Determining the age of tropical tunas in the Indian Ocean from otolith microstructures

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Abstract :

The Indian Ocean Tuna Tagging Program (IOTTP) provided a unique opportunity to assess the viability of estimating the age of tropical tunas from the micro-structural features of otoliths. Here, we analyzed the length measurements and micro-increment counts collected for 506 sagittal otoliths, of which 343 were chemically marked with oxytetracycline, for bigeye (*Thunnus obesus*), skipjack (*Katsuwonus pelamis*), and yellowfin tuna (*Thunnus albacares*). Our results show that the otoliths of tropical tunas grow more slowly than the rest of the body. Our findings confirm that both yellowfin and juvenile bigeye deposit daily increments in their otoliths, though ages are underestimated for large bigeye (>100 cm) when derived from micro-increment counts. Our results also indicate that skipjack otoliths are not suitable for age estimations during the adult phase, as evidenced by the poor agreement between micro-increment counts and days-at-liberty. We hypothesize that the income breeding strategy of skipjack could explain the variability observed in the deposition rates. Due to their complex micro-structural patterns, the reading of tropical tuna otoliths requires a degree of interpretation that can result in poor count precision and large variability in micro-increment counts, both among and within teams of readers. Age estimates were found to vary between readers, a factor which can eventually affect growth estimates and ultimately, impact on fisheries management decisions and outcomes. To address this, we recommend that reference collections of otoliths are developed, with a view to standardizing the reading process. Further, alternative methods, such as annual age estimations (as opposed to daily), and alternative structures, such as dorsal spines for skipjack, should be used to improve the accuracy of age estimations and the speed with which they can be made.

Highlights

► We confirm that yellowfin and juvenile bigeye deposit daily micro-increments in otoliths. ► Our results support previous findings that deposition rates in adult skipjack are highly variable. ► Age estimates are characterized by very low precision and strongly dependent on the reader. ► Variability in otolith reading can affect growth estimates. ► Reference collections are required to standardize the reading of tuna micro-increments.

Keywords : Daily age, Micro-increment, Mark-recapture, Oxytetracycline, Thunnus

1. Introduction

Information from age structures plays a significant role in fisheries science, with fish population
48 models largely based on age-dependent demographic features. Worldwide, millions of otoliths are
read annually to estimate fish age and provide essential information to improve the stock
assessment models which underpin fisheries management (Campana and Thorrold, 2001). Otoliths
51 are commonly used because uniquely, they do not absorb calcium. However, other calcified
structures, such as dorsal spines, scales, and vertebrae have also been widely used to provide annual
age estimates (Panfili et al., 2002). The chronological properties of otoliths have been known since
54 the 19th century, but gained wider recognition with the seminal article by Pannella (1971). Since
then, the growing demand for fish age estimates have led scientists to conduct further research in
the field of sclerochronology, focusing in particular on improving the preparation, conservation, and
57 reading of otoliths (Secor et al., 1995; Panfili et al., 2002; Begg et al., 2005).

In tropical environments, it is particularly difficult to estimate fish age using otolith increments
60 (annual or seasonal) because growth cycles are not related to environmental conditions (e.g., there
is less seasonal contrast in tropical waters as compared with temperate waters; Green et al., 2009).
In the 1970s, the sub-seasonal patterns in the micro-structural features (i.e., micro-increments) of
63 otoliths were investigated in several tropical fish species. This research revealed that these micro-
increments followed a circadian rhythm which was physiologically controlled and influenced by
environmental conditions (Pannella, 1971, 1974). Each micro-increment corresponds to a bipartite
66 structure which is composed of two alternating zones, an incremental (or accretion) zone and a
discontinuous zone. Each zone is characterized by a distinct composition of organic and mineral
fractions (Campana and Neilson, 1985; Campana, 1999). These early findings prompted the
69 significant growth in studies that used optical microscopes to investigate otolith micro-structures as
a way of estimating the age and growth of tropical tunas worldwide (Table 1). Counts of micro-

increments in sagittal otoliths were first used to estimate ages of yellowfin (*Thunnus albacares*; YFT) and skipjack tuna (*Katsuwonus pelamis*; SKJ) in the Eastern Pacific Ocean (Wild and Foreman, 1980). This study validated the presence of a daily deposition rate in the otoliths of YFT (size range: 40 cm – 110 cm fork length; F_L ; i.e., the length measurement taken from the tip of the snout of a fish to the fork of its tail) collected from oxytetracycline (OTC) mark-recapture experiments. SKJ, however, was found to exhibit a non-daily deposition rate. Subsequent studies conducted in the Pacific Ocean increased the number and extended the size range of fishes sampled and confirmed a daily micro-increment deposition rate for YFT between 40 cm and 148 cm F_L (Yamanaka, 1990; Uchiyama and Struhsaker, 1981; Wild et al., 1995; Lehodey and Leroy, 1999). More recently, Hallier et al., (2005) and Schaefer and Fuller (2006) validated a daily deposition rate for bigeye (*T. obesus*; BET) sized between 44 cm and 95 cm F_L in the Atlantic Ocean and between 38 cm and 135 cm F_L in the Eastern Pacific Ocean (Table 1). For SKJ, although further research (e.g., mark-recapture and captivity experiments) were conducted, none of the results pointed to a link between days-at-liberty and micro-increment counts (Table 1). There is also a growing body of literature investigating the use of annual (as opposed to daily) age structures to provide age estimates in tunas including vertebrae (Prince et al., 1985; Rodriguez-Marin et al., 2006), dorsal spines (Sun et al., 2001; Lessa and Duarte-Neto, 2004), and more recently, otoliths (Farley et al., 2003; Griffiths et al., 2010; Chen et al., 2012; Shih et al., 2014; Williams et al., 2013).

In the Western Indian Ocean, the few studies that have dealt with age estimates of tropical tunas have had contradictory results and none have investigated the micro-increment deposition rates for YFT and BET (Table 1). Stéquent et al., (1996) was the first to establish a von Bertalanffy (1938) growth curve for YFT based on otolith micro-structures. However, it resulted in an asymptotic length estimate that was inconsistent with YFT biology (i.e., $F_L > 270$ cm). In addition, the growth pattern estimated for juvenile YFT ($F_L < 60$ cm) differed considerably from the results of an

96 extensive analysis of length-frequency distributions which were based on purse-seine, gillnet, and
longline fisheries landings (IOTC, 2005; Viera, 2005). For BET, age and growth estimates were
made from micro-increment counts obtained using both an optical microscope and scanning
99 electron microscope, particularly for large fish ($F_L > 120$ cm) (Stéquent and Conand, 2000, 2004).
Finally, micro-increment deposition rates for SKJ derived from mark-recapture experiments were
found to vary greatly among individuals, suggesting that micro-increment counts are not suitable for
102 estimating the age of this species. However, this study was only based on a small, localized sample
of fish ($n = 8$) collected from Maldivian waters.

105 The Indian Ocean Tuna Tagging Program (IOTTP), which began in 2004, provided a unique
opportunity to improve research efforts into understanding the age and growth rates of tropical tuna.
An area of particular interest was the hypothesis that micro-increment deposition occurs at a rate of
108 one per day in the otoliths of YFT, BET, and SKJ in the Indian Ocean. More than 200,000 tunas
were tagged with conventional dart tags through the IOTTP and about 3% of these were also
injected with a fluorescent marker that is rapidly incorporated into the otoliths (Hallier, 2008).
111 Using recovered otoliths, the main objectives of this study were to (i) estimate the frequency and
consistency of micro-increment deposition in otoliths for the purposes of estimating the age of
tropical tunas, (ii) assess the influence of otolith readers on micro-increment counts (i.e., how the
114 age structures are interpreted by different individuals), and finally (iii) evaluate the influence of
different otolith readers on growth estimations (when they are based solely on otolith data).

117 **2. Material and Methods**

2.1. Tuna sampling and otolith extraction

The majority of otoliths and length data used in this study were collected through the Regional Tuna
120 Tagging Project (RTTP), the main component of the IOTTP, conducted by the Indian Ocean Tuna

Commission (IOTC). During 2006 – 2007, approximately 160,000 tunas were tagged with dart tags. Of these, about 6,000 fish were injected with OTC, a chemical that is rapidly incorporated by the
123 fish and leaves a fluorescent mark in their calcified tissues (Wild and Foreman, 1980; Campana and Neilson, 1985) (Table S1). Depending on the size of the fish, between 1.5 mL and 3 mL of OTC were injected intramuscularly into their back (Hallier, 2008). Tag recovery operations took place
126 across the entire Indian Ocean basin between 2004 and 2013. As of September 2013, more than 22,000 tunas with reliable length and species identification records had been recovered, including 536 OTC-tagged individuals (Table S1). Most of the reported recoveries (about 85%) were for fish
129 caught by European purse-seiners based in Victoria, Seychelles (Hallier 2008). The F_L of recaptured tunas was measured to the nearest 0.5 cm. Recovery positions and date information were accurately known for tags found at sea (27% of all recoveries). Uncertainty arose, however, when a tag was
132 recovered from a purse-seiners' well as they can contain fish from multiple fishing sets. In these cases, the location and time uncertainties associated with each recapture were derived from the logbook data and well maps.

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The RTTP tagging operations took place aboard two pole and line vessels, which mostly catch small- and medium-sized tunas. The tunas tagged ranged in size between 32 cm and 144 cm F_L ,
138 with 75% measuring between 48 cm and 59 cm F_L , and 95% measuring < 71 cm (Table S1). This gear selectivity at tagging resulted in the recovery of very few small fish with reliable fork length measurements. Of the total number of tunas recovered, only 1% measured < 45 cm and the smallest
141 fish measured 34.7 cm F_L . To complement the size range of tunas recovered by the purse seiners, an additional 40 otoliths were collected from 20 small YFT (19 cm – 29 cm F_L) and 20 small SKJ (20.5 cm – 25 cm F_L) that were caught in August 2007 in association with a fish aggregating device. This
144 device was anchored off the Indonesian coast (100°E longitude, 1.6°S latitude) and these fish were recovered as part of the West Sumatra Tuna Tagging Project (WSTTP; Anonymous, 2008). In

addition, data from a further 56 non-tagged YFT collected between April 2008 and April 2009 from
147 purse-seine landings in Victoria, Seychelles were considered in this analysis. In total, we used
otolith and length data obtained from 506 tunas collected between 2006 and 2012, including 343
that were OTC-marked, i.e., 142 BET (139 OTC-marked), 81 SKJ (43 OTC-marked), and 283 YFT
150 (161 OTC-marked). The majority of these fish were collected in the Western Indian Ocean (Fig. 1).
The final size ranges represented in these data were 46 cm – 142 cm F_L for BET, 20.5 cm – 63 cm
 F_L for SKJ, and 19 cm – 153 cm F_L for YFT (Fig. S1). While we consider that the size range for
153 YFT is comprehensive (Fig. S1c), there are some data coverage issues for BET and SKJ. The final
data set for BET only included eight fish > 100 cm F_L (Fig. S1a) and for SKJ, there was only one
fish in the 25 cm – 48 cm F_L size range (Fig. S1b).

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After decapitation, sagittal otoliths were extracted with forceps. They were cleaned with ultra-pure
water, and when necessary, ultrasound was used to remove adhering vestibular tissue. After
159 cleaning, the otoliths were stored in plastic micro-tubes for subsequent analyses. Not all of the
otoliths from recaptured tunas were prepared. The main criterion for selecting which otoliths were
prepared was the quality of information available for each fish. Only otoliths from fish with good
162 information (i.e., accurate dates, species identification, F_L at tagging and recapture, and times-at-
liberty for OTC-marked individuals) were selected.

165 2.2. Otolith analysis

2.2.1. Otolith preparation

All otoliths were prepared following the same protocol used at the Laboratoire des Sciences de
168 l'Environnement Marin in Brest, France (Stéquert, 1995). For consistency, only the left sagittal
otolith was used, although it has been shown that the number of micro-increments between the left
and right sagitta are not statistically different for tropical tunas (Wild and Foreman, 1980). The first

171 step in preparation was to set the otolith into a block of epoxy resin (Araldite® 2020 mixed with the
catalyst 2020-B). Two transversal cuts were then made either side of the nucleus to obtain an otolith
section of approximately 1 mm thickness. This section was then attached to a glass slide using
174 Crystal Bond® thermoplastic resin, a temporary mounting adhesive that enables the section to be
turned. Both sides of the section were then polished with a diamond suspension (3 µm grit). At this
stage of preparation, particular attention was paid to ensure that the nucleus was not sanded away.
177 This final otolith section (80 µm - 100 µm thickness) was then decalcified with a few drops of 10%
tri-sodium ethylene diaminetetraacetic acid (EDTA) for several seconds to enhance the contrast
between the micro-structural features. To reduce the risk of decalcifying the otolith too much and
180 making it too dark to read, the EDTA reaction was monitored using an optical microscope at 400x
magnification. The final otolith section was then rinsed with distilled water to finish the preparation
process. Hereafter, the term “otolith” refers to a prepared otolith section.

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2.2.2. Otolith readers

A total of seven readers analyzed the otoliths between 2008 and 2012. Although repeated counts
186 were undertaken, the number of repeats varied between preparations, according to available funds
and personnel, as well as IOTC priorities (Table 2). Thus, not all otoliths were read by all readers.
To assess the influence of individual readers on micro-increment counts, the seven readers were
189 grouped into four teams according to their prior experience in reading tuna otoliths (less than two
years versus more than two years), the amount of training they had received from former readers,
and their institute of affiliation (Table 2).

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2.2.3. Otolith measurements

The length of the otolith section (L_o) was measured along the counting path, from the nucleus (point
195 of original growth) to the last micro-increment deposited on the maximal growth axis. To account

for changing growth rates with age, this measurement was taken in two linear segments (L_1 and L_2), and L_o was estimated from the sum of these two segments (Stéguert et al., 1996; Fig. 2a). L_o measurements were completed by Teams 1-3 using an optical microscope (Olympus BX41 with 100x or 200x magnification) coupled with TNPC® 4.3 software. In addition, Team 2 also completed some readings using the easier and faster Leiss binocular and Axiovision software combination which is an alternative measuring method.. In total, otolith length measurements were made for 140 BET (46 cm – 141.6 cm F_L), 63 SKJ (20.5 cm – 63 cm F_L), and 223 YFT (19 cm – 153 cm F_L). Of these, 155 otoliths were measured using both the microscope and the binocular, and these data were used to assess the effects of the measurement method on otolith length measurements. Finally, for a small subset (eight otoliths), L_o measurements were repeated three times to estimate measurement accuracy.

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2.2.4. *Micro-increment counts*

All otoliths were randomly selected prior to reading (i.e., without any prior knowledge of how many times it had been counted or its corresponding fish identification or length). Readings were completed on dry otolith sections with transmitted light, using a light microscope (Olympus BX41 with camera at 1000x magnification: 10x ocular and 100x lens) and TNPC® 4.3 software. Micro-increment counts were made for two different otolith sections. Measurements of Section 1, from the OTC-mark to the otolith edge (I_m), allow for the periodicity of the deposition rate to be assessed (see section 2.3.2). Measurements of Section 2, from the nucleus to the otolith edge (I_t), provide estimates of absolute age and enable us to derive growth curves from which we can then assess the influence of the reader on growth estimation (see section 2.3.4). Counts were made on a computer screen using a manual cell-counter. Using a reading window of at least 60 μ m wide, micro-increments were counted along the outer edge of the ventral side, following the axis of maximal growth (Fig. 2b-d). For chemically-marked otoliths, an ultraviolet light was used to detect the

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fluorescent OTC-mark. No time corrections were required for full otolith sections, as it has been
222 shown that the larvae of tropical tunas deposit their first growth micro-increment one day after
hatching (Radtke, 1983; Wexler et al., 2007).

225 The interpretation of the deposition patterns observed in these otoliths was subjective. To start with,
full micro-increments had to be distinguished from sub-micro-increments, which are characterized
by faint and incomplete rings. In addition, overlapping micro-structures caused by irregular
228 incrementation were often observed (Fig. 2c). Finally, some otoliths presented with illegible sub-
sections. In these instances, a micro-increment count had to be interpolated from the surrounding
sub-sections (Fig. 2d). This type of interpolation has been found to be reasonable in cases where the
231 number of interpolated micro-increments is relatively small in comparison to the total micro-
increment count (Campana, 1992). The degree of interpretation required was found to vary in
accordance with the quality of otolith preparation; however, a quality index was not available in this
234 study. Difficulties with interpretation are generally assumed to decrease as the experience level of
the reader increases.

237 2.3. Statistical analyses

2.3.1. Modeling the relationship between otolith growth and somatic growth

For each species, otolith length L_O , was modeled as a function of F_L , with linear and non-linear
240 power regressions, to investigate the relationship between otolith growth and somatic growth.
Model parameters were estimated following the maximum likelihood approach using the “lm” and
“nls” functions implemented in R (R Development Core Team 2013). Gaussian error distribution
243 and homoscedasticity hypotheses were checked using the residuals. Model selection was based on
the Akaike information criterion (AIC) calculated for each model.

246 2.3.2. Modeling the deposition rate in tropical tuna otoliths

The relationship between times-at-liberty and micro-increment counts was investigated for OTC-tagged tunas based on the accuracy of the times-at-liberty. Uncertainty associated with the recapture
249 date (expressed in days) should be < 5% of the mean time-at-liberty derived from the expected mean recapture date. A total of 116 OTC-tagged tunas BET (46 cm - 141.6 cm F_L), 34 SKJ (48.5 cm - 60.2 cm F_L), and 112 YFT (47.9 cm - 135.4 cm F_L) were selected. The times-at-liberty varied
252 between 3 and 1,166 days for BET, 50 and 602 days for SKJ, and 8 and 969 days for YFT. For BET and SKJ, about 90% of the otoliths analyzed were collected from tunas that spent less than one year-at-sea. For YFT, these values were more balanced, with 25% of fish having spent more than
255 one year-at-sea and 5% having spent more than two years-at-sea.

For each reading team r , the number of I_m micro-increments was modeled as a linear function of
258 time-at-liberty D , following:

$$I_m = a_r \cdot D + b_r$$

where a corresponds to the pattern of deposition estimated by each team, and b is an additive error
261 term that results from several factors, such as reader experience or otolith morphology. Given none of the readers had any prior information on the fish whose otoliths they were reading and the otoliths of BET and YFT are indistinguishable, the intercept b was considered to be identical for
264 each of the two species for any given reading team. Model parameters were estimated using Bayesian inference as implemented in OpenBugs version 3.2.1 (Spiegelhalter et al., 2011). Gaussian error distribution and homoscedasticity hypotheses were checked using the residuals. Details on the
267 methodology used to generate prior distributions, simulations, and convergence diagnostics are available in the Supplementary Online Materials (SOM).

270 2.3.3. Precision in otolith reading

For all species and every team of readers, the relationship between the standard deviation and mean number of micro-increment counts was used to determine how overall count precision varied with age, i.e., how consistent micro-increment counts were between different age determinations. This relationship was based on data from a subset of otoliths which were read a minimum of six times ($n = 114$). The precision in age determination was then estimated for each team of readers and species using the coefficient of variation (CV) of micro-increment counts averaged across fish (Chang, 1982; Campana et al., 1995). Linear regression models and non-parametric Wilcoxon matched-pairs rank tests were then used to assess the consistency of age determinations between reading teams for otoliths that were read in common (Campana et al., 1995).

2.3.4. *Evaluating the reader effects on growth estimates*

The uncertainty associated with multiple otolith readings was modeled to estimate the true number of increments for each fish otolith. The number of increments counted for reading l of otolith i ($I_{i,l}$) was assumed to be distributed around the expected number of increments following a normal distribution (Dortel et al. 2013). This number was then converted into absolute age accounting for the potential biases of each reading team based on the species-specific regression models linking I_m and D (see section 2.3.2). The conversion assumed that these relationships were valid for tuna that were bigger and smaller than the specific size range of the OTC-tagged tunas considered. Somatic growth models were then fitted to the age and F_L data using Bayesian inference to assess the influence of reading method on growth estimates determined solely from otolith data. Growth was modeled using a Von Bertalanffy logK model, which allows fish to exhibit two successive and distinct growth phases over time (Eveson et al., 2004). Information on the asymptotic length parameter was provided by informative prior distributions derived from tuna size measurements (see SOM). The technical details of calculating the prior distributions and the posterior estimates are described by Dortel et al., (2013).

297 3. Results

3.1 Relationship between otolith length and fish length

For YFT, otolith length measurements were obtained from fish that represented the entire size range
300 caught by purse seine (20 cm – 150 cm F_L). In contrast, only a few otolith length measurements
were available for large BET (> 100 cm F_L) and very few measurements were collected from the 25
cm – 50 cm F_L size range for SKJ (Fig. 3). The measurement method used to estimate otolith length
303 (i.e., binocular or microscope), did not affect L_O measurements (Fig. S2). The repeated binocular
measurements indicated that there was a strong consistency between the number of readings and
small observation errors in L_O (Fig. S3). The mean CV of otolith length for the eight otoliths which
306 were measured three times was 1.5%. Otolith growth in tropical tunas of the Indian Ocean was
found to be strongly positive and non-linearly correlated with somatic growth, following allometric
relationships. Non-linear power regressions between F_L and L_O were found to be significant ($p <$
309 0.001) for all three tuna species (Fig. 3). Power regression models explained the variability in
otolith growth better than linear models (i.e., the AIC was lower for each species-specific model).
The allometric coefficients of the relationships were close to 0.6 and did not significantly differ
312 between species, i.e., 0.59 (SE = 0.021) for BET, 0.58 (SE = 0.023) for SKJ, and 0.6 (SE = 0.013)
for YFT. This result indicates that the otoliths in tropical tunas grow more slowly than the rest of the
body.

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3.2. Frequency of deposition

The relationship between micro-increment counts and days-at-liberty show that juvenile BET in the
318 Indian Ocean have a daily micro-increment deposition rate. For BET, the slope a of the relationship
between I_m and D was not found to be statistically different (i.e., very close to 1) for the three teams
of otolith readers (Table 3). However, this relationship was strongly influenced by the proportion of

321 juvenile BET in the data set while the relative age (i.e., time-at-liberty) of large individuals was underestimated. Micro-increment counts made by each of the three reading teams were smaller than actual times-at-liberty for $D > 400$ days (which corresponds with $BET > 100$ cm F_L ; Fig. 4a). The discrepancy between the observations and the regression model predictions increased with D , exceeding 200 days for $D > 1000$ days (which corresponds with $BET > 120$ cm F_L). Micro-increment counts in the otoliths of adult SKJ for the times-at-liberty indicated that their deposition rate during the adult phase displayed a high degree of variability and there were also differences in count values between and within the teams of readers (Fig. 4b). The slope of the regression models varied between 0.51 micro-increment per day ($m\ d^{-1}$) for Team 1 and 0.16 – 0.17 $m\ d^{-1}$ for Teams 2 and 4 (Table 3). For YFT (size range: 50 cm – 135 cm F_L), Team 2 found that the micro-increment deposition rate was daily while Team 1 estimated the rate to be $< 1\ m\ d^{-1}$. The mean deposition rate was 0.98 $m\ d^{-1}$ (SD = 0.03) for Team 2, but significantly $< 1\ m\ d^{-1}$ (mean = 0.88, SD = 0.02) for Team 1 (Table 3). In comparison to BET, no pattern in the model residuals was found for YFT, which indicated good agreement between the micro-increment counts and days-at-sea for the size range and times-at-liberty observed (Fig. 4c).

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The intercept b , for the relationships between I_m and D , represents the systematic bias in age estimates and differed between both the teams of reader and species. The least experienced Team 2, had the highest bias values for the three species amongst any of the teams of readers (+7.4 micro-increments for BET and YFT and +10.9 micro-increments for SKJ; Table 3). Teams 1 and 3 exhibited a small negative bias (< 1 micro-increment), while the bias of Team 4 was +7.4 micro-increments for SKJ.

3.3. Reader influence on micro-increments counts

345 Counting precision generally decreased as the age of the fish increased. The overall standard

deviation of micro-increment counts was found to significantly increase with the mean number of micro-increment counts ($p < 0.001$; adjusted Pearson's $r = 0.85$). This describes a typical
348 multiplicative error associated with the reading process (Fig. S4). Counting precision was generally low and differed considerably between the teams of readers and the three species. Team 4, who read 29 SKJ otoliths, was found to be the most precise, with a CV of 5.5% for micro-increment counts
351 (Table 4). By contrast, Team 3's readings of 137 BET otoliths, were characterized by low reproducibility, with a CV of almost 70%. Teams 1 and 2, who read otoliths from all three species, had mean CVs of 41.3% and 20.2%, respectively (Table 4). Within each team, precision also varied
354 greatly between species. For example, for Team 2, the CV for SKJ was $< 10\%$, but $> 23\%$ for YFT. Finally, precision also varied between individual readers for each particular species, e.g., for SKJ, CVs for each reader ranged from between 5.5% and 70% (Table 4). Overall, count precision did not
357 appear to be related to a particular species, but rather to the team of readers. Although no team's counting precision was very high, the less-experienced Team 2 was found to be more precise.

360 The pairwise comparisons of micro-increment counts for the otoliths that were read in common showed that there were major differences in the results of the reader teams. With the exception of BET otoliths (read by Teams 2 and 3; $p = 0.41$), the non-parametric Wilcoxon matched-pairs rank
363 test indicated that the micro-increment count estimates significantly differed between Teams 1 and 2 and Teams 1 and 3 for BET, between Teams 2 and 4 for SKJ, and between Teams 1 and 2 for YFT ($p < 2.10^{-5}$). Although the linear regression models showed significant positive correlations between
366 the micro-increment count estimates (adjusted Pearson's $r > 0.65$), the slope of each model was found to be significantly different than 1 (Fig. 5). For BET, there was, in general, a good agreement between the micro-increment counts (< 500) made between the different teams of readers (Fig 5a-
369 c). However, for counts between the 500 and 700 micro-increment range, Teams 2 and 3 counted more than Team 1 (Fig. 5a-b). Further complicating these differences is that within this micro-

increment range, the estimates of Team 3 were even higher than those made by Team 2, but became
372 lower for counts > 700 micro-increments (Fig. 5c). The highest variability in micro-increment
counts was observed for SKJ otoliths, which were characterized by wide discrepancies in count
estimates between Teams 2 and 4 (more than two-fold difference for several otoliths; Fig. 5d).
375 Finally, for YFT, the estimates appeared consistent between teams for micro-increment counts <
700, but Team 2 was found to count more micro-increments thereafter (Fig. 5c).

378 3.4. Reading team effect on growth curves

The absolute ages of 129 BET (46 cm – 141.5 cm F_L) and 215 YFT (19 cm– 152 cm F_L) were
derived from the species-specific relationships between I_m and D . No age estimation was made for
381 SKJ given the high variability observed in the micro-increment counts and the absence of a clear
relationship between I_m and D (see above). The shape of the growth curve estimated from the age-
length data was found to vary according to each team of readers. The growth curves estimated for
384 BET significantly differed between Team 1 and Teams 2 and 3 in the size and age range
encompassed by the otolith data (Fig. 6a). The growth rate k_L , estimated from Team 1's data was
found to be significantly higher than from Teams 2 and 3's data (Table S5). BET growth curves
387 derived from micro-increment counts of Teams 2 and 3 were similar for those fish aged one to four
years and diverged significantly for ages greater than four years, mainly due to the lack of data for
old fish. For YFT, differences in the age estimates derived between Teams 1 and 2 were not as great
390 as the differences observed between the micro-increment counts after the age conversion (which
took into account the reader bias; Fig. 6b). The growth curves were not statistically different for
those fish younger than two years, but they significantly differed for fish aged between 2.5 and 4.5
393 years.

4. Discussion

396 The IOTTP provided a unique opportunity to test the hypothesis that there is a daily micro-
increment deposition rate in the three key commercial tuna species of the tropical Indian Ocean. In
this program, OTC-marked YFT and BET were recovered around three years after their initial
399 tagging, which resulted in times-at-liberty that were more than twice as long as those observed in
the Eastern Pacific and Atlantic Oceans (Wild et al., 1995; Hallier et al., 2005; Schaefer and Fuller,
2006). Thus, this offered a significantly longer period of time against which to validate age reading
402 estimates. Although it was impossible to fully disentangle the effects of temporal variability on
micro-increment deposition rates from reading errors when relating times-at-liberty to micro-
increment counts, our findings show that both YFT (less than five years) and BET (less than three
405 years) deposit daily increments in their otoliths. This finding is similar to deposition rates observed
in the Pacific and Atlantic Oceans. However, when an interpretation bias is introduced by the
readers, it can result in an apparent non-daily deposition rate (e.g., for YFT; see below). This bias
408 can be accounted for in age estimations when reference data is available, such as the data provided
by the OTC-tagged tunas. Based on a comparison of micro-increment counts against times-at-
liberty values (> 300 days) for several fish, our results suggest that the micro-structural features in
411 SKJ otoliths are not suitable for age estimates during their adult phase. In addition, our results show
that (i) micro-increment count precision was generally low and strongly variable between readers,
(ii) counts tended to underestimate the age of the older, larger BET (> 100 cm), and (iii) the age
414 estimates from otoliths differed widely between readers and teams of readers. The overall
variability in otolith reading can strongly affect micro-increment counts and the derived age
estimates, and thus, the reader has a major influence on tuna growth estimates that are based solely
417 on otolith data. Therefore, we highly recommend the development of an otolith reference collection
made up of known-age or consensus-aged structures. These could then be used to train otolith
readers and standardize reading methods between laboratories involved in the aging of tunas.

4.1. Estimating SKJ growth

SKJ have particularly small otoliths that are characterized by irregular micro-incrementation, particularly in old fish. Our analysis of OTC-marked otoliths for SKJ revealed a large discrepancy between micro-increment counts and times-at-liberty, which is similar to the results observed in the Eastern Pacific Ocean (Wild et al., 1995) and Indian Ocean (based on a small dataset of otoliths collected around the Maldives; Adam et al., 1996). In addition, the high variability in micro-increment counts observed between and within teams of readers highlights the difficulties associated with interpreting SKJ otoliths. Our data set lacked OTC-marked fish in the 25 cm – 45 cm F_L size range, which hindered our assessment of whether a daily deposition rate occurred in the otoliths of immature SKJ (< 40 cm; Stéguert and Ramcharrun 1996, Grande et al. in press). Experiments on laboratory-reared SKJ, over time periods of up to 47 days, indicated that a daily deposition rate occurred in the otoliths of larvae, juveniles, and adult fish (Uchiyama and Struhsaker, 1981; Radtke, 1983; Tanabe et al., 2003a). In addition, Tanabe et al., (2003c) validated the occurrence of a daily deposition rate for small juvenile SKJ (< 4 cm) by analyzing the diel changes in the width of marginal micro-increments. Based on the assumption of a daily deposition rate, SKJ otoliths have been used to derive growth curves in the Eastern Indian (Kayama et al., 2004) and Western Pacific Oceans (Leroy, 2000; Tanabe et al., 2003b).

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Several hypotheses have been suggested to explain the variability observed in the micro-increment counts of SKJ otoliths. Environmental factors, such as temperature, food availability, and changes in the photoperiod have all been shown to affect the formation of daily growth increments in the otoliths of both temperate and tropical fish (Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977; Wright et al., 1991). SKJ may be exposed to less environmental variation than BET and YFT; although SKJ are able to dive to several hundred meters depth (Schaefer and Fuller, 2007), they

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spend most of their time in tropical surface waters which are characterized by small variations in temperature (Sund et al., 1981; Wild and Hampton, 1994). Furthermore, it might be expected that variations in environmental conditions and prey availability should affect otolith growth for SKJ and the juveniles of BET and YFT in the 30 cm – 60 cm F_L size range similarly, given that they all form multi-species schools and share similar habitats. Some authors have suggested that SKJ's maturation process and reproductive events may explain the temporal inconsistencies in their otolith growth (Wild and Foreman, 1980; Adam et al., 1996; Leroy, 2000), although evidence to support this hypothesis is limited. SKJ exhibit indeterminate fecundity and spawning in the Indian Ocean takes place year round, with peaks of heightened sexual activity (Stéquert and Ramcharrun, 1996; Grande et al., in press). They continue to feed throughout their spawning period, which is characterized by a continuous recruitment of oocytes which is enabled through a continuous energy supply from the liver that acts as an energy buffer (Grande, 2013). This “income breeding strategy” which allows for SKJ offspring to be provisioned using energy gained concurrently (as distinct from prior accumulation) may bring about changes in feeding intensity that subsequently trigger variations in the energy allocations between growth and reproductive phases and ultimately, could explain the variability observed in micro-incrementation.

When direct age reading data are not available, SKJ growth can be derived from mark-recapture experiments by relating observed changes in length between tagging and recovery to the time spent at sea (Maunder, 2002; Gaertner et al., 2008). Such models, however, are required to provide an age-length reference point which anchors the growth curve. For SKJ in the Indian Ocean Eveson et al., (this issue) assumed that the growth curve crosses the origin, i.e., the theoretical age at which fish growth is null and set to 0. Based on their model, SKJ growth would be very fast during their first year of life, reaching about 20 cm, 36 cm, and 45 cm F_L at three, six, and nine months, respectively. In this analysis, the results of Team 2, who analyzed juvenile SKJ otoliths (20.5 cm -

25 cm F_L ; $n = 14$) were consistent with the findings of Eveson et al., (this issue), suggesting these
471 fish were aged between three to five months. However, the readings of Team 4 suggested a faster
growth for early juveniles. In the Western Central Pacific, SKJ growth derived from otoliths also
showed fast growth during the first year with some variability between studies, for example, six-
474 month-old individuals were described as having lengths between 28 cm and 42 cm F_L (Struhsaker
and Uchiyama, 1976; Leroy, 2000; Tanabe et al., 2003b). The collection of otoliths in the 25 cm –
45 cm size range is currently in progress to facilitate complementary age-reading analyses which
477 will provide insights into the growth of SKJ juveniles in the Indian Ocean. In the interim, the use of
dorsal spines may be a valid alternative for aging adult SKJ. However, this method relies on the
assumption that there is an annual deposition of annuli in the spines and this assumption remains
480 untested (Valeiras et al., 2008; Wang et al., 2010).

4.2. Age estimation of YFT and BET from otoliths

483 Our results confirm that there is a daily deposition rate in the otoliths of YFT and juvenile BET in
the Indian Ocean, as previously observed in captive tunas (Uchiyama and Struhsaker, 1981; Wexler
et al., 2001) and wild populations of the Pacific and Atlantic Oceans (Wild and Foreman, 1980;
486 Wild et al., 1995; Hallier et al., 2005; Schaefer and Fuller, 2006). However, deposition rate
estimates were found to vary between readers, with one team of readers estimating a mean
deposition rate for YFT of $< 1 \text{ m d}^{-1}$. A daily frequency of micro-increment deposition in otoliths
489 has been observed for many tropical and temperate species and is explained by an endogenous
circadian rhythm that controls otolith growth (Pannella, 1971; Campana and Neilson, 1982; Radtke
and Dean, 1982; Campana, 1984). External factors, such as temperature or feeding frequency, have
492 been shown to regulate otolith growth, but micro-increment periodicity is only disrupted in extreme
cases of physiological stress (Morales-Nin, 2000; see above for the specific case of SKJ).
Therefore, we argue that the results for YFT from Team 1 are due to an interpretation bias as

495 opposed to other factors.

Within the IOTTP, validating age estimates using OTC-tagged tunas also enabled reader accuracy to
498 be assessed when micro-increment counts for YFT and BET were converted into ages. Age
validation is an integral part of the age determination process, whichever method of age estimation
(i.e., daily or annual) is selected or aging structure (i.e., otolith, dorsal spine, etc.) is examined
501 (Beamish and McFarlane, 1983; Neilson, 1992). Chemically tagging a percentage of tunas with
OTC was a relatively easy, low cost approach to age validation and active consideration should be
given to including a similar tagging component in future large-scale mark-recapture experiments.
504 Tagging larger individuals (> 80 cm F_L) might enable the recovery of tunas which have spent longer
than three years at sea, and hence extend the range of sizes and ages for which age estimates can be
validated (Farley et al., 2003). However, the recovery of large YFT and BET may continue to be
507 impaired by the low reporting rates generally seen for longline fisheries (Carruthers et al., this
issue).

510 Uncertainties in micro-increment counts (i.e., count precision and interpretation bias) can be
exacerbated by poor preparation. Firstly, a non-perpendicular section will require frequent changes
in microscope focus and the different reading axes will potentially result in a greater number of
513 count omissions or occurrences of double counting. Secondly, over-grinding the otolith generally
results in the removal of some micro-increments, particularly around the nucleus and at the otolith
edge. Errors such as these can be incorporated into estimates of age and can eventually propagate
516 into the estimates of somatic growth (Dortel et al., 2013). Finally, over-decalcification can blacken
the otolith and make it less readable. Whilst these preparation difficulties can be problematic, it is
also possible to take steps to ensure they are reduced as much as possible. However reading
519 uncertainties are mainly due to the natural complexity of tuna otoliths. In particular, several regions

of the otolith appear to be characterized by sub-daily, or split micro-increments, and overlapping micro-increments. Where these characteristics occur, the subjective opinion and experience of the reader may influence the micro-increment counts. Although low precision was seen in both teams, the less-experienced Team 2 was found to be more precise than the experienced Team 1. Team 2's efforts were solely devoted to reading otoliths whereas Team 1 was also required to work on additional, ongoing research projects. As such, we think that it is likely that this uninterrupted focus allowed Team 2 to develop greater counting precision. We would recommend that future large-scale mark-recapture experiments include a stratified sampling design for otoliths analysis (i.e., species, sex, size-range, area, gear), with different teams identified prior to the project, fully trained, and focused on aging. In this context, reference collections could be used and comparison exercises implemented to define a common reading method, prior to conducting the analysis. These tools could also be used to routinely assess aging errors or inconsistencies in the manner in which age is interpreted (Campana, 2001; Appelberg et al., 2005). Finally, integrated modeling approaches that combine different data sources, including age estimates from different readers, should be preferentially used for determining growth estimates (Dortel et al., submitted; Eveson et al., this issue).

The combination of a reduction in micro-increment width due to the allometric relationship between otolith and somatic growth and decreasing growth rates with age may result in some difficulties in identifying micro-increments in the otoliths of large tunas. A scanning electron microscope has been shown to give similar results to a light microscope for YFT and SKJ (Wild et al., 1995; Adam et al., 1996; Stéquent et al., 1996), but its preferential use has been advocated for large BET (> 120 cm F_L) because at these sizes, some micro-increments may be too small to be detected otherwise (Stéquent and Conand, 2004). This may partly explain underestimations of age in large BET (Williams et al., 2013), though this did not occur for YFT and micro-increment widths in large YFT and BET are

very similar ($\sim 1 \mu\text{m}$). Deriving age estimates from counts of annual (as opposed to daily) increment counts may be a more effective strategy for YFT and BET (Farley et al., 2006; Shih et al., 2014). This approach has been validated for BET $> 50 \text{ cm } F_L$ using 10 otoliths chemically tagged with strontium-chloride with times-at-liberty of longer than 6.5 years (Farley et al., 2003). Counting annual increments is quicker than counting daily micro-increments and appears more precise, though there can be some difficulties in identifying the first annulus and distinguishing between the partially formed increments at the otolith edge (Clear et al., 2000; Farley et al., 2003). The sister otoliths of OTC-tagged tunas that were not prepared for age reading could be used to confirm the applicability of the annual method for both YFT and BET.

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Table captions

Table 1. Summary of studies that have used otolith micro-structures to estimate the age and growth of tropical tunas in the Eastern Pacific Ocean (EPO), Western Central Pacific Ocean (WCPO), Atlantic Ocean (AO), and Indian Ocean (IO) outlining the otolith section that was read (Whole otolith (WO); External surface (ES); Frontal section (FS); Transverse section (TS)) and which experiment type was used to source the otoliths (mark-recapture experiments using oxytetracycline (MR) or captive experiments (CE)), where the number of tunas considered (N) are given for yellowfin (YFT), skipjack (SKJ), and bigeye (BET).

Table 2. The four teams of otolith readers and the reading equipment according to measurement method, used in this analysis. From left to right, the columns detail each team of readers's: institute of affiliation, prior experience reading tuna otoliths, assistance received from experienced readers, the number of readers in the team, the number of otoliths read for each species (i.e., bigeye (BET); skipjack (SKJ); and yellowfin tuna (YFT)), and the reading equipment (optical microscope (OM) linked to a computer screen and binocular (B)) used to measure the length of the otolith section (L_o), the number of micro-increments from the oxytetracycline mark to the otolith edge (I_m), and the number of micro-increments from the nucleus to the otolith edge (I_t).

Table 3. A summary of the linear models used to investigate the relationship between micro-increment counts from the oxytetracycline mark to the otolith edge (I_m) and times-at-liberty (D) by team of readers (mean, standard deviation (SD), and the 2.5% and 97.5% quantiles of the posterior distributions of the regression parameters).

Table 4. Number of otoliths read (N) and the coefficient of variation (CV; %) of the micro-increment counts by reading team for each of the three tuna species.

Table 1.

Basin	Species	Size range (cm)	N	Otolith reading method	Validation method	Validation size range (cm)	Deposition rate ($m\ d^{-1}$)	Reference
EPO	YFT	40-110	53	ES	MR	40-110	0.985	Wild and Foreman, 1980
		30-168	196	ES	-	-	-	Wild, 1986
		40-148	103	ES	MR	40-148	1.014	Wild et al., 1995
	SKJ	42-64	26	ES	MR	42-64	0.761	Wild and Foreman, 1980
		38-65	25	WO	CE	45-49.3	Qualitative	Uchiyama and Struhsaker, 1981
	BET	42-64	42	ES	MR	42-64	0.744	Wild et al., 1995
		30-149	254	FS	MR	38-135	0.999	Schaefer and Fuller, 2006
WCPO	YFT	7-93	14	WO	CE	52	Qualitative	Uchiyama and Struhsaker, 1981
		15-28	68	WO	CE	25-40	~1	Yamanaka, 1990
		16-79	139	FS	CE	25-40	~1	Yamanaka, 1990
		20-145	180	TS	MR	39-90	Qualitative	Lehodey and Leroy, 1999
	SKJ	3-80	51	WO	CE	42-64	Qualitative	Uchiyama and Struhsaker, 1981
		30-68	61	TS	-	-	-	Leroy, 2000
		1.3-4.0	72	WO	-	-	-	Tanabe et al., 2003a
		18-71	453	ES	CE	21-52	0.99	Tanabe et al., 2003b
	BET	24-34	54	ES	CE	24-34	0.996	Kayama et al., 2007
		33-58	9	WO	-	-	-	Matsumoto, 1998
		25-157	149	TS	-	-	-	Lehodey et al., 1999
AO	YFT	0.3-0.8	768	ES	-	-	-	Lang et al., 1994
		53-113	65	TS	-	-	-	Driggers et al., 1999
		5-179	132	TS	-	-	-	Shuford et al., 2007
	BET	29-190	255	TS	MR	44-95	0.97	Hallier et al., 2005
IO	YFT	30-140	151	TS	-	-	-	Stéquert et al., 1996
	SKJ	48-57	8	TS	MR	48-57	0.245	Adam et al., 1996
		42-66	25	ES	-	-	-	Kayama et al., 2004

BET	NA	154	TS	-	-	-	Stéquert and Conand, 2000
	30-165	164	TS	-	-	-	Stéquert and Conand, 2004

Table 2.

ID	Institute	Experience	Assistance	Number of readers	Species			Equipment	
					BET	SKJ	YFT	L_o measure	I_m and I_t counts
1	IRD	>2 y	Yes	3	89	18	197	OM	OM
2	IRD	<2 y	No	2	61	39	119	OM / B	OM
3	IRD	<2 y	Yes	1	137	-	-	OM	OM
4	SPC	>2 y	No	1	-	29	-	-	OM

Table 3.

Species	Reader team	N	Size range (cm)	Parameter	Mean	SD	Posterior quantiles	
							2.5%	97.5%
Bigeye	1	65	46-117.3	<i>a</i>	0.99	0.02	0.94	1.03
				<i>b</i>	-0.14	0.82	-1.63	1.58
	2	29	49.5-141.6	<i>a</i>	0.99	0.03	0.93	1.05
				<i>b</i>	7.39	2.51	3.21	12.29
	3	115	46-141.6	<i>a</i>	0.96	0.02	0.92	0.99
				<i>b</i>	-0.50	0.38	-1.17	0.21
Skipjack	1	9	48.5-56.9	<i>a</i>	0.51	0.08	0.34	0.66
				<i>b</i>	6.00	7.21	-7.65	20.47
	2	25	48.6-60.2	<i>a</i>	0.16	0.02	0.13	0.20
				<i>b</i>	10.89	2.83	0.86	15.32
	4	15	48.6-60.2	<i>a</i>	0.17	0.03	0.13	0.23
				<i>b</i>	7.39	4.36	-0.92	15.64
Yellowfin	1	90	49.8-135.4	<i>a</i>	0.88	0.02	0.84	0.92
				<i>b</i>	-0.14	0.82	-1.63	1.58
	2	39	47.9-135.4	<i>a</i>	0.98	0.03	0.92	1.04
				<i>b</i>	7.39	2.51	3.21	12.29

Table 4.

Species	Team 1		Team 2		Team 3		Team 4	
	N	CV	N	CV	N	CV	N	CV
Bigeye	89	62.9	61	21.2	137	67.8		
Skipjack	18	70	39	9.7			29	5.5
Yellowfin	197	32.8	119	23.8				
Total	304	41.3	219	20.2	137	67.8	29	5.5

Figure captions

Figure 1. The location of 415 tunas (137 bigeye, 57 skipjack, and 221 yellowfin) for which geographic coordinates were available. In cases where uncertainty around the location existed, the mean latitudes and longitudes of the relevant fishing sets were calculated to provide an approximate location.

Figure 2. Image of a yellowfin tuna otolith showing (a) the full transverse section with linear measurement segments L_1 and L_2 (used to compute L_O ; black arrows); (b) an otolith section showing the counting path (maximal growth axis) with detected micro-increments (white ticks); (c) an otolith section showing two zones where subjective interpretation is required, the black oval identifying where micro-increments had to be interpolated and the black rectangle identifying where there is some overlap in the micro-increments; and (d) an otolith section (black zone represents the otolith edge) illustrating differences in image resolution (left versus right sides of the dashed line) when the microscope is focused on the reading section. White arrows indicate the reading axis (b-d).

Figure 3. The relationship between otolith growth and somatic growth for (a) bigeye (BET; $n = 140$), (b) skipjack (SKJ; $n = 63$), and (c) yellowfin (YFT; $n = 223$), where L_O is the length of otolith section (μm) measured along the maximal growth axis, and F_L is the fork length (cm). The solid line indicates the power regression model fitted to the data.

Figure 4. The relationship between the micro-increment counts made from the OTC mark to the otolith edge (I_m) and time-at-liberty (D ; in days) for (a) bigeye (BET; $n = 116$), (b) skipjack (SKJ; $n = 34$), and (c) yellowfin (YFT; $n = 112$). Small vertical lines around the individual symbols indicate the standard deviation for I_m and the solid lines indicate the linear regression models fitted

to the data for each team of readers, with a 95% confidence interval.

600

Figure 5. A comparison between the micro-increment counts made by the different reading teams for (a-c) bigeye (BET), (d) skipjack (SKJ), and (e) yellowfin (YFT). The horizontal and vertical lines around the individual symbols represent the standard deviation around mean micro-increment counts. The thick solid lines represent the identity lines, and the dashed lines indicate the linear regression model fitted to the data. SKJ otoliths were only read once by Team 4.

606

Figure 6. Growth estimates for (a) bigeye (BET) and (b) yellowfin (YFT) based on the age estimates derived from micro-increment counts made by reading teams 1-3 for 129 BET and 215 YFT.

609

630 **Supplementary figure captions**

633 **Figure S1.** Size-frequency histograms of the tunas collected in the Indian Ocean between 2005 and 2012 by species (a) bigeye (BET; $n = 142$), (b) skipjack (SKJ; $n = 81$), and (c) yellowfin (YFT; $n = 283$), and by tag origin (West Sumatra Tuna Tagging Project (WSTTP) or Regional Tuna Tagging Program (RTTP)) or recoverer (Indian Ocean Tuna Ltd. Cannery; IOT).

636 **Figure S2.** A comparison between the length measurements of otolith sections (L_o ; μm) taken using the microscope and the binocular for a subset of 155 otoliths. Solid line indicates the regression model and dashed lines indicate the 95% confidence interval. The linear regression model fitted to the data indicates that there is a strong linear relationship between both reading methods (slope = 1.004; $p < 0.001$; Pearson's $r = 0.985$).

642 **Figure S3.** A comparison between the length measurements of otolith sections (L_o ; μm) made using the binocular by two different readers (A and B) for a subset of 38 otoliths. The correlation between the two sets of L_o measurements was found to be highly significant (slope = 0.98; $p < 0.001$; Pearson's $r = 0.99$).

648 **Figure S4.** The relationship between the mean and standard deviation of micro-increment counts for all tuna otoliths which were read a minimum of five times. The solid line indicates the linear regression model, I_m are the micro-increment counts made from the oxytetracycline (OTC) mark to the otolith edge, and I_t are the micro-increment counts made from the nucleus to the otolith edge.

Standard deviation of increment counts

654 **Supplementary table captions**

Table S1. The number and size ranges (in brackets; cm) of tunas tagged by conventional dart tags (DART) and oxytetracycline (OTC) tags and recovered through the Indian Ocean Regional Tuna Tagging Project, and the associated percent recovery rate (RR). Figures only represent tuna species (bigeye; BET, skipjack; SKJ, and yellowfin; YFT) for whom there was reliable data for species identifications and length measurements at tagging and recapture.

660

Table S2. Prior probability density functions used for the parameters of the regression model. U and N indicate Uniform and Normal distributions.

663

Table S3. Parameters and variables used in the somatic growth models.

Table S4. Prior distributions used for parameters of somatic growth models.

666

Table S5. Growth curve parameters according to age estimations of each team.

1. Complementary information on tagging-recovery operations

Table S1. The number and size ranges (in brackets; cm) of tunas tagged by conventional dart tags (DART) and oxytetracycline (OTC) tags and recovered through the Indian Ocean Regional Tuna Tagging Project, and the associated percent recovery rate (RR). Figures only represent tuna species (bigeye; BET, skipjack; SKJ, and yellowfin; YFT) for whom there was reliable data for species identifications and length measurements at tagging and recapture.

Species	Tagged		Recovered		RR (%)	
	DART	OTC	DART	OTC	DART	OTC
BET	31630 (32-102)	2407 (35-96)	4426 (37-189)	165 (46-150)	14	6.86
SKJ	75993 (32-77)	1482 (38-67)	10268 (39-153)	156 (40-69)	13.51	10.53
YFT	51841 (32-144)	1993 (34-141)	7899 (35-168)	215 (44-135)	15.24	10.79
Total	159464 (32-144)	5882 (34-141)	22593 (35-189)	536 (40-150)	14.17	9.11

2. Regression model between the time-at-liberty D , and the micro-increment count between the OTC mark and otolith edge I_m

2.1 Parameters and processes

In order to estimate the micro-increment deposition rate a , for each species, the number of increments made between the OTC mark and otolith edge I_m , was related to the time-at-liberty D , according to the following regression model:

$$I_m = a_r \cdot D + b_r$$

where r represents the team of otolith readers and the intercept b_r , includes the errors in counting and in interpreting missing increments for team. The prior distributions of these parameters are given in **Table S2**.

Table S2. The prior probability density functions used for the parameters of the regression models fitted for bigeye (BET), skipjack (SKJ), and yellowfin (YFT) expressed in micro-increments per day ($m\ d^{-1}$) where U indicates a uniform distribution and N indicates a normal distribution.

Species	Parameter	Unit	Prior distribution
YFT, BET	a	$m\ d^{-1}$	U(-10;10)
SKJ	a	$m\ d^{-1}$	U(-50;50)
YFT, BET, SKJ	b	m	N(0,50)

2.2. Statistical inference and convergence diagnostic

Estimates of the parameters were evaluated using three Markov Chain Monte Carlo (MCMC) simulations, using a Gibbs sampler as implemented in OpenBugs version 3.2.1 (Spiegelhalter et al., 2011). The convergence of the MCMC to the stationary posterior distribution was evaluated from the Gelman-Rubin diagnostic, based on the ratio of the inter-chain variance on intra-chain variance (this ratio must approach 1 to represent convergence; Gelman and Rubin, 1992). In this analysis, the Gelman-Rubin diagnostic (as computed from second half of MCMC chains), approached 1 for each parameter, indicating that convergence did occur. The marginal posterior distributions were drawn from 300,000 MCMC samples.

3. Modeling somatic growth

3.1. Bayesian fit of growth model

For modeling the somatic growth of yellowfin and bigeye, we used the Von Bertalanffy logK model developed by Laslett et al., (2002). Thus, the fork length of a fish i , at age A , is expressed as:

$$L_i = L_{\infty} \left(1 - \exp(-k_2(A_i - t_0)) \left(\frac{1 + \exp(-\beta(A_i - \alpha - t_0))}{1 + \exp(\beta\alpha)} \right)^{k_1 - k_2/\beta} \right) \times \varepsilon_i$$

All the parameters used in this equation are defined in **Table S3**. The corresponding prior distributions are given in **Table S4**. The prior distributions of k_1 , k_2 , and α are based on information from the literature. No information was available for β and t_0 ; thus, weakly informative distributions

were assigned.

717 The data set included little information on the asymptotic length L_{∞} ; however, it is a particularly
important parameter because it determines the shape of the second part of the growth curve. Thus,
supplementary information was provided for this parameter through the use of a generalized
720 extreme value distribution (GEV), using available biological knowledge of each species. This
approach allowed for the extrapolation of the behavior of the distribution tails from the greatest
values of a sample. This thus estimates the occurrence probability of extreme events (Borchani,
723 2010). This distribution was fit based on size measurement data of fresh fish collected between
1952 and 2011 from the European and Seychelles purse seine fisheries, Maldivian pole and line
vessels, and Taiwanese and Japanese longliners.

726

729 **Table S3.** Parameters and variables used in the somatic growth models.

Parameter	Unit	Description
L_i	cm	Fork length of fish i
A_i	y	Age of fish i
L_{∞}	cm	Asymptotic length
k_1	y^{-1}	First stanza growth rate coefficient
k_2	y^{-1}	Second stanza growth rate coefficient
α	y	Relative age of change in growth
β	y^{-1}	Transition rate between k_1 and k_2
t_0	y	Theoretical age of fork length 0
ε_i	cm	Process error for fish i

Table S4. Prior distributions used for parameters of somatic growth models.

Prior for yellowfin model	Prior for bigeye model
$L_{\infty} \sim \text{GEV}(173.141, 11.067, -0.3474)$	$L_{\infty} \sim \text{GEV}(187.622, 9.189, -0.3313)$
$k_1 \sim \Gamma(2.778, 0.211)$	$k_1 \sim \Gamma(4, 0.058)$
$K_2 = K_1 + \kappa$ with $\kappa \sim U(0, 3)$	
$\alpha \sim \Gamma(25, 1)$	
$\beta \sim U(0, 30)$	

	$t_0 \sim U(-2,0)$
$\varepsilon_i \sim N(0, \sigma^2)$	with $\sigma^2 \sim Inv\Gamma(0.01, 0.01)$

732

3.2. Model diagnostic

Estimates of growth parameters were evaluated using Bayesian inference with OpenBugs
 735 (Spiegelhalter et al., 2011). For each parameter, the value of th Gelman and Rubin (1992) diagnostic
 was close to 1, indicating convergence. The marginal posterior distributions of growth parameters
 were generated from 750,000 samples from three MCMCs. A burn-in period of 5,000 iterations was
 738 initially rejected and the chain was thinned to each 1,500 samples to estimate the statistics of the
 growth parameters.

741

744 **Table S5.** Growth curve parameters according to age estimations of each team.

Species	Reader team	N	Size range (cm)	Parameter	Mean	SD
Bigeye	1	69	46-105.3	L_{∞}	189.92	10.21
				k1	0.237	0.032
				k2	1.558	0.934
				t_0	-0.214	0.166
				α	3.948	1.754
				β	15.048	15.094
	2	46	46-141.6	L_{∞}	186.563	11.83
				k1	0.124	0.022
				k2	1.34	0.664
				t_0	-1.156	0.39
				α	3.669	0.929
				β	6.344	13.497
	3	113	46-141.6	L_{∞}	188.90	9.43
				k1	0.154	0.032
				k2	0.938	0.895
				t_0	-0.53	0.447
				α	4.602	2.634
				β	22.852	15.53
Yellowfin	1	170	19-147.5	L_{∞}	165.29	14.09
				k1	0.211	0.044
				k2	0.762	0.339
				t_0	-0.469	0.248
				α	2.069	0.54
				β	7.382	14.587
	2	108	19-152	L_{∞}	170.47	12.81
				k1	0.188	0.04
				k2	0.602	0.301
				t_0	-0.593	0.291
				α	2.698	0.697
				β	7.375	14.656

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