Abstract—The sectioned otoliths of four fish species from a tropical demersal trawl fishery in Western Australia revealed a series of alternating translucent and opaque zones in reflected light. The translucent zones, referred to as growth rings, were counted to determine fish ages. The width of the opaque zone on the periphery of the otolith section as a proportion of the width of the previous opaque zone (index of completion) was used to determine the periodicity of growth-ring formation. This article describes a method for modeling changes in the index of ring completion over time, from which a parameter for the most probable time of growth-ring formation (with confidence intervals) can be determined. The parameter estimate for the timing of new growth-ring formation for Lethrinus sp. 3 was from mid July to mid September, for Lutjanus vitta from early July to the end of August, for Nemipterus furcosus from mid July to late September, and for Lutjanus sebae from mid July to mid November. The confidence intervals for the timing of formation of growth rings was variable between species, being smallest for L. vitta, and variable between fish of the same species with different numbers of growth rings.

The stock assessments of these commercially important species rely on aging information for all the age classes used in the assessment. This study demonstrated that growth rings on sectioned otoliths were laid down annually, irrespective of the number of growth rings, and also demonstrated that the timing of ring formation for these tropical species can be determined quantitatively (with confidence intervals).

Quantitative determination of the timing of otolith ring formation from marginal increments in four marine teleost species from northwestern Australia

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The Pilbara fish trawl fishery, operating on the North West Shelf of Western Australia, has developed rapidly in the last ten years and is now the most valuable commercial scalefish fishery in Western Australia. Catch from this fishery was valued at $7 million (wholesale value) in 2001. In this multispecies fishery, Lutjanus vitta (Quoy and Gaimard, 1824) (brownstripe red snapper), Nemipterus furcosus (Valenciennes, 1830) (fork-tailed threadfin bream, also known as rosy threadfin bream), Lethrinus sp. 3 (Carpenter and Niem, 2001) (lesser spangled emperor, known locally as blue-spot emperor) made up 8%, 10%, and 20% respectively of the total scalefish trawl catch in 2000. The highly prized species, Lutjanus sebae (Cuvier, 1828) (red emperor), although comprising only 4% of the catch, is important because of its high market value.

In 1993 a research project was commenced to determine the fishing effort required for optimal level of catches in the Pilbara trawl fishery (Stephenson and Dunk1). The project relies on validated age composition data for L. vitta, L. sp. 3, N. furcosus, and L. sebae. The growth rings on otoliths have been shown to be formed annually for only one to three growth rings for N. furcosus (Sainsbury and Whitelaw, 1984), and for two to three growth rings for L. sebae (McPherson and Squire, 1992). After pooling of all age classes, Davis and West (1992) showed that growth rings of L. vitta were formed annually.

Determining age composition involves counting growth rings on hard parts of fish (otoliths, scales, spines, bones) and determining the timing of growth-ring formation. Sagittal otoliths are commonly used for aging teleost fishes and recent studies (Hyndes et al., 1992; Milton et al., 1995; Newman et al., 1996) have indicated that for some species sectioned otoliths give more reliable age estimates than whole, or broken-and-burnt otoliths. The periodicity of ring formation is commonly determined by the mark-recapture method in which fish are injected with chemical markers and the number of rings created between injection and recapture are compared (Ferreira and Russ, 1992; Francis et al., 1992; Newman et al., 1996).

An alternative to mark-recapture is marginal increment analysis in which the distance from the growth ring to the edge of the otolith, for a sample of fish, is tracked over time (Campana, 2001) and a sharp drop in this marginal increment, once a year, is taken as an indication of annual ring formation. The analysis is often performed on

1 Stephenson, P. C., and I. Dunk. 1996. Relating fishing mortality to fish trawl effort on the North West Slope of Western Australia. Final report of project 93/25 to the Fisheries Research and Development Corporation, 1995, 44 p. Western Australia Marine Research Laboratories, PO Box 20, North Beach, Western Australia 6092, Australia.
pooled age classes (Barger, 1985; Manickchand-Heileman and Kenny, 1990; Murphy and Taylor, 1990; Ross et al., 1995; Pearson, 1996; Morales-Nin and Moranta, 1997; Van der Walt and Beckley, 1997) or on a restricted number of age classes (Sainsbury and Whitelaw, 1984; McPherson and Squire, 1992).

Analysis with pooled data has limited value because there may be different patterns of growth-ring formation at different life stages (e.g. at sexual maturity) and pooled data may have interage differences masked by dominant age groups (Beamish and McFarlane, 1983; Hyndes et al., 1992). Studies in which data were pooled only for young and old fish, due to low fish numbers, reduced these problems and improved the credibility of the results (Hyndes et al., 1992; Fletcher and Blight, 1996; Hep et al., 2002).

Accounts of statistical analysis of the marginal increment data are rare. Davis and West (1992) used ANOVA to show that there were differences in the marginal increment of urohyal bones of L. vitta with time of year. As this seasonal pattern was the same for age classes 1 to 6, Davis and West (1992) pooled the data and used a graphical representation to show the time of formation of the annual rings.

This article describes a method for modeling changes in the index of completion of an otolith growth increment over time. This method enables quantitative determination of the most probable time of growth-ring formation (with confidence intervals) and is illustrated for the species L. vitta, L. sp. 3, N. furcosus, and L. sebae, from the Pilbara fish trawl fishery.

Materials and methods

Between October and November 1993 and between October and November 1994, samples of 30 fish of each species were randomly selected each month from fishery-independent trawl surveys. For the other months between January 1994 and March 1995, samples of 30 fish of each species were randomly selected each month from commercial catches. The samples came from an area between 115°30' E longitude and 120° E longitude; between the 50 meter and 100 meter depth isobaths.

The sagittal otoliths were extracted from each sampled fish and the right otolith was embedded in epoxy resin and then sectioned transversely through the otolith core to a thickness of 0.4 mm. A Gemmaster high speed saw with a 100 mm by 0.1 mm diamond tipped saw blade was used for sectioning. The otolith sections were set on 76 mm by 50 mm glass slides with casting resin and covered with cover slips. The sections were viewed with a dissecting microscope with an attached color video camera connected to a personal computer and a color monitor. Transmitted light revealed alternating wide opaque and narrow translucent zones. The translucent zones, referred to in the present study as growth rings, were counted to determine fish ages.

The distance from the outer extremity of the last wide, dark band to the otolith edge, \( w_i \), is referred to as the marginal increment and the distance between the outer edges of the second to last and the last dark band is denoted by \( w_{i-1} \). The distances \( w_i \) and \( w_{i-1} \) on the portion of the otolith ventral to the sulcus towards the proximal margin were measured on the computer screen. The index of completion, \( c_i \), was determined by using the formula of Tanaka et al. (1981)

\[
c_i = \frac{w_i}{w_{i-1}}
\]

and written to a file by using a computer program written in the programming language “HiSoft Basic” (version 2.0. MiccTron, Auburn Hills, MI).

The index of completion, \( c_i \), we expect to increase over time, and then decrease abruptly when a new growth ring is formed. The timing of formation of a new ring would occur at the same time for a fish species with the same number of rings, but there would be considerable variability in timing and detection between species and individuals (Fig. 1).

The increase in the index of completion over time, \( t \), is modeled as a strictly increasing function \( f(t, a, b, d) \) with the following parameters: maximum value, \( a \), rate of increase, \( b \), and horizontal translation, \( d \).

For our study, data were collected over a period of 18 months (October 1993 to March 1995) and the relation between the index of completion and time was expressed as two functions, denoted \( F_1 \) and \( F_2 \).

\[
F_1 : \hat{c}_1 = f(t, a, b, d_1) \quad \text{and} \quad F_2 : \hat{c}_2 = f(t, a, b, d_2)
\]

where \( \hat{c}_1 \) and \( \hat{c}_2 \) are the estimates of the index of completion;

\( t = \) the time in months from \( t = 0 \) (1 October 1993) to \( t = 18 \) (31 March 1995); and

\( d_1, d_2 \) are the translation parameters for functions \( F_1 \) and \( F_2 \) respectively.

If the point \((c_j, t)\) is associated with function \( F_i \), the value of the normal probability density function of the observed deviation from \( F_i \), evaluated at observation, \( i \), is given by

\[
\lambda_{ij} = \frac{1}{\sigma \sqrt{2\pi}} \exp \left( \frac{(c_j - \hat{c}_i)^2}{2\sigma^2} \right),
\]

and similarly the value of the normal probability density function of the observed deviation from \( F_2 \), evaluated at observation, \( i \), is given by

\[
\lambda_{2j} = \frac{1}{\sigma \sqrt{2\pi}} \exp \left( \frac{(c_j - \hat{c}_i)^2}{2\sigma^2} \right),
\]

where \( \sigma^2 \) is the variance of the residuals when \( F_1 \) is fitted to the data and where it is assumed to be equal to the variance of the residuals when the function \( F_2 \) is fitted.

To ensure the tractability of the subsequent analysis, we assume that the probability, \( P \), of a point with index of completion \( c_j \), at time \( t \), being represented by \( F_1 \), is given by the logistic function

\[
P = \frac{1}{1 + \exp \left( \ln(19) \left( \frac{R - t}{S - R} \right) \right)},
\]

where \( R \) is the maximum value of the annual ring for species in this study.
where \(R, S,\) and \(R-(S–R)\) are the values of \(t\) corresponding to the 50\(^{th}\), 95\(^{th}\), and 5\(^{th}\) percentiles of the logistic function. The probability that the index of completion is associated with \(F_2\), rather than \(F_1\), is calculated as \(1–P_t\).

Figure 1 illustrates typical values of the index of completion at time \(t\) and the functions \(F_1\) and \(F_2\) representing these points before and after new growth-ring detection. The most likely time at which a new growth ring is detected is given by the value of \(t\) when \(P_t=0.5\). The likelihood functions \(\lambda_1\) and \(\lambda_2\) are illustrated for \(t = 10.4\) months. When \(\lambda_{1,i}\) is high, \((c_i, t)\) is likely to lie closest to \(F_1\) and when \(\lambda_{2,i}\) is high, \((c_i, t)\) is likely to lie closest to \(F_2\).

As a point \((c_i, t)\) will be associated with either \(F_1\) or \(F_2\) (but not both), it follows that the likelihood function \(K\) is given by

\[
K_{i,i} = \lambda_{1,i}P_i + \lambda_{2,i}(1–P_i).
\]

That is,

The overall log-likelihood associated with all the observed points \((c_i, t)\), for \(i = 1\) to \(n\) in a particular age class is given by

\[
\sum_{i=1}^{n} \ln(K_{i,i}) = \sum_{i=1}^{n} \ln[\lambda_{i,i}P_i + \lambda_{2,i}(1–P_i)].
\]

The parameters of the functions \(F_1\) and \(F_2\) (i.e. \(a, b, d_1\), and \(d_2\), as well as \(\sigma, R,\) and \(S\)) were estimated separately for each value of the number of rings by maximizing the log-likelihood.

The value of \(t = R\) corresponds to the month where a value of the index of completion is equally likely to be in either \(F_1\) or \(F_2\); that is, the point where the drop in the index of completion occurs. The value of \(S\) and \(R-(S–R)\) correspond to the 95\(^{th}\) and the 5\(^{th}\) percentiles for the time at which a new growth ring is likely to be detected, indicating reliability of the estimate of the time of ring formation \(t = R\).

Results

The plots of index of completion versus time reflected this growth pattern in the four species we studied, with the growth rate decreasing as the time of new growth-ring detection approached.

The temporal pattern of growth of the otolith suggests the index of completion could be modeled with a logistic function

\[
F(t,a,b,d) = \frac{a}{1 + \exp \left[ \ln 19 \left(\frac{d-t}{b}\right) \right]},
\]

with the maximum value \(a = 1\), phase shift \(d\), and rate of increase \(b\).

A characteristic of otolith growth is that the distance between growth rings decreases each year, thus, the rate of increase in the marginal increments will be greater for fish with few rings and less for fish with many rings. On the other hand, the index of completion, being the ratio of
the marginal increment to the width of the previous band, would be expected to be constant at the same time of year for a particular species, regardless of the ring count.

Thus, during the maximization of the objective function

$$\sum_{i=1}^{n} \ln(K_{i,j}),$$

the rate of increase parameter $b$ is assumed constant for all ring counts for a species, but the other parameters ($d_1$, $d_2$, $R$, and $S$) are estimated for each number of rings for each species.

Figure 2 shows the pattern of changes in the index of completion for $L$. sp. 3 for otoliths with two to eleven growth rings from 1 October 1993 ($t=0$) to 31 March 1995 ($t=18$). The solid circles (●) represent those $(c_p, t)$ most likely represented by $\hat{c}_1$ and lying closest to the function $F_1$ and the solid triangles (▲) are those most likely represented by $\hat{c}_2$ and lying closest to the function $F_2$. The logistic function, $P_r$, indicates the probability that points $(c_p, t)$ are most likely represented by function $F_1$.

In the other three species, $L$. vitta, $N$. furcosus, and $L$. sebae, the points representing index of completion, $(c_p, t)$ and functions, $F_1$, $F_2$, and $P_r$ are illustrated in Figures 3, 4,
Index of completion at time \( t \), \((c_i, t)\), for \( L. vitta \) for growth-ring categories 2, 3, 4, 5, 6, 7, 8, and 9–12 sampled between the months 1 October 1993 \((t=0)\) to 31 March 1995 \((t=18)\). The solid circles (●) represent those \((c_i, t)\) most likely represented by \( \hat{c}_1 \) and lying closest to the function \( F_1 \) and the solid triangles (▲) are those most likely represented by \( \hat{c}_2 \) and lying closest to the function \( F_2 \). The logistic function, \( P_t \), indicates the probability that points \((c_i, t)\) are most likely represented by function \( F_1 \).

Figure 3

Discussion

With different starting values for the parameters, the method we described found that the time of detection of growth-ring formation for the four species was consistent. Although the timing varied considerably for different numbers of growth rings, the estimate was generally similar for each species.

Other marginal increment studies on these species produced estimates of the times for growth-ring formation...
that are consistent with those determined in the present study (Table 2). Davis and West (1992) found that the time of formation of a new translucent growth-ring on urohyal bones for *L. vitta* was October, later than the timing found in our study. Sainsbury and Whitelaw (1984) found the marginal increment values on whole otoliths from *N. furcosus* had low values in July 1979 and in May 1980 (earlier than observed in the present study for sectioned otoliths) but the sampling reported by Sainsbury and Whitelaw (1984) was very sparse: four sampling times in 1979 and two in 1980. McPherson and Squire (1992) reported that the mean monthly marginal increment of the first two age classes for *L. sebae* appeared to have a minimum between July and September that is consistent with the present study.

In our study, the growth zones on *L. vitta* were generally clearly defined; the opaque zone was easily distinguished from the translucent zone, and there were few discontinuities (areas of dissimilar structure or optical density within the growth zone). This clear definition was especially noticeable for the outer growth zones of the otolith for older fish which often had very clear dark zones. This finding is consistent with the small confidence intervals for this species, especially in the fish with a greater number of growth rings in their otoliths. The growth rings on *L. sp. 3* and *N. furcosus* had poor contrast and had many discontinuities which made the analysis difficult. For young *L. sebae*, there were many discontinuities within the growth zones which made locating the translucent zone difficult. For fish with two to four growth rings, low values of the index of completion occurred when \( t = 7 \) and also when \( t = 12 \) (Fig. 5). For the older *L. sebae* (where the number of rings is greater than or equal to 12) the wide zone was very dark and by increasing the magnification, the marginal increment could be measured relatively easily. The narrow confidence limits for the timing of growth-ring formation for *L. sebae* are consistent with this explanation but the small number of data points results in less reliable measures in the timing of new ring formation.

The time of formation of the new growth ring was slightly earlier for *L. vitta* than for *L. sp.3, N. furcosus*, or *L. sebae*. The calculation of an earlier growth-ring formation may be attributed to the more clearly defined translucent zone in *L. vitta* which may be detectable earlier in

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**Figure 4**

Index of completion at time \( t, (c_r, t) \), for *N. furcosus* for growth-ring categories 2, 3, 4, 5, 6, and 7–9 sampled between the months 1 October 1993 (\( t=0 \)) to 31 March 1995 (\( t=18 \)). The solid circles (●) represent those \( (c_r, t) \), most likely represented by \( \hat{c}_1 \) and lying closest to the function \( F_1 \) and the solid triangles (▲) are those most likely represented by \( \hat{c}_2 \) and lying closest to the function \( F_2 \). The logistic function, \( P_t \), indicates the probability that \( (c_r, t) \) are most likely represented by function \( F_t \).
Index of completion at time $t$, $(c_s, t)$, for *L. sebae* for growth-ring categories 2–3, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13–14, and 15–19 sampled between the months 1 October 1993 ($t=0$) to 31 March 1995 ($t=18$). The solid circles (●) represent those $(c_s, t)$ most likely represented by $\hat{c}_1$ and lying closest to the function $F_1$ and the solid triangles (▲) are those most likely represented by $\hat{c}_2$ and lying closest to the function $F_2$. The logistic function, $P_I$, indicates the probability that $(c_s, t)$ are most likely represented by function $F_{1}$. 

**Figure 5**
Table 1
Parameter estimates for the fit of two functions to the index of completion data. The parameters are the rate of increase, $b$, the phase shifts $d_1$ and $d_2$, the time of new growth-ring detection $t = R$ with the confidence interval ($5^{th}$ and $95^{th}$ percentiles), and the standard deviation, $\sigma$, of the observed values of index of completion for points fitted to function $F_1$ and $F_2$.

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<th>$n$</th>
<th>$b$</th>
<th>$d_1$</th>
<th>$d_2$</th>
<th>$R$</th>
<th>Month</th>
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<td>3.1</td>
<td>14.9</td>
<td>11.6 ±2.6</td>
<td>Sep</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>22</td>
<td>17.4</td>
<td>2.1</td>
<td>13.9</td>
<td>9.6 ±0.1</td>
<td>Jul</td>
</tr>
<tr>
<td></td>
<td>13–14</td>
<td>23</td>
<td>17.4</td>
<td>4.7</td>
<td>14.6</td>
<td>13.3 ±0.4</td>
<td>Nov</td>
</tr>
<tr>
<td></td>
<td>15–19</td>
<td>21</td>
<td>17.4</td>
<td>4.0</td>
<td>17.6</td>
<td>11.5 ±0.2</td>
<td>Sep</td>
</tr>
</tbody>
</table>

Table 2
The timing of growth-ring formation for the four species in the present study and for comparative studies.

<table>
<thead>
<tr>
<th></th>
<th>Lutjanus sp. 3</th>
<th>L. vitta</th>
<th>Nemipterus furcosus</th>
<th>L. sebae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present study</td>
<td>July–September</td>
<td>July–September</td>
<td>July–September</td>
<td>July–November</td>
</tr>
<tr>
<td>Davis and West (1992)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>McPherson and Squire (1992)</td>
<td></td>
<td></td>
<td>July–September</td>
<td></td>
</tr>
</tbody>
</table>
the year than it is in the other three species. Similarly, the apparent earlier timing of new ring creation in our study, compared to the findings of Davis and West (1992) may have been due to the fact that the translucent zone can probably be detected closer to the time of formation in sectioned otoliths than in urchyls (Reshetnikov and Claro, 1976).

In summary, modeling the change in index of completion over time enabled estimates to be made of the time of the formation of a new growth ring (with confidence intervals) for four tropical species. Although the index of completion was modeled with a logistic function in the present study, alternative functions (e.g. sine or linear), gave very similar results. The technique is a useful addition to marginal increment analysis because it can be used in place of previous subjective methods to determine quantitatively the timing of new ring formation.

Acknowledgments

This project was financed by the Fisheries Research and Development Corporation (FRDC) (project 94/25) and the Department of Fisheries, Western Australia where the main author was employed for the duration of the project. The authors thank Mike Moran (Department of Fisheries, Western Australia) for obtaining FRDC funding and providing critical advice and encouragement. The senior author also thanks Robert Black (University of Western Australia) for his valued suggestions and encouragement. Stephen Newman (Department of Fisheries, Western Australia) provided advice on reading and interpretation of otolith bands, Iain Dunk (Department of Fisheries, Western Australia) collected samples, sectioned otoliths, and acted as the second reader for fish aging and marginal increment analysis. Tony Paust, Ken Bryers, Justin Chidlow, Daryn Payne (Department of Fisheries, Western Australia) assisted in sample collection. I also acknowledge the assistance of M. G. Kailis, Kraus Fishing Company, and Westmore Seafoods whose vessels were used for sample collection, and two anonymous referees for their constructive comments.

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