Aquaculture Technical Paper No. 543, FAO, Rome.

Morton, R., and Bravington, M. 2008. Comparison of methods for estimating age composition with application to Southern Bluefin Tuna (*Thunnus maccoyii*). Fisheries Research, 93: 22–28.

Neilson, J. D., and 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.

Neilson, J. D., Manickhand-Heileman, S., and Singh-Renton, S. 1994. Assessment of hard parts of blackfin tuna (*Thunnus atlanticus*) for determining age and growth. International Council for the Conservation of Atlantic Tunas, ICCAT Collective Volume of Scientific Papers, 42: 36–376.

Ortiz de Zárate, V., Megalofonou, P., De Metrio, G., and Rodríguez-Cabello, C. 1996. Preliminary age validation results from tagged-recaptured fluorochrome label albacore in the north east Atlantic. ICCAT Collective Volume of Scientific Papers, 43: 331–338.

Powers, J. E. 1983. Some statistical characteristics of ageing data and their ramification in population analysis of oceanic pelagic fishes. NOAA Technical Report, National Marine Fisheries Service, 8: 19–24.

Reeves, S. A. 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES Journal of Marine Science 60: 314–328.

Schaefer, K. M. 2001. Reproductive biology of tunas. *In* Tuna: Physiology, Ecology and Evolution, 19, Fish Physiology, pp. 225–269. Ed. by B. A. Block, and D. E. Stevens. Academic Press, New York.

Schaefer, K. M., and 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. Bulletin of the Inter-American Tropical Tuna Commission, 23: 35–76.

Schaefer, K. M., Fuller, D. W., and Miyabe, N. 2005. Reproductive biology of bigeye tuna (*Thunnus obesus*) in the eastern and central Pacific Ocean. Bulletin of the Inter-American Tropical Tuna Commission, 23: 3–31.

Secor, D. H., Dean, J. M., and Laban, E. H. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute and the Belle W. Baruch Institute for Marine Biology and Coastal Research, South Carolina.

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

Stéquert, B., Panfili, J., and 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.

Sun, C. L., Huang, C. L., and Yeh, S. Z. 2001. Age and growth of the bigeye *Thunnus obesus* in the western Pacific Ocean. Fishery Bulletin, 99: 502–509.

Tomoyuki, I., and Sachiko, T. 1996. Age and growth of juvenile southern bluefin tuna *Thunnus maccoyii* based on otolith microstructure. Fisheries Science, 62: 892–896.

Wild, A. 1986. Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. Bulletin of the Inter-American Tropical Tuna Commission 18: 421–482.

Wild, A., and Foreman, T. J. 1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Bulletin of the Inter-American Tropical Tuna Commission, 17: 507–560.

Wild, A., Wexler, J. B., and Foreman, T. J. 1995. Extended studies of increment deposition rates in otoliths of yellowfin and skipjack tunas. Bulletin of Marine Science, 57: 555–562.

Williams, A. J., Farley, J. H., Hoyle, S. D., Davies, C. R., and Nicol, S. J. 2012. Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. PloS One 7, e39318. doi: 10.1371/journal.pone.0039318.

Yamanaka, K. L. 1990. Age, growth and spawning of yellowfin tuna in the southern Philippines. Indo-Pacific Tuna Development and Management Programme (IPTP) Working Paper 21, 1–87.

Handling editor: David Secor