Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region

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Abstract. Biological parameters such as age, growth and age (or size) at maturity are vital for accurate stock assessments and management plans to ensure that fisheries develop sustainably. Despite this, very few validated age studies have been conducted for large tropical pelagic species within the Australian region. Age and growth parameters were estimated for bigeye tuna, *Thunnus obesus* (Lowe, 1839), sampled from longline fisheries in the Australian region using validated techniques based on counts of annual increments. Poor increment clarity reduced the number of otoliths included in the final analysis to only 50% of the 3200 selected for reading (39–178-cm fork length). Microincrement analysis confirmed the position of the first two annual increments in these otoliths. A maximum age of 16 years was obtained, but over 80% of fish in the Australian catch were <5 years old. Growth is most rapid in the first few years of life and asymptotic length is reached at about age 9 to 10 years. The von Bertalanffy growth parameters were estimated at $L_\infty = 169.09$, $k = 0.238$, and $t_0 = -1.706$ for the south-west Pacific Ocean and $L_\infty = 178.41$, $k = 0.176$, and $t_0 = -2.500$ for the eastern Indian Ocean. These parameters were significantly different, suggesting that there is little mixing between populations in the Pacific and Indian Oceans. Length at 50% maturity for females sampled in northern Queensland was estimated to be 102.4-cm fork length.

Extra keywords: age composition, longevity, microincrements, otoliths, stock structure.

Introduction

Accurate estimates of fish age are essential for calculating growth, mortality, longevity and age at maturity, which are important for age-based stock assessments and the development of appropriate management plans. Age and growth information can be obtained from a variety of different sources such as length–frequency data, tagging and direct ageing of calcified tissues such as otoliths, scales and vertebrae (Pauly 1983). Estimating age through modal progression of length–frequencies, however, is often considered imprecise when length modes merge as fish grow, whereas estimating growth using tag–return data is generally limited to small/young fish because most tagged fish are recaptured within a few years of release. Counts of increments on calcified tissues such as otoliths, on the other hand, have been widely used to obtain estimates of annual age, and these estimates are considered accurate if the ageing method has been validated (Beamish and McFarlane 1983). It had long been thought, however, that otoliths from tropical species could not be used to estimate age because the tropical environment lacked seasonal variation in factors such as temperature,

resulting in the absence of clear annual growth checks. Several studies have now shown that this is not the case, and otoliths of many tropical reef species and some tropical pelagic species also exhibit seasonal growth patterns that can be interpreted for age determination (see review in Morales-Nin and Panfili 2005).

Bigeye tuna, *Thunnus obesus* (Lowe, 1839), is a large pelagic species inhabiting tropical and subtropical waters of the Pacific, Indian and Atlantic Oceans. It is considered one of Australia's most valuable tuna species, yet little is known about key biology parameters such as its age and growth within the Australian region. On the east coast, bigeye is caught in an Eastern Tuna and Billfish Fishery (ET&BF) with over 1000 tonnes landed annually in 2001–2003 (Caton and McLoughlin 2005). On the west coast of Australia, the longline catch of bigeye in the Southern and Western Tuna and Billfish Fishery (SWT&BF) is much smaller than in the east (200–400 tonnes caught annually since 1998) but is a valuable component of that fishery (Caton and McLoughlin 2005). These Australian fisheries form part of the larger fisheries in either the Western and Central Pacific Ocean where

60 000–80 000 tonnes of bigeye are caught annually, or the eastern Indian Ocean where 40 000–60 000 tonnes are caught annually (Lawson 2004; Anon 2005). North of the SWT&BF, is the large Indonesian longline fishery that targets bigeye and yellowfin tuna (*Thunnus albacares*) in a known tuna spawning area within its Exclusive Economic Zone and on the high seas. In 1996–2001, an estimated 20 000–30 000 tonnes of bigeye were caught annually by that fishery (Anon 2005).

Within the Pacific and Indian Oceans, the annual age of bigeye has been estimated using scales and vertebrae (Yukinawa and Yabuta 1963; Tankevich 1982), but neither technique was validated. Sun *et al.* (2001) estimated the annual age of bigeye using dorsal spines from fish up to 189-cm fork length and used edge type analysis to indirectly validate the annual periodicity of the increments counted. Most recent studies have used counts of microincrements in otoliths to estimate daily age (Hampton *et al.* 1998; Matsumoto 1998; Lehodey *et al.* 1999; Kato 2001; Stequert and Conand 2004), although none directly validated the periodicity of these increments. Oxytetracycline mark–recapture experiments in the eastern Pacific and eastern Atlantic Oceans, however, confirmed the daily deposition of microincrements in otoliths of small bigeye in these regions (Anon 2002; Hallier *et al.* 2005). The maximum age obtained from studies so far have ranged between 7 and 10 years. Tag–return data, however, suggested that bigeye may live significantly longer than this (Hampton and Gunn 1998; J. Hampton, personal communication).

Clear *et al.* (2000) developed validated techniques to estimate the annual age of bigeye using otoliths through a strontium chloride mark–recapture experiment in the Coral Sea. They could not, however, validate the 1st annual increment because the smallest fish tagged and released (assumed to be 0+) had not been recovered. This led us to investigate the use of microincrement counts to confirm the position of the first annulus in sectioned otoliths, and use counts of annual increments in otoliths to estimate longevity, determine the age structure of the catch of bigeye within the Australian region, investigate sexual and regional differences in growth, and estimate mean length/age at maturity of bigeye from the spawning area in the north-western Coral Sea.

Material and methods

Terminology

The language used to describe otolith structure often varies between studies, creating some confusion. In brief, 'growth zones' are the opaque and translucent 'bands' visible along sectioned sagittal otoliths that form 'growth increments'. Under transmitted light, the opaque zone appears dark and the translucent zone appears light. Growth zones can be on a micro (daily) or macro (annual) scale, and the analysis of these is referred to as 'microincrement' and 'annual increment' analysis respectively. A 'final count' refers to the estimated number of opaque growth zones (e.g. Fig. 1) present in the otolith after consecutive readings. A 'sister' otolith is the second otolith of a pair from the same fish (e.g. sister sagittal otoliths).
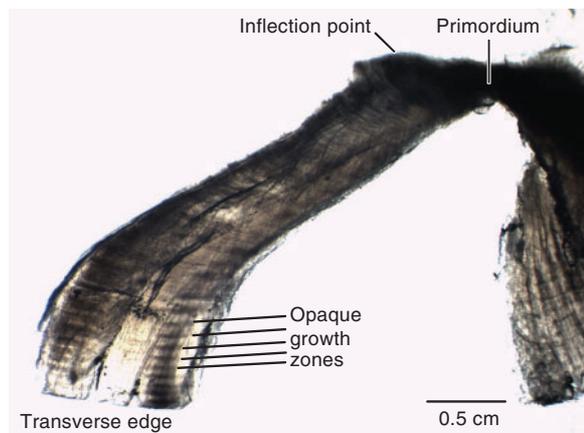
Fig. 1.   Transverse section of a bigeye tuna otolith showing clear annual opaque growth zones at the terminal edge (5 marked) and the region of unclear increments towards the primordium.

Sampling and laboratory processing

Sagittal otoliths selected for age estimation were sampled from bigeye caught in the south-west Pacific and eastern Indian Oceans. Sampled fish were caught in two low latitude areas (Northern Queensland (Qld) and Indonesia (south of Bali)) and two higher latitude areas (southern Queensland/New South Wales (Qld/NSW) and Western Australia (WA)) by three longline fisheries (Australian, Japanese and Indonesian) (Table 1, Fig. 2). Otoliths sampled from the Australian fishery were collected by scientific observers aboard the vessels or by technicians at processing factories and fish markets between October 1999 and December 2002. The otoliths collected at processing factories were randomly sampled from fish landed on a given day, but not all days were monitored during the year. Otoliths sampled from the Japanese fishery were collected by scientific observers onboard the vessels between July 1992 and September 1997. The remaining otoliths, sampled from the Indonesian fishery, were sampled at the port of Benoa (south Bali) as part of a catch-monitoring program in conjunction with the Research Institute of Marine Fisheries in Indonesia (Davis and Andamari 2002) between October 2000 and July 2002.

Fork length was measured to the nearest cm for all fish. Some length measurements were made 'over the body' ($n = 861$). These measurements were adjusted to standard length using a regression based on 'over the body' and standard length measurements made on a subsample of 22 fish ranging in size from 95 to 150 cm:

$$y = (0.8948x) + 5.4251$$

where y is the standard fork length and x is the tape measurement over the body of the fish ($r^2 = 0.983$). A Kolmogorov–Smirnoff test was used to compare the length distributions of fish with age estimates sampled in the Pacific and Indian Oceans. Dressed weight (weight after the gills, guts and fins were removed and discarded) was measured to the nearest 0.1 kg for most fish sampled and sex was recorded where possible.

Of the otoliths collected, 3200 were selected based on area of capture and length of fish, with the aim of estimating ages of fish from a representative sample of the size range of bigeye caught in each fishery (stratified sampling), although priority was given to fish with sex identified (Table 1). Otoliths were weighed to the nearest 1 mg ($n = 2483$) and the maximum length was measured to the nearest 0.1 mm for a subset ($n = 1173$). We tested for differences in the otolith length to fish length relationship between oceans using analysis of covariance (ANCOVA). Where necessary, the data were log-transformed to meet the assumptions of normality and homoscedasticity.

Ocean	Region	Australian			Japanese			Indonesian			Total *n*
		M	F	U	M	F	U	M	F	U	
Pacific	N. Qld	468	377	23	–	–	–	–	–	–	868
Pacific	Qld/NSW	57	56	964	26	27	–	–	–	–	1130
Indian	WA	–	–	547	128	134	–	–	–	–	809
Indian	Bali	–	–	–	–	–	–	192	199	2	393
Total		525	433	1534	154	161	–	192	199	2	3200
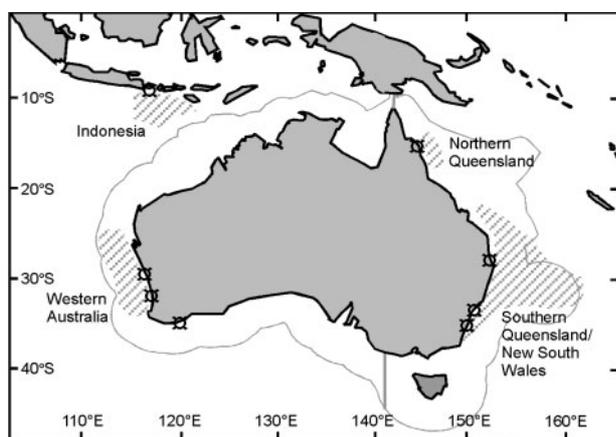
Fig. 2. Regions of bigeye catches (shaded) and locations of fishing ports (¤) sampled for otoliths. The Australian Fishing Zone is shown by grey line.

Annual age determination

Otoliths were embedded in clear casting polyester resin and four or five serial transverse sections were cut from each (one section including the primordium) and polished to ∼350-μm thick. Otolith sections were examined under compound and dissecting light microscopes using transmitted light, and the 'best' section for clarity and interpretability was chosen for reading. The number of visible opaque growth zones was counted along the ventral 'long' arm of each otolith using the techniques developed by Clear *et al.* (2000), and a confidence score of 1 (poor) to 5 (excellent) was assigned to each reading. Otoliths were read two or three times by the same reader without reference to the previous reading, length of fish or date of capture. If the successive readings were in agreement, this estimate was used as the final increment count for the otolith. However, if the readings differed, a further reading was conducted with knowledge of the previous readings to decide on a final count. The final count was assigned an overall confidence based on the mean of the individual confidence scores. If no obvious pattern could be seen in the otolith section, a count was not made. The Average Percentage Error method of Beamish and Fournier (1981) was used to examine intra-reader consistency in replicate otolith readings (precision of readings).

To assign each fish to its correct age-class, a birth date of 1 January and an opaque growth zone formation date of 1 June were assumed, and the final count was adjusted according to capture date. Although bigeye are known to spawn year-round in equatorial waters when surface water temperatures are >24°C (Schaefer 2001; Schaefer *et al.* 2005),

spawning is generally restricted to the summer months in both the tropical western Pacific and tropical eastern Indian Oceans (Kikawa 1962; Mohri *et al.* 1997); the most likely sources of recruits to the ET&BF and SWT&BF. 1 January is also the internationally accepted birth date when biological birth date is unknown (Williams and Bedford 1974). We assigned 1 June as the date that opaque zones form because our results indicate that opaque zones form during winter. For all fish caught after 1 January, but before 1 June, we added 1 year to the final increment count for the otolith. Given the variation in both birth date and time of increment formation, the resulting age estimates will be approximate.

The otoliths were viewed using an image-analysis system; images were acquired with a video camera (Phillips, Eindhoven, Holland) mounted on a Leitz orthoplan microscope (Leitz, Wetzlar, Germany) into a Macintosh computer (www.apple.com, verified October 2006). NIH Image software (developed at the USA National Institutes of Health and available at http://rsb.info.nih.gov/nih-image/, verified September 2006) was used to process and enhance the images and measure otolith increment widths. The distance from the inflection point (Fig. 1) to the first three opaque growth zones (if present and clearly defined) and to the terminal edge of the otolith were made along the external side of the otolith section. For consistency, measurements were only made on sections that contained the primordium. Marginal increment analysis (MIA) and edge type analysis (ETA) (see review in Campana 2001) were used to determine if the timing of increment formation during the year could be ascertained. The marginal increment of otoliths was calculated by measuring the distance from last-formed opaque growth zone to the terminal edge of the otolith (incomplete annual increment) as a proportion of the previous complete annual increment. This analysis was restricted to otoliths with a final increment count of 2 and 3 years. For the ETA, the terminal edge of each otolith section was scored on the presence of an opaque or translucent zone. This analysis was restricted to otoliths with an increment count of 5 or more years (because increments are more obvious), and where the region near the terminal edge of otolith section showed distinct alternating opaque and translucent growth zones. The data were pooled across years and areas (within each ocean) due to the low number sampled for some months.

To examine the temperature experienced by bigeye in the Australian region, mean monthly Reynolds V2 sea surface temperature (SST) data were obtained from NOAA–CIRES Climate Diagnostics Center, Boulder, CO, USA (http://www.cdc.noaa.gov/, verified September 2006) from 1997 to 2002 for the areas sampled: Qld (15–20°S, 145–155°E); Qld/NSW (20–40°S, 150–160°E); WA (25–35°S, 110–115°E); and Bali (10–15°S, 115–120°E).

Microincrement analysis

To confirm the location of the first few annual increments (or more specifically the opaque growth zones) in sectioned otoliths, the 'sister' otoliths from 113 pairs were selected for a direct comparison of

micro- and annual increments. Otoliths for microincrement analysis were randomly selected from fish between 81- and 120-cm fork length from northern Qld, Qld/NSW and WA. A fork length of 120 cm is the maximum length recommended for microincrement analysis using light microscopy by Lehodey *et al.* (1999).

Otoliths were embedded in polyester resin and a transverse section containing the primordium was prepared and polished to 50–75-µm thick. The surface of the section was partially decalcified with 5% ethylenediaminetetraacetic acid (EDTA; pH 7.4) to emphasise the increments. The number of visible microincrements was counted on each otolith under high magnification on a dissecting microscope and a reliability score based on the entire reading was given to each otolith as excellent, good or doubtful. All counts were made from the primordium to the terminal edge, and assuming daily increment formation, these provided an estimate of age. When present, the distance from the inflection point to the 365th increment (age 1; Y1), the 730th increment (age 2; Y2) and to the edge of the otolith (ZT) was measured and compared with the location of the opaque zones in the corresponding sister otolith. All measurements were made along the external side of the ventral edge of the section – the same path as for the annual opaque growth zone measurements.

Growth and catch-at-age

To include as much data as possible for analysis, age estimates from the age validation study of Clear *et al.* (2000) were combined with the current data ($n = 46$; same sample locations as in the current study). These additional otoliths were sampled from the same time and area range as the current study. The von Bertalanffy growth function was fitted to the combined length-at-age data by sex, sampling location and ocean using the equation:

$$L_t = L_\infty(1 - e^{-k(t-t_o)})$$

where L_t is the fork length (cm) at age t, L_∞ is the theoretical maximum fork length, k is the growth parameter (per year) and t_o is the theoretical age (years) at zero length. The equation was fitted using the non-linear regression function. Growth parameters were estimated using the least square method and growth functions were compared using a modified analysis of the residual sum of squares (ARSS; Chen *et al.* 1992).

To determine the age structure of bigeye caught in the Australian fisheries, age–length keys were developed for the south-west Pacific and eastern Indian Oceans using our sample of aged fish collected in 2001. Age–length keys give the proportion of age from fish in each 5-cm length class, which enabled the conversion of catch-at-length data to catch-at-age. The ET&BF and SWT&BF were not sampled sufficiently for length, but weight data was collected for a large proportion of the catch (78% between mid-1997 and mid-2001; Campbell *et al.* 2003). Individual weight data collected between January and December 2001 ($n = 22\,269$ in the ET&BF and 1962 in the SW&TBF) were converted to lengths using:

$$L = (W/a)^{1/b}$$

where $a = 2.6696 \times 10^{-5}$ and $b = 2.948$ for the ET&BF (Campbell and Dowling 2003), and $a = 2.74 \times 10^{-5}$ and $b = 2.908$ for the SWT&BF (Stobberup *et al.* 1998).

Length and age at maturity

To estimate length at maturity for bigeye tuna caught off northern Qld, ovaries were removed from 635 fish in conjunction with otolith sampling by technicians on board two Australian longliners between August 2000 and September 2002. Very few samples were collected between December and April in those years, because bigeye were rarely caught. The majority were caught in the area 146–148°E, 15–18°S (69%) or 150–154°E, 18–19°S (27%). A visual assessment of the developmental
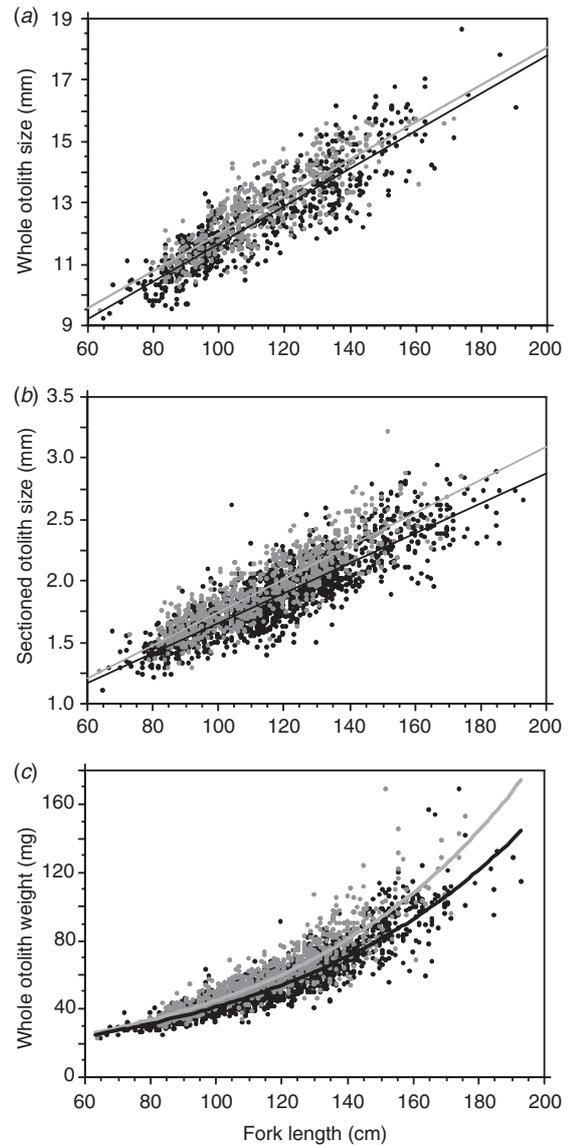
Fig. 3. Relationship between fork length and (*a*) whole otolith size ($n = 1173$), (*b*) sectioned otolith size ($n = 2295$) and (*c*) whole otolith weight ($n = 2483$) for bigeye sampled in the eastern Indian Ocean (grey) and south-west Pacific Oceans (black).

stage was made based on the macroscopic appearance of the ovaries using the scheme developed by McPherson (1992) and each fish was classified as either mature or immature based on the presence of vitellogenic oocytes.

An estimate of length at 50% maturity for females was obtained from a logistic regression:

$$P(maturity|L) = (\exp(a + bL))/(1 + \exp(a + bL))$$

where P is the estimated proportion of mature individuals at fork length L, and a and b are parameters that define the shape and position of the fitted curve. The predicted length at 50% (L_{50}) maturity was calculated as:

$$L_{50} = -a/b$$

Age at 50% maturity was estimated using the von Bertalanffy equation we estimated for the south-west Pacific Ocean.

Results

Otolith growth

Fish length and otolith size had a linear relationship (Fig. 3*a*,*b*; r^2 ranged between 0.717 and 0.779). Significant differences in these relationships (otolith growth) were detected between the eastern Indian Ocean (WA and Bali) and the south-west Pacific Ocean (northern Qld and Qld/NSW) (ANCOVA; $P < 0.001$). Otolith weight increased exponentially with fish length (Fig. 3*c*; $r^2 = 0.858$ south-west Pacific Ocean and $r^2 = 0.853$ eastern Indian Ocean).

Annual age determination

The clarity and interpretability of annual increments varies substantially between otoliths. In general, the first two or three annual opaque zones deposited appear broad, diffuse and often contain multiple translucent and opaque sub-annual bands. Subsequent opaque zones are usually darker and more obvious, and in large otoliths the distance between the opaque zones becomes regular in width and appearance towards the terminal edge of the otolith (Fig. 1).

The mean average percentage error (APE) between blind readings was 5.98%. Not surprisingly, the precision of readings was related to the confidence score from the readings: lower precision being correlated with lower confidence scores. If only those otoliths with a mean confidence score of ≥ 2.5 (from consecutive readings) are included, mean APE decreased to 4.34% – a precision level above that recommended by Morison *et al.* (1998). When successive readings of these otoliths differed, 97% were by only ± 1 year, indicating a high level of precision.

A final increment count was assigned to 2185 (68%) of the otoliths read. Of these, only 1611 were included in the final data analysis because age estimates with mean confidence scores below 2.5 were not included. There was no significant difference in mean otolith size between otoliths included and excluded from the final analysis (unpaired *t*-tests by 5-cm length class; $P > 0.05$) suggesting that otolith size does not appear to influence the otolith readability in bigeye tuna. Overall, a slightly greater proportion of otoliths sampled from higher latitudes (Qld/NSW and WA; both 55%) were included in the final analysis compared with otoliths sampled from lower latitudes (Northern Qld and Bali; 39 and 51% respectively). When age estimates from Clear *et al.* (2000) were included ($n = 46$), the final analysis included fish ranging in length from 39 to 178 cm in the south-west Pacific and 64 to 176 cm in the eastern Indian Oceans, although 95% were from fish between 80 and 160 cm (Fig. 4). No significant difference was found in the distribution of lengths of fish with age estimates between the two oceans (Kolmogorov–Smirnov test, $D = 6.86$, $P = 0.0647$).

The monthly marginal increment (MI) data for 2–3-year old bigeye caught in the Pacific Ocean showed a cyclic pattern, with a minimum occurring from May to July (Fig. 5*a*).
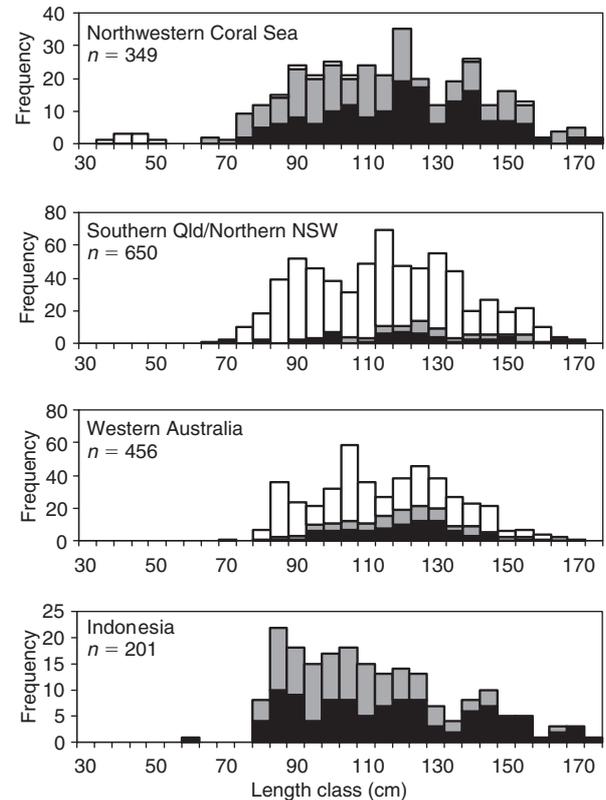
Fig. 4. Length–frequency distribution of bigeye with otoliths used in the final age analysis. Black = male, grey = female, white = unknown sex.

The ETA suggests that opaque zones form from May to August in the otoliths of older fish (5+ years). The mean monthly SST data for the two regions sampled showed a cyclic pattern, with the lowest temperatures occuring in July to September (Fig. 6). The seasonal SST range (difference between the warmest and coolest months) for Qld and Qld/NSW was 4.5°C and 5.4°C respectively. For bigeye sampled in the eastern Indian Ocean, a cyclic pattern was not evident in the MI data, whereas the ETA showed that opaque zones were more common at the otolith edge from April to June (Fig. 5*b*). The mean monthly SSTs were lowest in July to September south of Bali, and August to October in WA (Fig. 6). The seasonal temperature extremes for Bali and WA were 3.1°C and 4.0°C respectively. The high standard errors associated with the MI data, and the presence of opaque zones at the otolith edge year-round, highlights the variability in the timing of growth zone formation present in the data.

Microincrement analysis

Of the 113 otoliths read for microincrement analysis, 73 were given a reliability score of excellent or good. Increment counts ranged from 544 to 1300 corresponding to 1.5 and 3.6 years respectively, assuming that microincrements form daily. A linear relationship ($r^2 = 0.731$) was found between

(*a*)

(*b*)
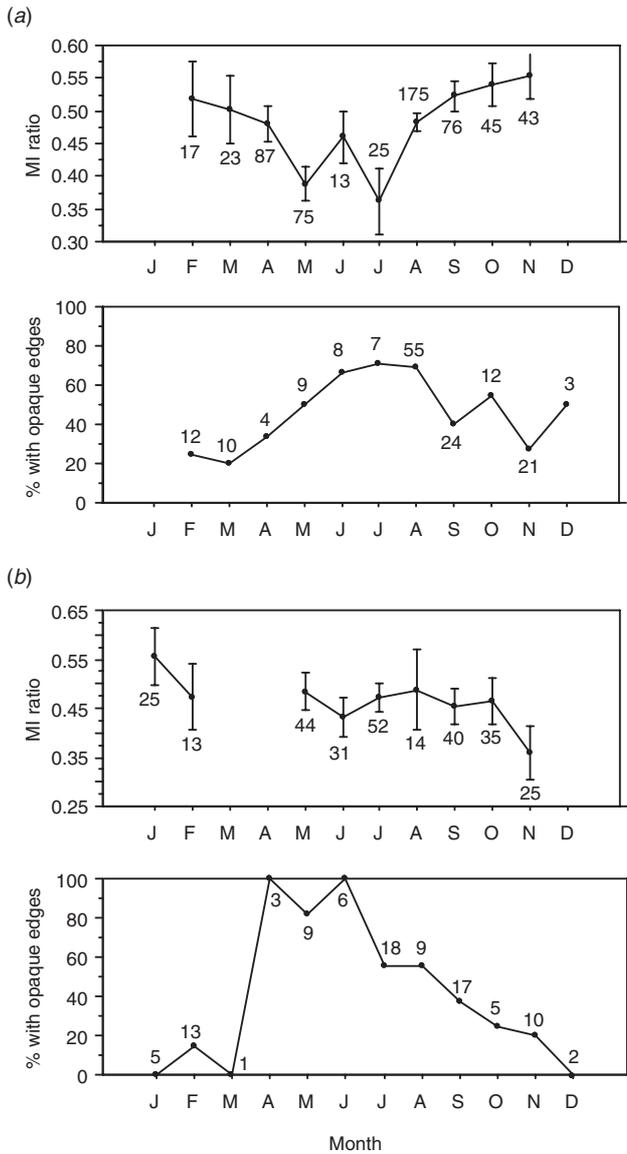
Fig. 5. Mean monthly marginal increment(MI) ratio (proportion of the previous annual increment) for bigeye aged 2+ and 3+, and proportion of otoliths with opaque edges for bigeye aged ≥5+, in the (*a*) south-west Pacific and (*b*) eastern Indian Oceans. Error bars show ±1 s.e. of the mean, and numbers indicate sample sizes.

Fig. 6. Mean and standard deviation monthly Reynolds sea surface temperature (SST) by sampling area: northern Qld (□), Qld/NSW (○), WA (●), and Bali (■).
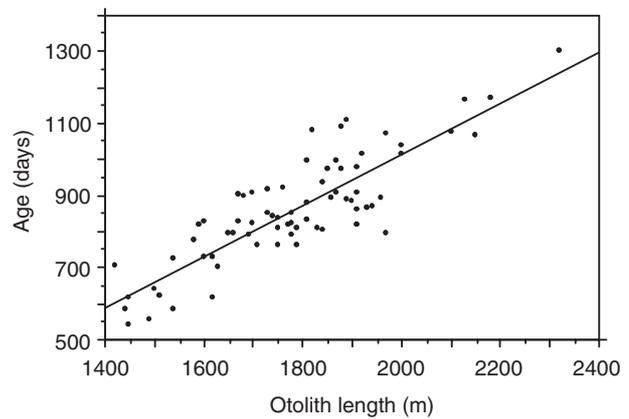
Fig. 7. Relationship between estimated age (days) from microincrement count and sectioned otolith length (distance from the inflection point to the edge of the otolith; ZT). Only otolith readings with a readability score of good or excellent are included.

otolith length (ZT) and estimated daily age (Fig. 7). The distance from the inflection point to the 365th increment (Y1) and the 730th increment (Y2) were consistent with the estimated positions of the first two annual opaque zones in 53 corresponding sister otoliths that could be directly compared. The position of Y1 and Y2 along the otolith occurred after the corresponding opaque zone in 89% of otoliths, confirming that the first two annual increments were successfully identified in these otoliths.

The mean distance to Y1 was 1124 μm (± s.e. 9.5) and to Y2 was 1639 μm (± s.d. 11.9). No significant differences were detected in the means of Y1 or Y2 between the four regions (ANOVA; $P = 0.829$ for Y1 and $P = 0.739$ for Y2). This is confirmed by the multiple comparisons analysis using the Bonferroni test ($P > 0.05$). By comparing the mean of Y1 and Y2 with histograms of the distance to the first three opaque zones from annual age analysis (Fig. 8), it is clear that the first few annual increments are being successfully identified in sectioned otoliths. This comparison of micro and annual increments also shows that the first annual opaque zone is not deposited exactly 1 year after birth.

Growth and catch-at-age

Age estimated for bigeye ranged from 1 to 16 years. Large variations in age were detected within all length classes, showing that growth is highly variable in bigeye tuna. Of the age estimates included in the final analysis, sex was known for 783 (47.3%). A small but significant difference in von Bertalanffy growth parameters was found between
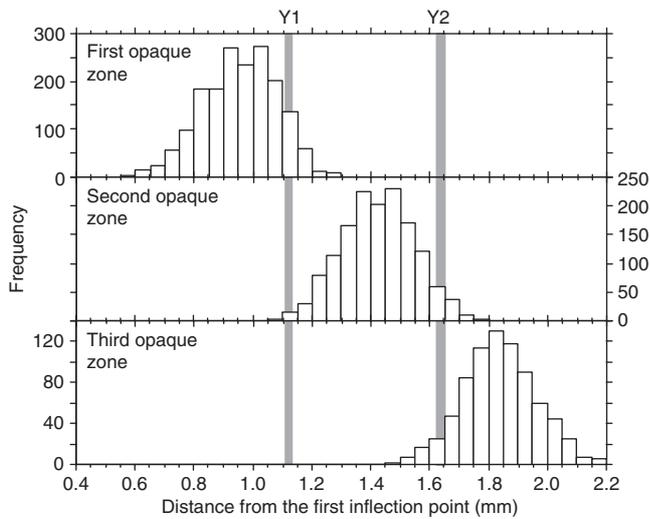
Fig. 8. Histograms of the distance from the inflection point to the first, second and third opaque zones on otoliths measured for annual age estimation. Grey stripes represent the mean distance ± s.d. to the 365th increment (age 1; Y1) and the 730th increment (age 2; Y2) from microincrement analysis.

males and females sampled in the south-west Pacific Ocean (ARSS; $F = 2.99$; d.f. 3, 422, $P = 0.031$) but not in the eastern Indian Ocean (ARSS; $F = 0.30$; d.f. 3, 349, $P = 0.825$). In the south-west Pacific Ocean, estimated growth parameters (L_∞, k, t_o) for males are 172.21, 0.222, −2.045 and for females are 161.73, 0.252, −2.066. Asymptotic length was also found to be slightly greater for males (185.1 cm) than females (174.7 cm) in the eastern Indian Ocean.

Using all length-at-age data, the estimated growth parameters were found to be significantly different between all sampling locations, except between WA and Bali (Table 2). The comparisons suggest that the smallest differences in growth occurred between sampling locations in the same ocean, and the largest differences occurred between sampling locations in different oceans. The von Bertalanffy growth parameter k was greater for bigeye sampled in the south-west Pacific Ocean compared with the eastern Indian Ocean (Fig. 9). Estimates of L_∞ were close to the observed maximum length of bigeye caught in the region, and were slightly larger for the Indian Ocean fish. Mean length-at-age for fish sampled in the south-west Pacific were generally larger than for fish in the eastern Indian Ocean (Fig. 9).

The catch of bigeye in both the ET&BF and the SWT&BF in 2001 consisted predominantly of small/young fish, with the 2- to 4-year age classes being most abundant (Fig. 10). In the ET&BF, 105–125-cm fish dominated the catch in 2001, giving a higher abundance of 3-year olds compared with the SWT&BF, where slightly smaller fish (85–120 cm) dominated.

Table 2. Comparison of von Bertalanffy growth models between sampling locations and oceans using analysis of the residual sum of squares (ARSS)

Sampling location compared		F	d.f.	P
WA	Bali	1.16	3, 651	0.300
N. Qld	Qld/NSW	3.75	3, 993	0.011
N. Qld	WA	4.46	3, 502	0.004
Qld/NSW	Bali	5.28	3, 845	<0.001
N. Qld	Bali	5.94	3, 544	<0.001
Qld/NSW	WA	12.68	3, 1100	<0.001
Pacific Ocean	Indian Ocean	14.04	3, 1650	<0.001
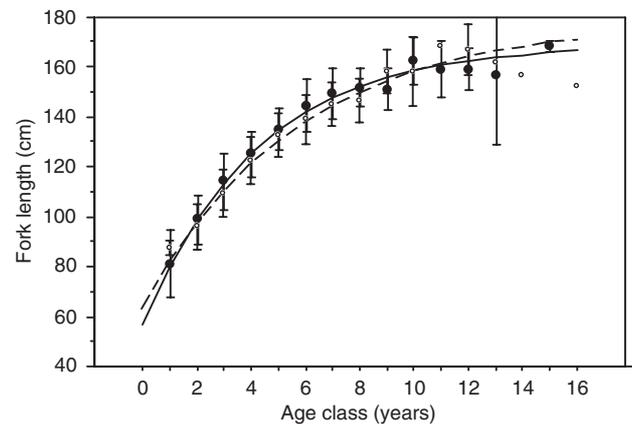
Fig. 9. Mean length-at-age ± 1 standard deviation for bigeye tuna caught in the south-west Pacific (●) and eastern Indian (○) Oceans. Von Bertalanffy growth curves fitted to the raw length-at-age data are shown. Estimated growth parameters (L_∞, k, t_o) for south-west Pacific Ocean bigeye are 169.09, 0.238, −1.706 and eastern Indian Ocean bigeye are 178.41, 0.176, −2.500 (dashed line).

Length and age at maturity

Off northern Qld, females classed as mature were predominantly caught from August to November in 2000 and from October to December in 2001 (98%) and these months were selected as the best for estimating size at maturity. The size of females sampled for ovaries during these months ranged from 61 to 172 cm, with a mode between 100- and 115-cm fork lengths. The smallest mature female sampled was 80 cm, although 288 (96%) of females classed as mature were ≥100-cm fork length. Using the logistic curve fitted to the maturity data, length at 50% maturity (L_{50}) was estimated to be 102.4 cm (Fig. 11). Of the females in the 100–104.9-cm length class (the class encompassing female L_{50}) sampled off northern Qld, 88% were estimated to be 2-year olds. Using the estimated von Bertalanffy growth parameters for the south-west Pacific Ocean, a fish of 102.4-cm fork length would be 2.2 years old. If the von Bertalanffy growth parameters of Hampton *et al.* (1998) based on counts of (assumed) daily increments were used to estimate age, a fish of 102.4-cm fork length would be 2.4 years old.
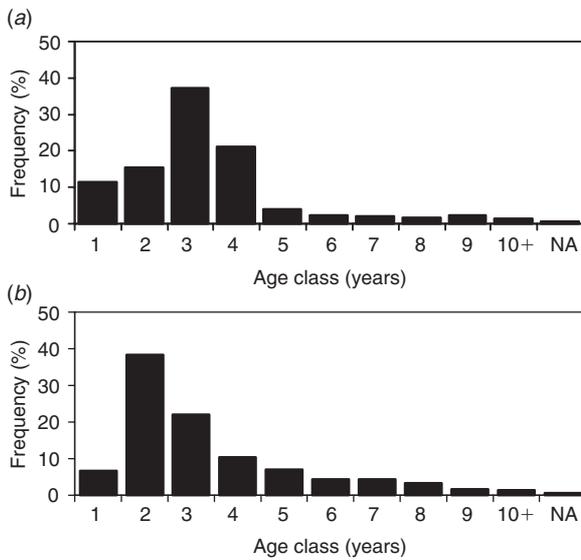
Fig. 10. Length (2-cm classes) and age distribution of bigeye caught in the (*a*) Eastern Tuna and Billfish Fishery and (*b*) Southern and Western tuna and Billfish Fishery in 2001. NA = age not assigned as key did not cover the full range of lengths.
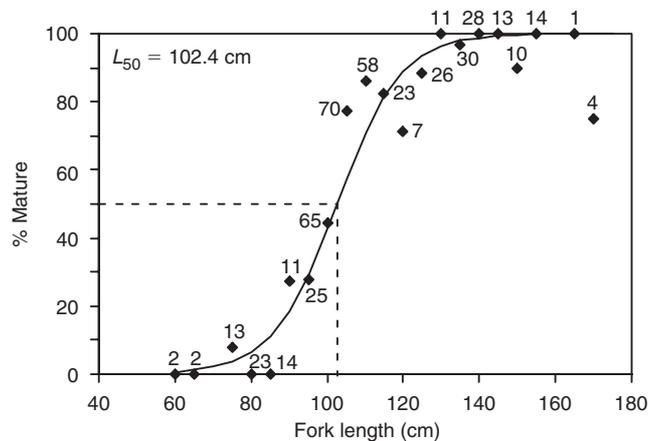
Fig. 11. Proportion of mature female bigeye tuna in the north-western Coral Sea by 5-cm length classes ($n = 450$). Data restricted to the spawning season (August–November 2000 and October–December 2001). Maximum likelihood fit of the logistic regression model is shown for the restricted data. Dotted lines show length at 50% maturity. Number of fish sampled is shown for each size class.

Discussion

Age estimation

The annual age of bigeye was directly validated by Clear *et al.* (2000) during a mark–recapture study using strontium chloride. This work confirmed that the 2nd to 9th opaque zones are formed annually for fish caught off northern Qld. Similar validation has not been undertaken for bigeye caught elsewhere, or for fish older than 9 years, so results for these fish should be considered preliminary.

The precise time that annual increments form in otoliths remains inconclusive, although there was some indication from marginal increment and edge type analysis that opaque zones form during early winter in 2–3-year olds, and slightly earlier for older fish. The lack of a consistent pattern in the marginal increment and edge type data may be due in part to poor measurement precision associated with the first few increments, problems associated with resolving increments at the otolith edge (Campana 2001), low samples sizes for some months, and/or variability in the timing of increment formation between individuals, age classes, years, or areas (e.g. equatorial *v.* temperate latitudes). These factors would obscure trends in annual increment formation when samples are pooled across years and areas. Sun *et al.* (2001) used edge type analysis on dorsal spines to suggest that February to September was the period of slow growth for bigeye caught in the north-west Pacific Ocean, which coincided with the spawning period of fish in the region. Our comparison of micro- and annual increments, however, shows that the first annual opaque zone is rarely deposited 1 year after birth, suggesting that spawning does not control opaque-zone formation for bigeye caught in Australian waters.

We found that the clarity of annual increments in otoliths varied considerably between fish, reducing the number that could be analysed to only 50%. In all otoliths, the first few increments are generally indistinct, but become more distinct and regularly spaced as the otolith grows (fish matures). In southern bluefin tuna (*Thunnus maccoyii*) otoliths, annual slow-growth zones form during winter (Eveson *et al.* 2004), suggesting that changes in water temperature experienced by the fish during annual cyclic migrations between cold southern waters in winter and warmer waters in summer (either the Great Australian Bight (GAB) for juveniles or south of Bali for adults) (Farley and Davis 1998; Gunn and Block 2001) influence otolith growth. It has been shown through both conventional and archival tagging, however, that juvenile bigeye show high levels of regional fidelity within in the ET&BF and in the wider Pacific Ocean (Gunn *et al.* 2005; Hampton and Williams 2005). If this is the case and surface temperature influences otolith growth in bigeye, the small annual fluctuations experienced in the areas sampled (only 3.1 to 5.4°C) and the fast juvenile growth rates may be responsible for the lack of distinct increments close to the primordium in many otoliths. This is supported to some extent by the link found between otolith clarity and latitude; a greater proportion of the otoliths sampled from lower latitudes in both oceans (where the annual SST fluctuation was greatest) were interpretable. Gunn *et al.* (2005), however, found that some bigeye tagged in the Coral Sea embarked on large-scale cyclic migrations possibly after reaching maturity. It is unknown if bigeye in the eastern Indian Ocean undertake similar migrations, although Mohri *et al.* (1997) suggested that bigeye in the Indian Ocean undertake a seasonal pattern of movement between the tropics (~10°S) in summer and higher

latitudes (∼30°S) in winter based on Japanese longline catch-and-effort data in the 1960–1980s. It seems plausible that if larger variations in temperature (or other factors such as prey availability) are experienced by migrating fish, the clarity of increments in their otoliths may be increased. Conversely, fish that remain in warm tropical waters year-round, or those that only migrate periodically, may have reduced otolith clarity. Combined tagging and otolith studies are needed to examine the timing and nature of these migrations, and whether they relate to otolith clarity.

Growth and catch-at-age

Bigeye is a relatively long-lived species of tuna. Growth is most rapid in the first few years of life and asymptotic length is reached at about age 9 to 10 years. The maximum age of 16 years is consistent with the recent recapture of a 168-cm tagged bigeye 12 years after release as a 2-year old in the south-west Pacific Ocean (J. Hampton, personal communication). The maximum age obtained for bigeye in previous direct ageing studies in the Pacific and Indian Oceans have ranged between 7 and 10 years (Tankevich 1982; Sun *et al*. 2001; Stequert and Conand 2004). These low figures are not surprising given that very few large fish (>140 cm) were sampled, apart from Sun *et al*. (2001), who collected dorsal spines from bigeye up to 189-cm fork length. Stequert and Conand (2004), however, questioned the reliability of using dorsal spines due to vascularisation of the core and interpretation problems, and recommended that this structure only be used for fish up to age 3 years. By comparison, only two tuna species have a greater reported maximum age than bigeye: Atlantic bluefin tuna (*Thunnus thynnus*) is estimated to reach 16–17 years (Ólafsdóttir and Ingimundardóttir 2004; Rodríguez-Marín *et al*. 2004) and southern bluefin tuna can live in excess of 30 years (Kalish *et al*. 1996).

The von Bertalanffy growth model has traditionally been used to describe growth of pelagic tuna species. It has been shown, however, that this model does not adequately describe the growth of small bigeye because of changes in the pattern of growth between juvenile stages (Lehodey *et al*. 1999). Analysis of daily age and tagging data showed that the growth of bigeye slows at around 60–70 cm, which led to the development of a modified von Bertalanffy model (Lehodey *et al*. 1999). Given that we used very few fish <70-cm fork length ($n = 14$) in our analysis, the growth curves obtained using the traditional von Bertalanffy model are appropriate for our purposes.

We have shown that males sampled in the south-west Pacific Ocean have slightly faster growth rates and higher L_∞ than females, although these differences were not as pronounced as reported for eastern Pacific bigeye (Shomura and Keala 1963; Kume and Joseph 1966; Suda and Kume 1967). The estimates of L_∞ from the combined length-at-age data (169.0 cm for the Pacific and 178.4 cm for the Indian Ocean) are generally smaller than estimated in earlier studies (see comparisons in Lehodey *et al*. (1999) and Sun *et al*. (2001)), but are similar to that estimated by Hampton *et al*. (1998) for the western and central Pacific Ocean (166.3 cm) and Stequert and Conand (2004) for the western Indian Ocean (169.0 cm). Both of these studies used counts of assumed daily increments on otoliths to estimate the age of fish up to age 3. To estimate the age of larger fish, Hampton *et al*. (1998) used tag–recapture data, whereas Stequert and Conand (2004) continued to use daily increment counts but used a scanning electron microscope to resolve the microincrements. The estimates of t_o obtained in the current study are lower than obtained in all previous studies, which is due primarily to the absence of small fish (<75 cm) in our samples resulting in higher estimated length-at-age for young fish (≤2-year age class).

The different growth rates of bigeye from the eastern Indian and south-west Pacific Oceans supports the hypothesis of separate populations in the Pacific and Indian Oceans. Similar differences were detected in otolith morphology – otoliths from the south-west Pacific were on average larger for the fish length than those from the eastern Indian Ocean. These findings are important but not surprising given that the tropical/subtropical distribution of bigeye would not allow for substantial mixing between the Pacific and Indian Oceans south of Australia. However, the results appear to be in conflict with genetic studies that have not found clear evidence of separate stocks or sub-structuring of bigeye in the Indo-Pacific region based on examination of mitochondrial DNA and DNA microsatellites (Alvarado-Bremer *et al*. 1998; Chow *et al*. 2000; Grewe *et al*. 2000). The Indonesian throughflow (Godfrey 2001) has been proposed as the region where bigeye larvae and juveniles are transported from the Pacific to the Indian Ocean, and that this mixing is the likely explanation of the genetic similarities (Chow *et al*. 2000). However, as only a small degree of mixing is required to reduce genetic heterogeneity between geographically distant populations (Waples 1998), analysis of genetic variation may not be sufficiently good a descriptor of stock structure for fisheries management purposes. It also seems surprising that genetic differences were not detected in bigeye sampled from the Indian and Pacific Oceans, given that some evidence has been found for restricted gene-flow between areas within each of these oceans (Grewe and Hampton 1998; Grewe *et al*. 2000; Appleyard *et al*. 2002).

Our study provides the first validated age–length keys and estimated catch-at-age for bigeye in Australian waters. Although fish aged ≤5 years dominated the catches in the ET&BF and SWT&BF in 2001, the age frequency distributions differed between the fisheries, providing further evidence of separate stocks in the eastern Indian and south-west Pacific Oceans. Campbell *et al*. (2003) showed that seasonal and regional fluctuations occur in the size of bigeye caught in the ET&BF, and that these fluctuations were

the result of variations in the recruitment and migration of cohorts. For example, the mean weight of bigeye caught by area and quarter varied from 20.7 to 38.7 kg in 2001. Campbell *et al.* (2003) indicated that poor recruitment of the 1997 and 1999 cohorts occurred in the ET&BF, whereas the 1998 cohort dominated the catch. These variations in recruitment are evident in the estimated age distribution for the ET&BF where 3-year olds dominated in 2001. By comparison, the dominance of 2-year olds in the SWT&BF in 2001 indicates a relatively large recruitment of the 1997 cohort in the region and poor recruitment of the 1998 cohort. This suggests that other factors such as environmental conditions are influencing year-class strength and that little mixing occurs between the populations.

Length and age at maturity

The smallest mature female sampled in northern Qld was 80-cm fork length, although most (96%) were greater than 100-cm fork length. Most previous studies report higher minimum length at first spawning of 90–110 cm (Kume 1962; Tankevich 1982; Sun *et al.* 1999; Schaefer *et al.* 2005). Our estimate of length at 50% maturity of 102.4 cm is substantially lower than that estimated for the eastern and central Pacific Ocean of 135 cm based on histological classification (Schaefer *et al.* 2005). There are several possible explanations for these differences. First, macroscopic staging is not recommended as the most appropriate method to estimate maturity because mature but post-spawning or resting females may be misclassified as immature (Schaefer 2001). However, if this type of misclassification occurred in our study, it would result in an overestimation of mean length at maturity. Further, we limited our analysis to data collected during the period of highest reproductive activity, which significantly reduces the chance of misclassifying mature females as immature/resting.

Second, there is some evidence to suggest that bigeye maturity estimates vary depending on the area and/or depth sampled. In the Coral Sea (northern Qld), Hisada (1973) and McPherson (1992) both reported smaller estimates of minimum length at maturity for bigeye caught in a Japanese handline area (64 and 100 cm respectively) compared with sub-surface longline-caught fish in the wider area (100 and 122 cm respectively). Differences in maturity levels with sampling depth have also been found for yellowfin tuna (Hisada 1973; Suzuki 1988; McPherson 1991). It has been hypothesised that the mature fish move to the surface to spawn when temperatures are ≥26°C where they are caught by handlines, whereas less mature fish remain in the cooler and deeper waters where they are caught by deeper-set longlines (Hisada 1973). The difference in maturity levels found with depth highlights the importance of obtaining samples from both surface and sub-surface fisheries for maturity data. The ovaries obtained in the current study were sampled from bigeye caught by Australian longliners operating predominantly

in the handline area. The longlining technique used, however, fished to depths up to 160 m (Gunn *et al.* 2005), which is similar to the fishing depths used in the longline area (Ward 1996). At times, the Australian fishers also use a method similar to the handline fishery to entice bigeye to the surface and onto the lines using baited hooks thrown directly at fish (Hampton and Gunn 1998). As a result, the ovaries sampled for the project were from a combination of depths and the results may better represent length at maturity for the population in the area. Further structured sampling would provide the data required to resolve this issue of differences in maturity estimates with area/depth.

Finally, given that the level of bigeye mixing between the Coral Sea and wider Pacific Ocean appears to be low (Gunn *et al.* 2005; Hampton and Williams 2005), it is not surprising that different life-history traits, such as length at maturity, are observed between regions. Differences in maturity estimates for yellowfin tuna have been linked to regional differences in productivity, temperature and length of the spawning season (Cole 1980; Itano 2000), and may explain to some extent the different maturity estimates obtained for bigeye in northern Qld and the eastern and central Pacific Ocean of Schaefer *et al.* (2005).

Conclusions and recommendations

This study establishes an understanding of several of the key biological parameters required for age-based stock assessments and population modelling of bigeye tuna in Australian waters. Counting of annual increments has allowed us to estimate the age of bigeye beyond the limit of microincrements, and the estimates of longevity reported are a significant result for bigeye. It is essential, however, that as strontium-injected fish are recaptured in the future, analysis of otoliths for validation purposes continues, especially for fish that have been at liberty for long periods or fish assumed to be aged 0+ when released. Similarly, as very few large fish were sampled, and none sampled were over 180-cm fork length, it is recommended otoliths from large fish (>150 cm) continue to be collected and analysed to provide a better estimate of length-at-age for these larger, older fish. In addition, a large-scale detailed histological study of bigeye maturity is required for the Coral Sea region to confirm the preliminary results in the current study and to determine other key biological parameters such as spawning frequency and batch fecundity. Similar reproductive work is also required for eastern equatorial Indian Ocean bigeye.

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