

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 relies 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).

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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 relied 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; Hesp 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)

$$c_i = \frac{w_i}{w_i - 1} \quad (1)$$

and written to a file by using a computer program written in the programming language "HiSoft Basic" (version 2.0. MichTron, 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

$$F_1 : \hat{c}_1 = f(t, a, b, d_1) \text{ and } F_2 : \hat{c}_2 = f(t, a, b, d_2), \quad (2)$$

where \hat{c}_1 and \hat{c}_2 = 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 = the translation parameters for functions F_1 and F_2 respectively.

If the point (c_i, t) is associated with function F_1 , the value of the normal probability density function of the observed deviation from F_1 , evaluated at observation, i , is given by

$$\lambda_{1,i} = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(c_i - \hat{c}_1)^2}{2\sigma^2}\right),$$

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

$$\lambda_{2,i} = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(c_i - \hat{c}_2)^2}{2\sigma^2}\right),$$

where σ^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_i , of a point with index of completion c_i , at time t , being represented by F_1 , is given by the logistic function

$$P_i = \frac{1}{1 + \exp\left[\ln(19) \frac{(R-t)}{(S-R)}\right]}, \quad (3)$$

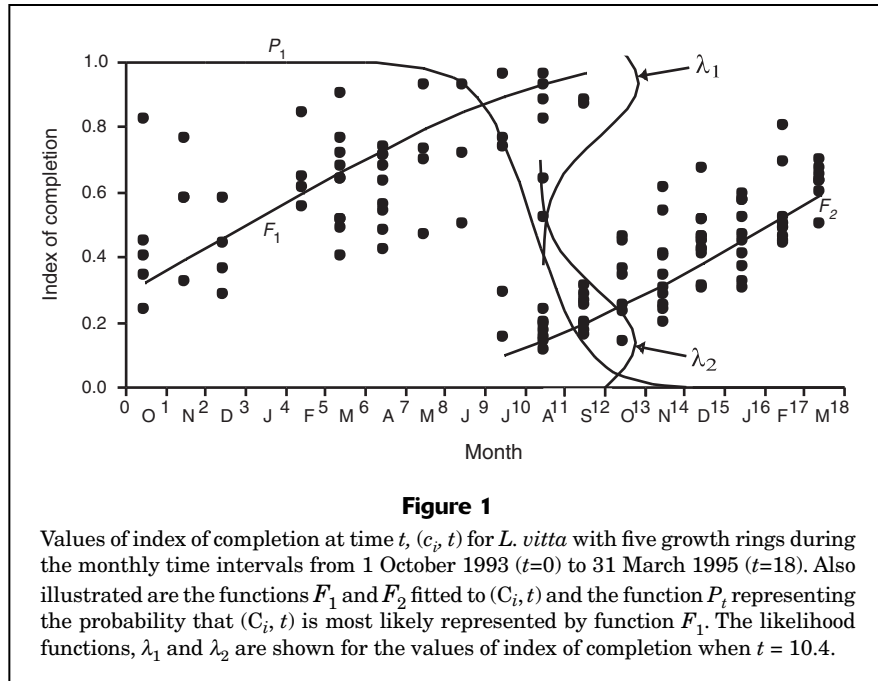


Figure 1
 Values of index of completion at time t , (c_i, t) for *L. vitta* with five growth rings during the monthly time intervals from 1 October 1993 ($t=0$) to 31 March 1995 ($t=18$). Also illustrated are the functions F_1 and F_2 fitted to (C_i, t) and the function P_t representing the probability that (C_i, t) is most likely represented by function F_1 . The likelihood functions, λ_1 and λ_2 are shown for the values of index of completion when $t = 10.4$.

where R, S , and $R-(S-R)$ are the values of t corresponding to the 50th, 95th, and 5th 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 λ_1 and λ_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

the probability of the observed deviation from F_1 , given that the point is associated with F_1	×	probability that the point is represented by F_1	+	the probability of the observed deviation from F_2 , given that the point is associated with F_2 .	×	probability that the point is represented by F_2 .
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That is,
$$K_{t,i} = \lambda_{1,i}P_t + \lambda_{2,i}(1 - P_t).$$

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

$$\sum_{i=1}^n \ln(K_{t,i}) = \sum_{i=1}^n \ln[\lambda_{1,i}P_t + \lambda_{2,i}(1 - P_t)].$$

The parameters of the functions F_1 and F_2 (i.e. a, b, d_1 , and d_2 , as well as σ, 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 on 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 95th and the 5th 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

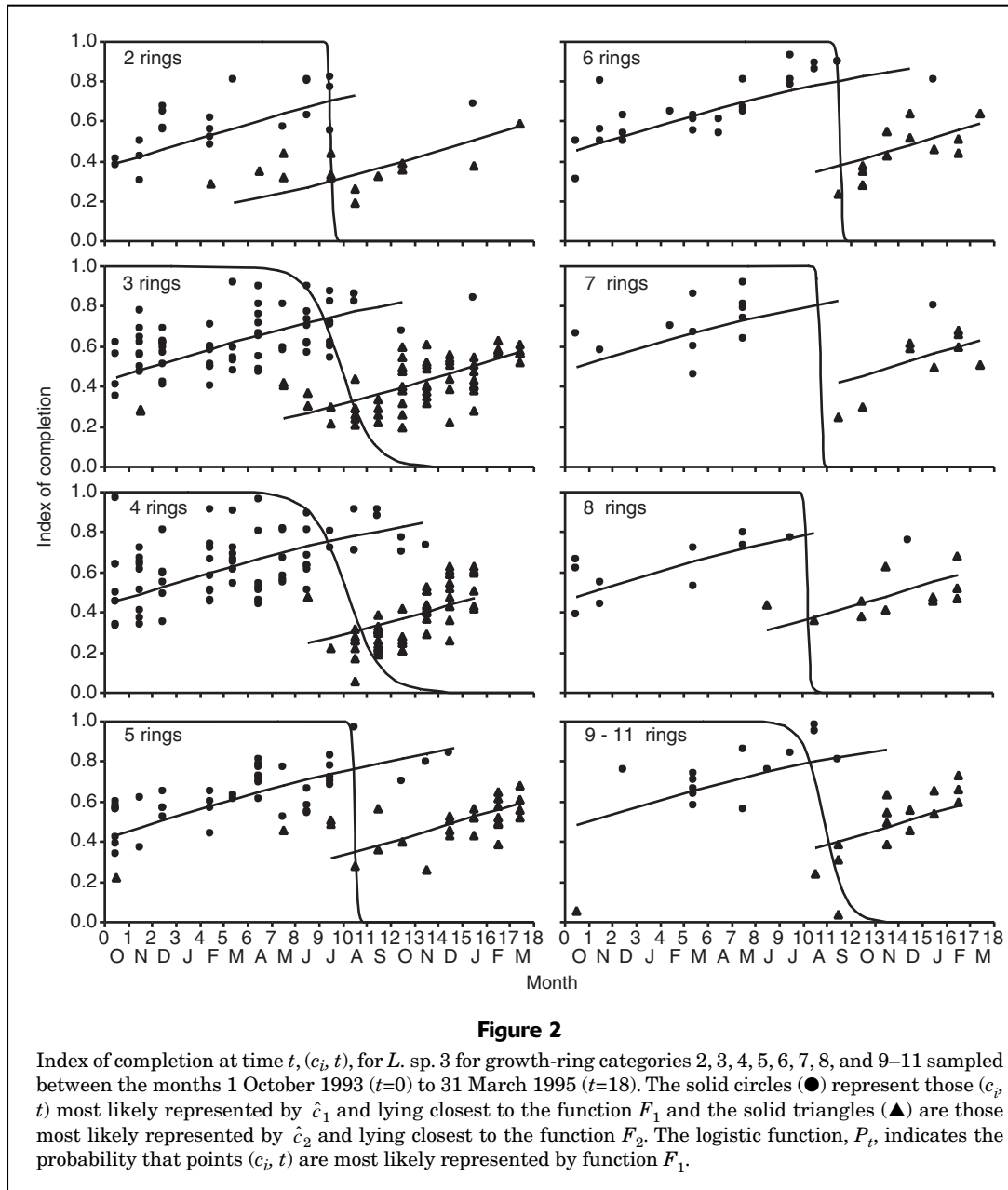
The plots of index of completion versus time reflected this growth pattern in the four species we studied, with the growth rate decreasing as the time of new growth-ring detection approached.

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

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

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

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

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 data were pooled for the older age classes (nine or more growth rings) because of the small numbers of old fish in the samples. The points indicating the values of index of completion, c_i , are represented with different symbols according to whether they are most likely to be represented by \hat{c}_1 (lying closest to the function F_1) or most likely to be represented by \hat{c}_2 (lying closest to the lower line F_2). The function P_i represents the probability of points being represented by line F_1 . The time where $P_i=0.5$ is the most likely time of detection of the formation of a new growth ring.

In the other three species, *L. vitta*, *N. furcosus*, and *L. sebae*, the points representing index of completion, (c_i, t) and functions, F_1 , F_2 , and P_i are illustrated in Figures 3, 4,

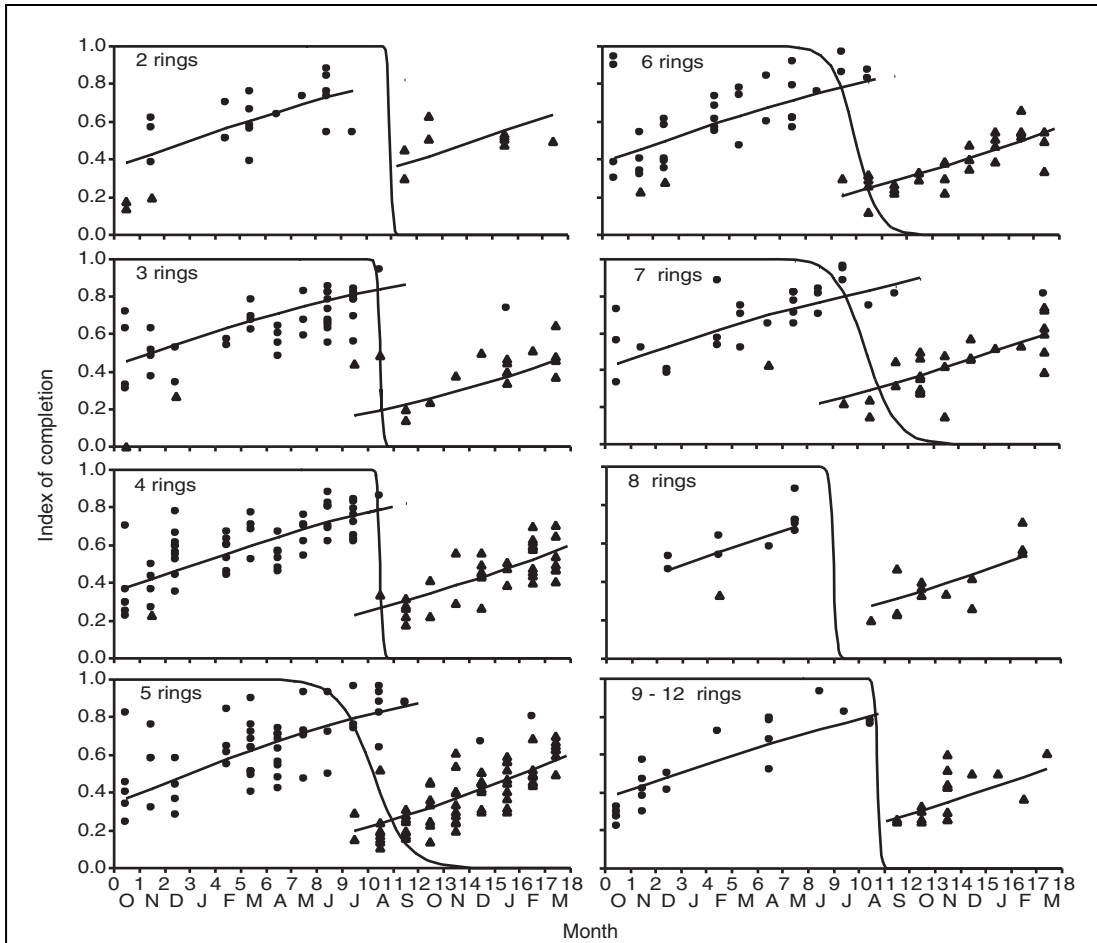


Figure 3

Index of completion at time t , (c_p, 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_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_t , indicates the probability that points (c_p, t) are most likely represented by function F_1 .

and 5. Because of the smaller numbers of fish, the data was pooled for *L. vitta* with 9–12 growth rings, for *N. furcosus* with 7–9 growth rings, and for *L. sebae* with 13–14 and 15–19 growth rings.

The estimates of the parameters b , d_1 , d_2 (the rate of increase and phase shift of F_1 and F_2), R , the time of formation of a new growth ring, with the range $\pm(S-R)$, and the standard deviation (σ) for the four species are listed in Table 1.

The estimated time of formation of a new ring varied between age classes and occurred for *L. sp. 3* from mid July to mid September, for *L. vitta* from early July to early September, for *N. furcosus* from mid July to late September, and for *L. sebae* from mid July to mid November.

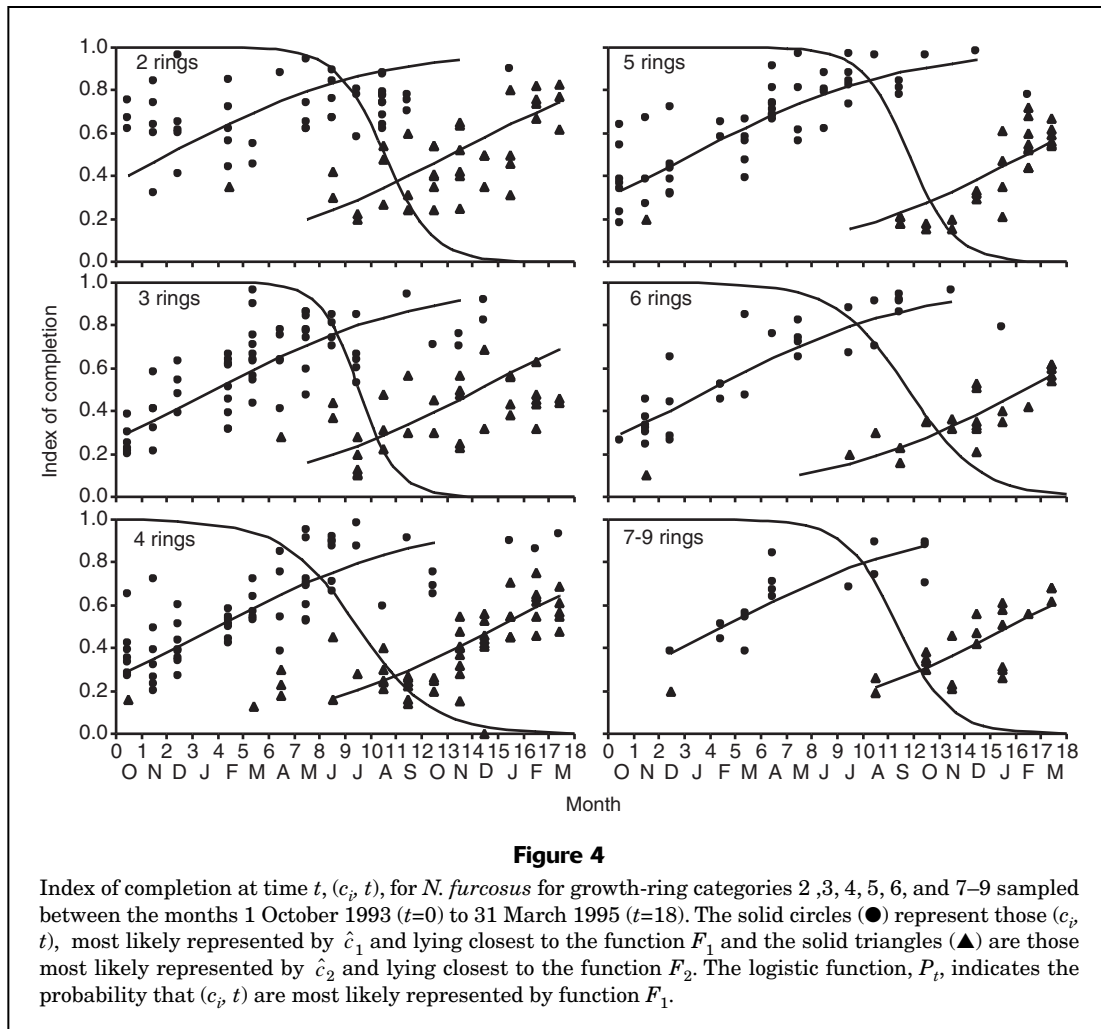
The confidence intervals are small for *L. sp. 3* and *L. vitta* and generally larger for *N. furcosus* and *L. sebae* where reading increments was more difficult. The confidence interval was smaller for *L. sebae* with 12–19 growth rings because the clarity of the rings generally improved for older fish.

The difference between the phase shift for functions F_1 and F_2 , that is d_2-d_1 , was between 11 to 13 months. This difference indicated an annual cycle of growth-ring formation. The standard deviation, σ , of the values of index of completion was lowest for *L. vitta* (0.1–0.14) and highest for *L. sebae* (0.11–0.21) and *L. sp. 3* (0.11–0.24).

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

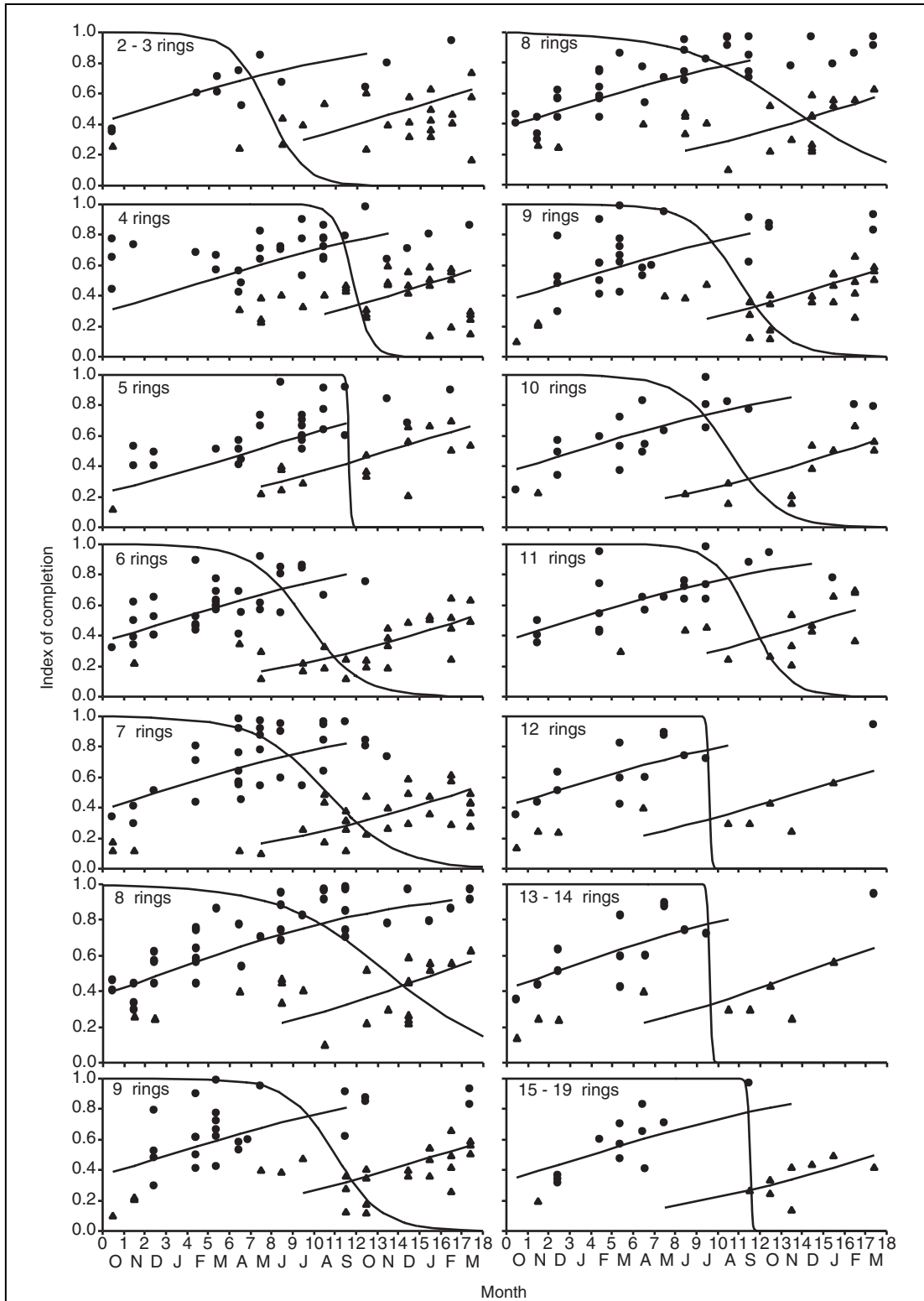


Figure 5

Index of completion at time t , (c_p, 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_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_t , indicates the probability that (c_p, t) are most likely represented by function F_1 .

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 (5th and 95th percentiles), and the standard deviation, σ , of the observed values of index of completion for points fitted to function F_1 and F_2 .

	rings	n	b	d_1	d_2	R	Month	σ
<i>Lutjanus sp. 3</i>	2	36	20.3	3.6	15.3	9.5 \pm 0.1	Jul	0.14
	3	134	20.3	2.0	15.4	9.9 \pm 2.0	Jul	0.13
	4	146	20.3	1.7	16.2	10.2 \pm 2.1	Aug	0.13
	5	72	20.3	2.3	14.8	10.5 \pm 0.1	Aug	0.24
	6	38	20.3	1.7	14.9	11.5 \pm 0.2	Sep	0.11
	7	22	20.3	0.6	13.7	10.7 \pm 0.1	Aug	0.12
	8	22	20.3	1.1	14.0	10.2 \pm 0.1	Aug	0.12
	9–11	29	20.3	0.9	14.2	10.9 \pm 1.3	Aug	0.15
<i>Lutjanus vitta</i>	2	31	15.8	3.0	14.3	10.9 \pm 0.1	Aug	0.13
	3	62	15.8	1.5	18.3	10.5 \pm 0.2	Aug	0.14
	4	96	15.8	3.4	15.9	10.5 \pm 0.2	Aug	0.10
	5	127	15.8	2.7	16.3	10.2 \pm 2.0	Aug	0.12
	6	66	15.8	2.5	16.5	10.0 \pm 1.3	Aug	0.12
	7	56	15.8	2.0	15.4	10.3 \pm 1.7	Aug	0.11
	8	24	15.8	3.3	15.8	9.0 \pm 0.2	Jul	0.10
	9–12	39	15.8	3.1	16.2	11.1 \pm 0.2	Sep	0.10
<i>Nemipterus furcosus</i>	2	85	11.9	2.0	13.1	10.6 \pm 2.7	Aug	0.18
	3	95	11.9	3.9	14.2	9.5 \pm 2.2	Jul	0.17
	4	116	11.9	4.0	15.0	9.5 \pm 4.3	Jul	0.14
	5	82	11.9	3.3	16.4	11.8 \pm 2.6	Sep	0.11
	6	53	11.9	4.0	16.4	11.8 \pm 4.2	Sep	0.10
	7–9	39	11.9	4.5	15.8	11.4 \pm 3.0	Sep	0.10
<i>Lutjanus sebae</i>	2–3	34	17.4	1.9	14.4	7.8 \pm 2.5	May	0.17
	4	62	17.4	5.0	15.9	11.9 \pm 1.2	Sep	0.21
	5	43	17.4	5.1	13.4	11.6 \pm 6.7	Sep	0.14
	6	60	17.4	3.3	17.0	9.6 \pm 3.7	Jul	0.13
	7	63	17.4	2.6	17.0	10.6 \pm 4.9	Aug	0.16
	8	60	17.4	2.8	15.8	13.5 \pm 7.6	Nov	0.15
	9	52	17.4	3.2	15.9	11.0 \pm 3.3	Sep	0.19
	10	32	17.4	3.3	15.9	10.6 \pm 3.4	Aug	0.15
	11	34	17.4	3.1	14.9	11.6 \pm 2.6	Sep	0.17
	12	22	17.4	2.1	13.9	9.6 \pm 0.1	Jul	0.12
	13–14	23	17.4	4.7	14.6	13.3 \pm 0.4	Nov	0.21
	15–19	21	17.4	4.0	17.6	11.5 \pm 0.2	Sep	0.11

Table 2

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

	<i>Lutjanus sp.3</i>	<i>L. vitta</i>	<i>Nemipterus furcosus</i>	<i>L. sebae</i>
Present study	July–September	July–September	July–September	July–November
Davis and West (1992)		October		
Sainsbury and Whitelaw (1984)			May–July	
McPherson and Squire (1992)				July–September

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 urohyals (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.

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