Ageing of three species of tropical snapper (Lutjanidae) from the Gulf of Carpentaria, Australia, using radiometry and otolith ring counts

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Abstract.—A radiometric ageing method was used to resolve conflicting results from ageing tropical lutjanids based on annual ring counts in whole and sectioned otoliths. The number of rings detected in sectioned otoliths of *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae* from unexploited populations in the Gulf of Carpentaria, Australia, were 1.6 to 2.4 times the number found in whole otoliths. To obtain an independent estimate of age, we measured $^{210}Pb/^{226}Ra$ radioactive disequilibria of both whole and cored otoliths. As all species had high levels of ^{226}Ra, they could be aged with relative accuracy by this method. Samples of whole otoliths and cores with a similar ring count had similar radiometric ages. In samples whose sectioned and whole-otolith ages differed by more than 4 years, the whole otolith ring count agreed better with the radiometric age (for an uptake activity ratio R=0.0). This result stands in marked contrast to the radiometric age validation of section counts for slow-growing, long-lived fish inhabiting temperate to subtemperate waters. In this region, all species lived less than 10 years and grew to a maximum size of up to 600 mm SL. They reached a similar length in one year, but *L. erythropterus* grew faster than the other two species thereafter. The sexes had the same growth rates. Our results were similar to those found for these species elsewhere and suggest that in tropical fishes, such as lutjanids, rings observed in sectioned otoliths and other hard parts may not be formed annually. Where possible, ages derived from counts in these structures should be verified by independent methods.

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Tropical fishes can be difficult to age because many species do not deposit annual rings in their hard parts (Longhurst and Pauly, 1987). Lutjanids, which are highly valued commercial fishes in the tropical Indo-Pacific region, often have ring patterns in their hard parts that are difficult to interprete (e.g. Davis and West, 1992). The age and growth of many lutjanid species have been well studied and the results of these studies have formed the basis of age-structured stock assessments upon which the management of these fisheries is based (e.g. Sainsbury, 1988).

In the western Pacific, *Lutjanus malabaricus* has been the most widely studied lutjanid, as it is the main catch of trawl and line fisheries in northern Australia, adjacent Indonesian waters, and in the South China Sea. The reported maximum age (up to 10 yr) and growth parameters differ both between regions (Lai and Lui, 1974, 1979) and within one area (northern Australia: Lai and Lui, 1979; Chen et al., 1984; Edwards, 1985; McPherson and Squire, 1992). These studies estimated age from growth rings in vertebrae (Lai and Lui, 1979; Chen et al., 1984; Edwards, 1985) or in whole otoliths (McPherson and Squire, 1992). The latter method may underestimate the age of longer-lived species because of the difficulty of distinguishing all the growth rings (Casselman, 1974).

The timing of formation of annual growth rings in *Lutjanus* from northern Australia has not been fully verified. Several authors (Lai and Lui, 1974, 1979; Chen et al., 1984; Yeh et al., 1986; Davis and West, 1992) have concluded that the outer ring is probably deposited annually, but the season when this ring is formed varies between studies and species. Such ambiguities cast doubt on the validity of the conclusions and suggest that differences in the estimated growth rate and age of *Lutjanus* populations may be related to problems of interpretation rather than to biological differences.

A radiometric method has recently been used successfully to estimate the age of long-lived fishes (Bennett et al., 1982; Fenton et al., 1991). This method uses the known decay rates of isotopes of Radium-226 (^{226}Ra) and Lead-210 (^{210}Pb) in bony parts to estimate the age of fish. It does not rely on operator interpretation to estimate age and therefore is particularly useful for ageing long-lived species where the growth rings are often not clearly defined (Casselman, 1974).

The objectives of the present study were 1) to estimate the age and growth of *Lutjanus malabaricus*, *L. erythropterus*, and *L. sebae* from the Gulf of Carpentaria by counting rings in whole and sectioned otoliths; and 2) to use the ^{210}Pb/^{226}Ra radiometric ageing method to make an independent age estimation of the same fish.

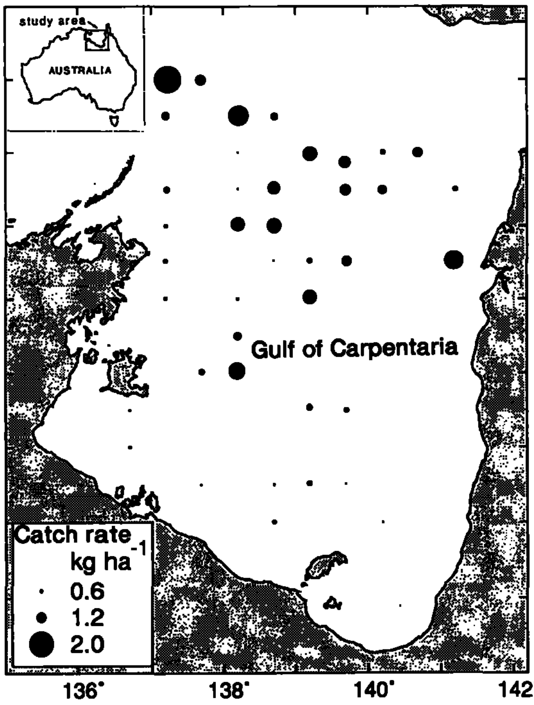

Figure 1

Map of the Gulf of Carpentaria showing the distribution and relative abundance of *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae* during a systematic survey in November 1990.

Materials and methods

Sampling

Most samples of *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae* were collected during a systematic survey of the Gulf of Carpentaria between long. 136° and 142°E in November 1990. Two similar random-sampling surveys were made across the northern Gulf of Carpentaria (north of lat. 14°30'S) in November 1991 and January 1993. Samples of *Lutjanus malabaricus* were also collected during a survey of eight areas in the Gulf of Carpen-taria by the commercial trawler *Clipper Bird* in June 1990 (Fig. 1). Details of survey design, trawl gears, and trawl durations are given in Blaber et al.(1994).

Commercial-sized *Lutjanus malabaricus* (1–3 kg) were obtained from fish retained for sale after the June 1990 survey. During the systematic survey in November 1990, all specimens of the three target species of lutjanids were retained for ageing studies. In November 1991 and January 1993, only fish from length classes underrepresented in previous samples were processed. All fish were measured (standard length [SL] in mm), weighed (±1 g), and sexed, and both sagittae were removed, dried, and stored in labelled bags for future analysis.

Radiometry

Radioanalysis requires about 1 g of sample material; therefore, fish were pooled to obtain the necessary sample weight. For juveniles, up to four otoliths were required to obtain this weight. Otoliths used for radioanalysis were chosen in two ways. First, for each species, otoliths from juvenile, maturing, and mature fish that had the same sectioned-otolith ages, similar otolith weights, and similar sizes, and came from the same region of the Gulf of Carpentaria were pooled for radioanalysis. Second, otoliths of the same whole-otolith age and from fish of similar size were abraded with a mechanical sander to a central core approximating the weight (see Table 2), length, and shape of the otolith of a fish whose whole-otolith age was 3 (otolith length=11.6 ± 0.7 for *L. erythropterus*; 12.7 ± 0.4 for *L. malabaricus*; and 11.4 ± 0.4 for *L. sebae*). The exception was sample 2490 for which otoliths were ground to a core age of 2 (weight 0.156 ± 0.005 g; otolith length 9.2 ± 0.16 mm; n=92). The otolith nucleus at the center of the cores was located by examining intact otolith morphology and by sectioning other samples (Campana et al., 1990). This age is less than the age at sexual maturity for all species.

The method of radioanalysis of the otoliths is detailed in Fenton et al. (1990, 1991). It involves measuring the specific activity of ^{226}Ra:^{210}Pb by alpha-spectrometry. Because of the extremely small specific activities measured (0.01–0.1 dpm·g^{-1} for Polonium–210 [^{210}Po]), cleanliness is of the utmost importance in the analytical procedure. Every item of laboratory ware that contacted the otolith solutions and otoliths was chemically decontaminated in alkaline 0.05M Na_4EDTA (pH 10.5). The otoliths were washed and rinsed several times in this solution, then washed several times in 0.1M HCl (<10 s) and finally washed twice in water.

Our analyses of ^{210}Pb, via its short-lived daughter-proxy ^{210}Po, and ^{226}Ra were made with high-resolution alpha-spectrometers according to the methods of Fenton et al. (1990). The mean ^{210}Po reagent blank was 0.0071 ± 0.0012 dpm. Recovery of ^{210}Po was always at least 90% and instrument background counts (for ^{208}Po and ^{210}Po) were less than one count·d^{-1}. ^{226}Ra was analyzed by a direct alpha-spectrometry method and chemical yield was measured by gamma spectrometry of a Barium–133 (^{133}Ba) tracer (Fenton et al., 1990, 1991). Mean activity of the ^{226}Ra blanks was 0.0174 ± 0.0026 dpm, which was lower than in previous studies (e.g. Bennett et al., 1982; Fenton et al., 1991) owing to careful control of reagents. Recovery of ^{226}Ra (as estimated by the recovery of ^{133}Ba tracer) was greater than 85% for all samples.

Data analysis

The ages of whole otoliths were calculated on the basis of a single constant (linear) growth rate by the equation originally derived by Bennett et al. (1982):

$$A = 1-(1-R)\frac{1-e^{-\lambda t}}{\lambda t}, \qquad (1)$$

where A=the ratio of the activity of ^{210}Pb to ^{226}Ra activity at time t ($^{210}\mathrm{Pb}/^{226}\mathrm{Ra})_t$; R=ratio of ^{210}Pb to ^{226}Ra at the time of deposition [($^{210}\mathrm{Pb}/^{226}\mathrm{Ra})_0$]; and λ=decay constant for ^{210}Pb (0.03114 yr^{-1}). Assumption of a single linear mass growth rate produces radiometric ages that are greater than those that would result from assumption of an exponential (nonlinear) rate, the bias always favoring a higher value (Campana et al., 1993). It should be understood that using this assumption (linear mass growth of the otolith) will produce age estimates that always overestimate the real age.

For otolith cores, ages were calculated from Smith et al.'s (1991) equation:

$$A = \left(1-e^{-\lambda(t-T)}\right)+\left(1-(1-R)\frac{\left(1-e^{-\lambda T}\right)}{\lambda T}\right)e^{-\lambda(t-T)}, \qquad (2)$$

where all parameters are the same as in the previous model, except T, which is the estimated age of the otolith core. A linear mass growth model was assumed only up to the age of the core. The initial uptake $^{210}\mathrm{Pb}/^{226}\mathrm{Ra}$ activity ratio was generally assumed to be R=0.0. This is the most conservative value, and so radiometric age estimates derived with this value must overestimate the maximum possible age of the sample. The above equations were solved numerically by a Newton-Raphson iteration method (Fenton et al., 1991).

Stable element analysis

The levels of lead and barium in otoliths are presumed to act as stable equivalents of ^{210}Pb and ^{226}Ra and so can be used to assess the uptake of the radioactive isotopes and to normalize the radiometric data (Fenton and Short, 1992). Therefore, the concentrations of stable lead, barium, strontium (Sr), and calcium (Ca) in each otolith sample were measured for an aliquot of each dissolved otolith solution used in the radiometric analysis. Each solution was analyzed by inductively coupled plasma mass spectrometry for lead and barium and by inductively coupled plasma atomic emission spectrometry for strontium and calcium.

Otolith ageing

Pairs of otoliths from each fish were cleaned of excess tissue, dried at 60°C for 24 h, weighed (± 0.1 mg) and measured along the longitudinal axis with dial calipers (± 0.05 mm). One otolith of each pair was embedded in polyester resin and cross-sectioned with a diamond saw (Augustine and Kenchington, 1987). Thin sections (approximately 200 µm) of each otolith were bonded to microscope slides with thermoplastic cement. Each section was polished on both faces with 800-grit wet-and-dry carborundum paper before being examined with a video-enhanced light microscope attached to a microcomputer with precise distance-measuring software. The rings (presumed annuli) were counted and the distance between them measured along the dorsal axis adjacent to the sulcus, where they were most clearly distinguishable. In whole otoliths, the rings were counted against a strong background point light source.

Counts of rings in all whole and sectioned otoliths were made independently by two readers. When the ring counts differed, the otoliths were reexamined by both readers. If the counts still differed by more than one, the data were discarded (<5% of all otoliths). If counts differed by one, the higher value was chosen (10% of otoliths). The relative frequency of these discrepancies was similar for all species.

Data analysis

The length-at-age data were fitted to the reparameterized von Bertalanffy growth curve of Francis (1988). This method has the advantage that the parameters estimated are independent and can be compared directly between species and populations.

Most previous studies of lutjanid age and growth have fitted the von Bertalanffy growth equation to data on length at age (e.g. Lai and Lui, 1979; Manooch, 1987; Davis and West, 1992). However, the estimated parameters L_∞, K, and t_0 either do not have direct biological meaning (e.g. Knight, 1968; Schnute and Fournier, 1980; Ratkowsky, 1986) or are extrapolations from the data (Ratkowsky, 1986). Francis (1988) extended the equation of Schnute and Fournier (1980) to derive a new set of parameters L_1, L_2, and L_3 (his l_ϕ, l_χ, and l_w), which correspond to the length at the lower, middle, and upper limits of any arbitrarily defined age range, such that:

$$L_t = L_1 + (L_3 - L_1)\left(1 - r^{2(t-\phi)/(w-\phi)}\right)\Big/(1 - r^2), \quad (3)$$

where $r = (L_3 - L_2)/(L_2 - L_1)$; L_t is the mean length of a fish at age t; and L_1, L_2 and L_3 are the length at the lower, middle, and upper limits of two arbitrary ages ϕ and w. By fitting a curve of this form, extrapolations beyond the data are avoided, as the three fitted parameters are chosen from within the range of the data and hence can be directly compared with the results of previous studies.

In this study, we set $\phi = 1$ ring and $w = 6$ rings for each species. This equation has the advantage that the age range to be examined can be chosen by the investigator, rather than having to be the largest and smallest age classes found, as required by the Schnute and Fournier (1980) equation. These parameters (L_1, L_2, and L_3) can also be expected to have similar properties to those of Schnute and Fournier (1980) and not to show the high negative correlation between L_∞ and K (Francis, 1988).

All parameters were estimated by an iterative least-squares method (SAS NLIN procedure with the Marquardt option; SAS, 1989). Vaughan and Kanciruk (1982) found that this procedure consistently showed the least bias in parameter estimates, converged rapidly, and provided more precise estimates than did standard linear techniques. A measure of goodness-of-fit was obtained by calculating an r^2 value from the residual and the explained sums of squares derived from the least-squares regression.

Relationship of ring counts in whole and sectioned otoliths with radiometric ages

The estimated age from ring counts in whole and sectioned otoliths used in the radiometry were compared for all species by two methods. First, the relationship between radiometric age and whole and sectioned otolith ages of the same fish were plotted. If the slope of the relationship was not significantly different from 1, the results of the two methods were considered to be in close agreement. Second, the two ageing methods were compared with the radiometric ages with a Wilcoxon matched-pairs ranks test (Conover, 1980). The two hypotheses tested were 1) that whole otolith ring counts underestimated true age (radiometric age) or 2) that sectioned otolith ring counts overestimated true age.

Results

Radiometry

Lutjanus erythropterus—The specific activity of ^{226}Ra and the ^{210}Pb/^{226}Ra activity ratio differed among the three samples of *L. erythropterus* (Tables 1 and 2). The activity ratio was highest in the cored sample (0.118 ± 0.031; Table 2). Ring counts in whole otoliths were linearly related to otolith mass (Fig. 2A) and ring count in sectioned otoliths, though the relationship was significantly weaker ($P<0.05$). Radiometric age estimates were calculated on the basis of a single constant (linear) growth rate for otolith mass, which removes the need to include the mass growth relation in the radiometric age calculation (Eq. 1). Under the assumption of a constant growth model, radiometric age estimates were most similar to those obtained from the ring counts in whole otoliths (Table 2). The match was best for the cored otolith sample where model assumptions are less stringent (sample 2673).

Lutjanus malabaricus—The specific activity of ^{226}Ra in *L. malabaricus* otoliths differed among samples and among size classes (Tables 1 and 2). The ^{210}Pb/^{226}Ra activity ratios ranged from less than 0.027 to 0.212 and varied to a similar degree in cored and whole-otolith samples (Table 2). Otolith weight was linearly related to the number of rings in whole otoliths (Fig. 2B), and this relationship was stronger than that for counts from sectioned otoliths

Table 1

Elemental composition of otoliths of three species of *Lutjanus* used in the radiometric analysis. Whole = whole otoliths used; cored = otoliths cored to age 3+ (*L. erythropterus*) or 2+(*L. malabaricus* and *L. sebae*). Numbers in parentheses represent repeated analyses of a sample in which several otoliths of similar whole and sectioned age had been combined.

Species	Sample	Whole/or cored	^{226}Radium dpm·g^{-1} (± 1σ)	^{210}Lead dpm·g^{-1} (± 1σ)	Lead (Pb) (ppm)	Barium (Ba) (ppm)	Pb/Ba mass ratio	Strontium (Sr) (ppm)	Calcium (Ca) (ppm)	Sr/Ca mass ratio
L. erythropterus	2065	Whole	0.2277 ± 0.0132	0.0174 ± 0.0047	0.08	18.7	0.004	2,800	395,000	0.0071
	2066	Whole	0.1623 ± 0.0087	0.0070 ± 0.0035	0.19	11.5	0.016	2,720	398,000	0.0068
	2673	Cored	0.1331 ± 0.0087	0.0157 ± 0.0040	0.66	9.2	0.071	—	—	—
L. malabaricus	2062(2)	Whole	0.2390 ± 0.0111	−0.0025 ± 0.0045	0.27	8.2	0.033	2,915	462,000	0.0063
	2063	Whole	0.0728 ± 0.0066	0.0067 ± 0.0042	3.49	6.5	0.537	3,330	470,000	0.0071
	2063(2)	Whole	0.0582 ± 0.0049	−0.0010 ± 0.0025	0.22	13.4	0.016	1,990	321,000	0.0062
	2063(3)	Whole	0.0916 ± 0.0053	0.0072 ± 0.0017	0.55	4.8	0.114	2,240	399,000	0.0056
	2064	Whole	0.2118 ± 0.0164	0.0173 ± 0.0024	2.28	5.8	0.390	3,000	395,000	0.0076
	2438	Whole	0.1014 ± 0.0064	0.0068 ± 0.0036	0.41	5.3	0.080	2,005	426,000	0.0047
	2439	Whole	0.2942 ± 0.0141	0.0133 ± 0.0043	0.06	7.5	0.008	2,250	415,000	0.0054
	2440	Whole	0.1080 ± 0.0068	0.0135 ± 0.0029	0.18	6.2	0.029	2,910	438,000	0.0067
	2489	Cored	0.1678 ± 0.0088	0.0356 ± 0.0055	<0.09	6.7	<0.014	2,160	407,000	0.0053
	2490	Cored	0.1219 ± 0.0078	0.0180 ± 0.0037	<0.09	6.2	<0.014	2,040	416,000	0.0049
L. sebae	2068	Whole	0.1036 ± 0.0064	0.0139 ± 0.0034	3.13	8.7	0.360	2,360	396,000	0.0060
	2069	Whole	0.1046 ± 0.0058	0.0312 ± 0.0037	1.38	8.1	0.170	2,510	398,000	0.0063
	2070	Whole	0.0460 ± 0.0042	0.0100 ± 0.0023	0.46	5.0	0.092	—	—	—
	2647	Cored	0.2143 ± 0.0114	0.0373 ± 0.0049	0.50	11.5	0.043	—	—	—
	2648	Cored	0.1756 ± 0.0099	0.0458 ± 0.0052	0.66	9.4	0.071	—	—	—

Table 2

Results of radiometric and direct ageing otoliths of *Lutjanus malabaricus, L. erythropterus* and *L. sebae* from the Gulf of Carpentaria. Radiometric ages were calculated by using a constant growth rate model and by using $R = 0.0$ (where R = initial ^{210}Pb:^{226}Ra activity ratio at time of deposition). All errors in radiometric age estimates expressed at 1σ level (n = number of otoliths in sample). SE = Standard error. Numbers in parentheses represent repeated analyses of a sample in which several otoliths of similar whole and sectioned age had been combined.

Species	Sample	n	Mean length (mm) ± SE	Mean otolith mass (g) ± SE	Whole otolith age	Sectioned otolith age	^{210}Pb:^{226}Ra activity ratio	Radiometric age
L. erythropterus	2065	3	316 ± 2	0.3315 ± 0.0186	3	3	0.076 ± 0.021	5.1 ± 1.5
	2066	2	364 ± –	0.3875 ± –	3.3	6	0.043 ± 0.022	2.8 ± 1.5
	2673	3	368 ± 7	0.4750 ± 0.0507	4	9	0.118 ± 0.031	5.5 ± 1.1
L. malabaricus	2062(2)	2	310 ± –	0.4852 ± –	3	3	<0.027 (95% CL)	<1.8 (95% CL)
	2063	2	350 ± –	0.5775 ± –	4	6	0.092 ± 0.058	5.7 +4.3,–4.0
	2063(2)	2	348 ± –	0.6170 ± –	4	6	<0.069 (95% CL)	<4.6 (95% CL)
	2063(3)	3	346 ± 7	0.6118 ± 0.0133	4	6	0.079 ± 0.019	0.8 ± 0.8
	2064	3	443 ± 7	1.5591 ± 0.0493	6.7	14	0.082 ± 0.013	5.6 ± 0.9
	2438	4	250 ± 2	0.2517 ± 0.0063	3	3.5	0.067 ± 0.036	4.5 +2.6,–2.5
	2439	1	650	2.1155	9	13	0.045 ± 0.015	3.0 ± 1.0
	2440	1	560	2.1111	7	19	0.125 ± 0.028	8.8 + 2.2,–2.1
	2489	4	455 ± 10	1.6185 ± 0.1349	9	13	0.212 ± 0.035	8.7 +1.5,–1.4
	2490	5	422 ± 7	1.1055 ± 0.0501	8	8	0.148 ± 0.032	6.1 ± 1.2
L. sebae	2068	4	222 ± 5	0.2429 ± 0.0261	2	3	0.134 ± 0.034	9.5 + 2.7,–2.6
	2069	2	304 ± –	0.6152 ± –	3.5	7	0.298 ± 0.039	24.2 +4.2,–3.9
	2070	2	399 ± –	1.5658 ± –	5.5	15	0.217 ± 0.054	16.4 +5.1,–4.6
	2647	3	400 ± 15	1.4462 ± 0.0184	5	12.3	0.174 ± 0.023	7.1 ± 1.0
	2648	2	462 ± –	2.1000 ± –	7	15.5	0.261 ± 0.033	11.2 +1.5,–1.4

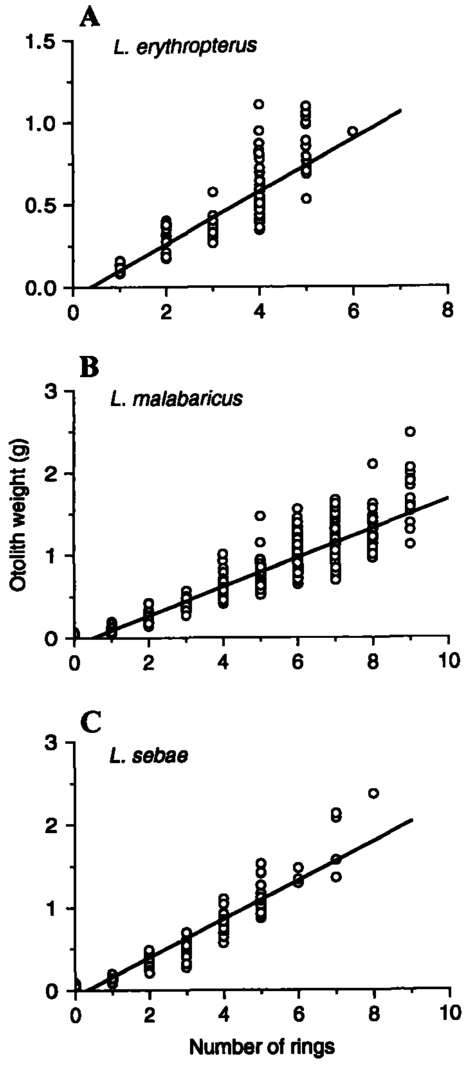

Figure 2

The relationship between otolith weight and the number of rings counted in whole otoliths of (**A**) *L. erythropterus*, (**B**) *L. malabaricus*, and (**C**) *L. sebae*.

($P<0.05$). Under the assumption of a constant mass growth model, radiometric age estimates were again most similar to those found for whole otolith ring counts. The match was best for samples of cored otoliths (2489, 2490) where assumption of a mass growth model is almost absent (Table 2).

Lutjanus sebae —The specific activity of ^{226}Ra and the ^{210}Pb/^{226}Ra activity ratio varied less between samples in *L. sebae* than in the other species (Tables 1 and 2). As with the other species, otolith weight was linearly related to the ring counts of whole otoliths; therefore, a single constant growth rate was assumed in interpretation of the radiometric data (Fig. 2C). The radiometric age estimates of intact otolith samples of juveniles (2068, 2069, 2070), based on the assumption of no allogenic ^{210}Pb uptake in the otoliths (R=0.0), were higher than the ring counts for both sectioned and whole otoliths (Table 2). Samples 2068 and 2069 were probably subject to high rates of allogenic ^{210}Pb uptake, as indicated by the high stable Pb/Ba mass ratios (Table 1). Radiometric ages of both sets of cored otoliths were most similar to the age estimates based on whole otolith counts. However, both these samples (2647 and 2648) had very low stable Pb/Ba mass ratios (Table 1). Modelled radiometric ages of *L. sebae* samples (both whole and cored) for different values of R indicate that R = 0.10 best matches the ring count of whole otoliths (Table 3).

Lead:Barium ratios

The stable lead:barium ratios of all samples were plotted against radiometric age assuming an initial activity ratio R = 0.0 (Fig. 3). Neither *L. malabaricus* nor *L. erythropterus* showed an increase in the ratio with increasing age. However, in four of the five *L. sebae* samples radiometric age increased rapidly with increasing stable lead (Fig. 3).

Otolith ageing

Lutjanus erythropterus—The growth curves of *L. erythropterus* based on ring counts in whole otoliths

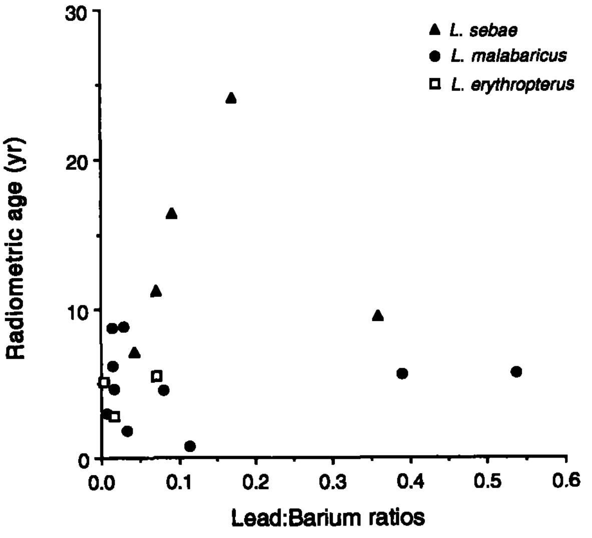

Figure 3

Plot of the relationship between radiometric age and lead:barium ratios for the three species of *Lutjanus*.

Table 3

Radiometric age estimates of samples of both whole and cored(*) *Lutjanus sebae* otoliths for a range of initial uptake $^{210}Pb/^{226}Ra$ activity ratios (*R*). [ ] denotes best match of radiometric age to whole age. Standard errors of samples 2069 and 2070 were unavoidably large, resulting in a poor agreement with either whole or sectioned ages. For whole otoliths, radiometric age estimates assumed linear mass growth for otoliths throughout. For cored otoliths, radiometric age estimates assumed linear mass growth for otoliths only to age 2+, thereafter they were irrelevant.

Sample number	Mean whole otolith age	Mean sectioned otolith age	Radiometric age (yr) for various *R* values			
			$R_{0.0}$	$R_{0.05}$	$R_{0.1}$	$R_{0.15}$
2068	2	3	9.5+2.7,–2.6	6.0+2.7,–2.5	[2.5+2.5,–1.9]	0.3±0.4,–0.3
2069	3.5	7	24.2+4.2,–3.9	20.4+4.1,–3.8	16.6+4.0,–3.7	12.5+4.1,–3.5
2070	5.5	15	16.4+5.1,–4.6	12.8+4.9,–4.5	9.1+4.9,–4.4	[5.4+4.7,–3.8]
2647*	5	12.3	7.1±1.0	6.0±0.9	[4.3±0.9]	1.9±0.9
2648*	7	15.5	11.2+1.5,–1.4	9.6+1.5,–1.4	[7.8+1.5,–1.4]	5.5±1.4

differed from those obtained from sectioned otoliths (Figs. 4A and 5). Fewer rings were counted in whole than in sectioned otoliths but they were linearly related (Fig. 6A; whole otolith count=0.40 × (sectioned otolith count) + 1.02; r^2=0.69, $F_{1,170}$=368.7, P<0.0001). However, the length-at-age data overlapped for all the size classes detected in whole otoliths (Fig. 4A). Both sexes had similar growth parameters based on whole otlith ring counts (P>0.3) (Table 4) and lived to a similar age.

Lutjanus malabaricus—The growth curves expressing the best fit of length-at-age data from both sectioned otoliths and whole otoliths show significant differences (P<0.05) in the estimated growth rates (Fig. 4B). More rings were counted in sectioned otoliths than in whole otoliths from the same fish (Fig. 6B), but were linearly related (whole otolith count=0.64 × (sectioned otolith count) + 0.79; r^2=0.81, $F_{1,869}$=3614.7, P<0.001).

Growth parameters of the reparameterized von Bertalanffy equation of male and female *L. malabaricus* did not differ except for L_3; this parameter was larger in males (P<0.05). Not all fish collected were sexed, but the growth parameters of the combined equation differed from that obtained from the subsets that were sexed (Table 4).

Lutjanus sebae—Ages based on counts of sectioned and whole otoliths differed significantly in *L. sebae* over 350 mm SL (P<0.05; Fig. 4C). More rings were detected in the otoliths of these fish when they were sectioned than when examined intact, although the number of rings detected by the two methods were linearly related (Fig. 6C; whole otolith count=0.50 × (sectioned otolith count) + 0.19; r^2=0.80, $F_{1,140}$=546.0, P<0.0001).

The growth parameters of the reparameterized von Bertalanffy equation were similar for both sexes (Table 4). *Lutjanus sebae* were larger at one year (L_1)

Table 4

Growth parameters (SL ± SE) of the reparameterized von Bertalanffy growth equations for *Lutjanus malabaricus*, *L. erythropterus*, and *L. sebae* (1–6 rings) from the Gulf of Carpentaria (r^2 = nonlinear estimate of goodness-of-fit).

Species	Sex	*n*	L_1 ± SE	L_2 ± SE	L_3 ± SE	r^2
L. erythropterus	both	172	75.40 ± 11.67	335.21 ± 2.73	457.12 ± 10.01	0.93
	females	61	75.03 ± 17.57	346.66 ± 5.07	477.29 ± 15.64	0.95
	males	30	86.06 ± 22.0	337.47 ± 4.50	468.66 ± 18.55	0.94
L. malabaricus	both	878	78.09 ± 2.99	298.94 ± 1.72	424.92 ± 1.37	0.95
	females	159	195.37 ± 27.37	329.09 ± 4.31	423.19 ± 2.70	0.70
	males	73	100.63 ± 15.50	313.62 ± 6.91	442.67 ± 4.54	0.92
L. sebae	both	144	122.27 ± 3.22	287.28 ± 2.18	451.50 ± 3.27	0.97
	females	14	99.92 ± 17.84	277.43 ± 8.58	443.96 ± 7.54	0.99
	males	9	113.50 ± 3.98	284.83 ± 5.30	461.10 ± 4.41	0.99

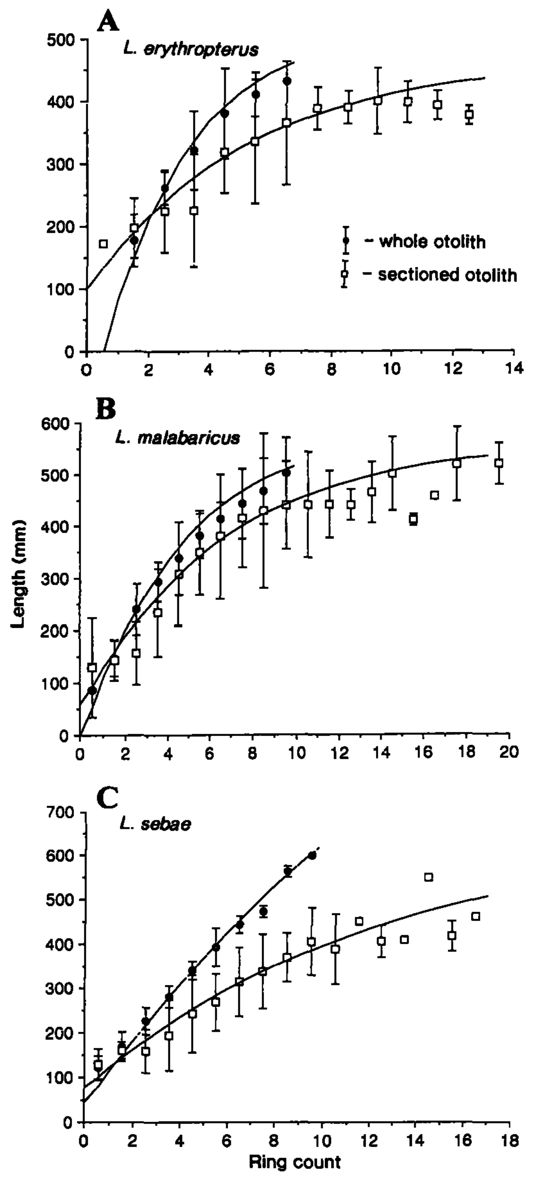

Figure 4

Plot of the mean length-at-age (±) range and the growth curves of the three species of *Lutjanus* based on ring counts in whole and sectioned otoliths.

than were other species ($P<0.05$). However, at six years of age (L_3) they were about the same size as *L. erythropterus* but were larger than *L. malabaricus* ($P<0.05$).

Relationship of ring counts in whole and sectioned otoliths with radiometric ages

There was a significant linear relationship between both whole and sectioned otolith ring counts and radiometric age (Fig. 7; $P<0.001$ in both cases). The slopes of the lines of best fit differed ($\beta=1.04 \pm 0.11$; $r^2=0.84$ for whole otolith ring counts and $\beta=1.83 \pm 0.06$; $r^2=0.87$ for sectioned otolith ring counts). Because the initial activity ratios of the *L. sebae* samples (*R*) were obviously greater than 0.0 in at least the whole otolith samples, these were not included in the analyses.

There was no significant difference between whole otolith ring counts and radiometric ages for all species combined ($T=53.5$; $P>0.30$, $n=15$) or for *L. malabaricus* ($T=17.5$; $P>0.15$, $n=10$). However, for all species combined we found that the sectioned ring counts were significantly greater than the radiometric age of the same fish ($T=6.5$; $P<0.001$, $n=15$). The sectioned ring counts of *L. malabaricus* were also greater than the radiometric ages ($T=2$; $P<0.005$, $n=10$).

Discussion

This is the first study to use $^{210}Pb/^{226}Ra$ activity ratios to verify the age of relatively short-lived tropical fishes. Previous studies that have used these ratios to estimate age have focussed on species that live to at least 70 years (Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1991). In the Lutjanidae, natural levels of ^{226}Ra in the otoliths were high, which helped to minimize the variances in the $^{210}Pb/^{226}Ra$ activity ratio and hence the errors in the age estimates. Radiometry provided strong evidence that the rings counted in whole otoliths were the best estimate of the true age of the three lutjanids studied.

The radiometric methods we used tend to overestimate age because the assumptions concerning the otolith mass growth model and rate of incorporation of allogenic ^{210}Pb were conservative. The only conceivable mechanism that would lead to underestimation of ages radiometrically would be a significant loss of radon (^{222}Rn) from otoliths during growth (West and Gauldie, in press).

Radon is the daughter of ^{226}Ra and the only gaseous precursor of ^{210}Pb in the decay chain. Its mean lifetime is only 4.8×10^5 seconds, and its effective (physical) diffusivity in otoliths would be about 0.5×10^{-12} $m^2 \cdot s^{-1}$. Radon diffusion out of otoliths would be further retarded by adsorption to organic matter (Wong et al., 1992). Simple calculations based on the known microstructure of otoliths (Campana and Neilson, 1985) and on the existing data on radon emanation (Morawska and Phillips, 1993) show that significant loss of radon from otoliths is extremely unlikely, as previously suggested from empirical studies (Fenton and Short, 1992).

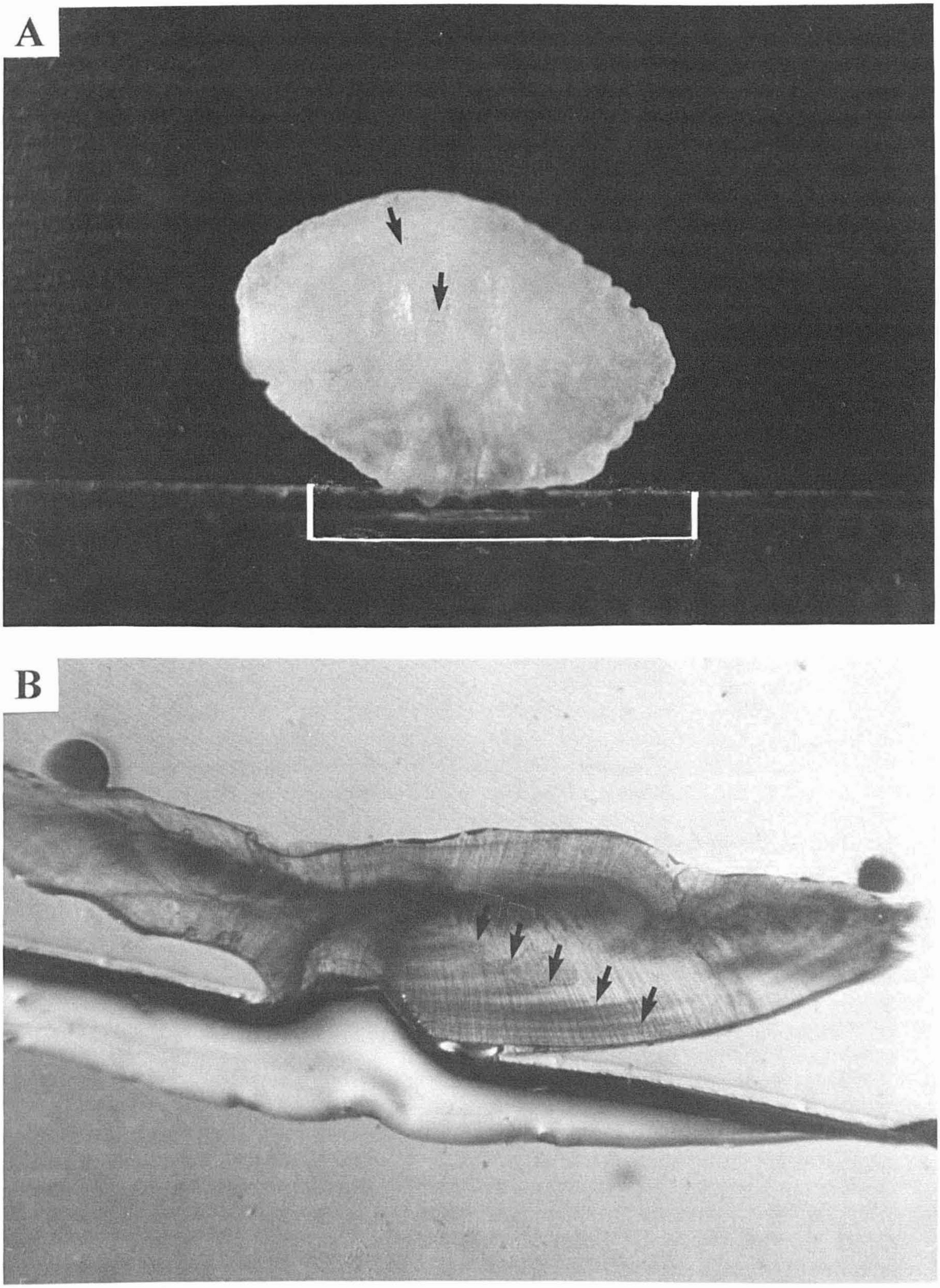

Figure 5

Photographs of an otolith of a 270-mm *L. erythropterus* showing the discrepancy between the number of rings seen by examining (**A**) the intact otolith (2 rings) and (**B**) after sectioning (5 rings). Scale=1 cm.

Why ages derived from whole and sectioned otoliths were significantly different remains unclear. The differences in ring counts increased with the size of the fish, and the slope of the regression (whole vs. sectioned ring count) was steepest for the fastest-growing species, *L. erythropterus*. The otoliths were large (up to 30 mm long, and weighing 3 g), so the daily rings during periods of reduced or variable growth of younger fish were still relatively widely spaced. Thus, what would appear as a diffuse, single hyaline zone in a whole otolith examined against reflected light may have appeared in section as a group of hyaline and opaque zones. These problems in otolith interpretation were most marked in *L. erythropterus* and led to the greatest discrepancy in ring counts.

Studies of the age and growth of *Lutjanus malabaricus* from northern Australia and the South China Sea used ring counts in vertebrae (Lai and Liu, 1974, 1979; Edwards, 1985), sectioned otoliths (Chen et al., 1984), and whole otoliths (McPherson and Squire, 1992). Their estimates were similar to the estimates we obtained from whole-otolith ageing, although *L. malabaricus* from the Great Barrier Reef appear to grow much faster and live at least one year less than those found in other areas (McPherson and Squire, 1992). However, the previous studies and our study provide different estimates of the von Bertalanffy growth parameters L_∞ and K (Table 5). These differences may have major impacts on age-structured fishery models (e.g. yield per recruit) that use these parameters to estimate optimal yield.

Lutjanus erythropterus and *L. sebae* from the Gulf of Carpentaria grew at similar rates to those reported from other parts of northern Australia (Ju et al., 1988; McPherson and Squire, 1992) and elsewhere within their range (Druzhinin and Filatova 1980; Yeh et al., 1986; McPherson and Squire, 1992). However, the growth of *L. sebae* in the Gulf of Carpentaria did not decline as they approached the maximum age observed. This may have been caused by an error in the ring count in otoliths of older fish or because the older age classes were not caught in the trawls. The maximum size of L. sebae in Australian waters has been reported to be between 1.0 and 1.4 m (Allen,

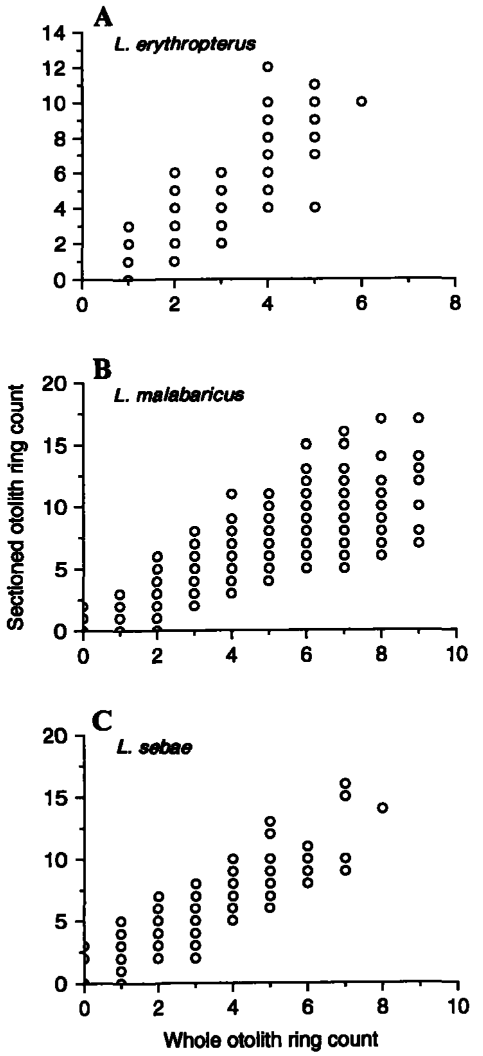

Figure 6

Plot of the relationship between whole and sectioned otolith ring counts of the three species of *Lutjanus*.

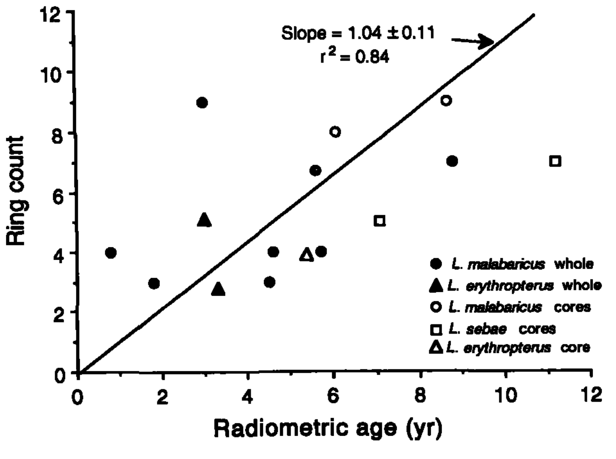

Figure 7

The relationship between radiometric age (yr) and whole otolith ring counts of all samples (except *L. sebae* whole otolith samples).

Table 5

Von Bertalanffy growth parameters of tropical *Lutjanus* from northern Australia and elsewhere within their range (W=whole otoliths; S=sectioned otoliths; V=vertebrae; U=urohyal; Sc=scales).

Species	Locality	Sex	Method	K	L_∞	Maximum age	Reference
L. erythropterus	Gulf of Carpentaria	Both	W	0.30	565	6	Present study
	Great Barrier Reef	F	W	0.44	500	7	McPherson and Squire (1992)
		M	W	0.41	500	7	McPherson and Squire (1992)
	Northwest Shelf	Both	V	0.21	603	7	Ju et al. (1988)
L. malabaricus	Arafura Sea	Both	V	0.17	707	10	Edwards (1985)
		Both	V	0.12	790	8	Lai and Lui (1979)
	Gulf of Carpentaria	Both	W	0.22	592	9	Present study
	N.W. Australia	Both	V	0.13	768	8	Lai and Lui (1979)
		Both	V	0.25	715	10	Chen et al. (1984)
	S. China Sea	Both	V	0.14	790	11	Lai and Lui (1974)
	Great Barrier Reef	F	W	0.23	696	7	McPherson and Squire (1992)
		M	W	0.18	820	7	McPherson and Squire (1992)
	Vanuatu	Both	S	0.31	600	—	Brouard and Grandperrin (1984)
L. sebae	Gulf of Aden	Both	Sc	0.16	660	11	Druzhinin and Filatova (1980)
	Gulf of Carpentaria	Both	W	0.06	1483	9	Present study
	N.W. Australia	Both	V	0.13	678	10	Yeh et al. (1986)
	Great Barrier Reef	F	W	0.18	851	8	McPherson and Squire (1992)
		M	W	0.15	736	8	McPherson and Squire (1992)
L. vittus	N.W. Australia	F	U	0.37	267	7	Davis and West (1992)
		M	U	0.22	346	8	Davis and West (1992)

1985; Grant, 1985) or 16 to 22 kg (Grant, 1985; Allen and Swainston, 1988), which is much greater than we recorded (5 kg). This species may, therefore, live more than 10 years. Indeed, large *L. sebae* (over 800 mm) from the Great Barrier Reef are known to live on deep coral reefs at depths greater than 60 m[1]; the deepest part of the Gulf of Carpentaria is only 55 m. This suggests that fish may move from this region as they grow.

Our radiometric ageing results have several important implications beyond the verification of the age structure of each species. First, they demonstrated that for species that have a high otolith ^{226}Ra specific activity, ^{210}Pb/^{226}Ra activity ratios can be used to age fish as young as 3 years with accuracy. Previously these radioisotopes have only been used to age long-lived species (>10 yr; Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1991). Other radioisotope pairs (^{228}Th:^{228}Ra) have been used to age short-lived tropical species (Campana et al., 1993), but these are only useful for fish up to 5 years old because of the short half-life of Th–228.

Second, for relatively short-lived species, radiometric ageing of whole otoliths and cores using a single-phase linear model of otolith mass growth rate gave similar results. Campana et al. (1990) and Smith et al. (1991) argued that new material accreting to the outer surface of the otolith may not accrete ^{226}Ra in similar specific activities to the juvenile ($t\approx0$). This would invalidate the use of a simple otolith mass growth model to interpret the radiometric data for otoliths of postjuvenile fish. However, even with a single-phase linear mass growth model (a two-phase model would have reduced the age estimates), we were able to verify that the ring counts in whole otoliths were a more accurate measure of the true age than counts from sectioned otoliths (in accord with core radiometric ages). However, we agree with Smith et al. (1991) that otoliths should be cored for radiometric ageing, if possible, which would avoid the use of an otolith mass growth model.

The third point that arises from our analyses relates to the ratio of allogenic to radiogenic lead in *Lutjanus* otoliths. We set the uptake activity ratio value at zero (R=0.0) because higher values would have lowered the age estimates (e.g. Smith et al., 1991). However, from the stable lead/barium ratios and the high age estimates of two of the *L. sebae* samples (2068 and 2069) it appears that, at least for this species, the juveniles may be taking up more allogenic ^{210}Pb than the adults (Fenton and Short, 1992). There was no systematic increase in the Pb/Ba mass ratios of *L. malabaricus* and there is insufficient data for *L. erythropterus* to be conclusive (Fig.

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[1] Williams, D. Australian Institute of Marine Science, PMB No. 3, Townsville 4810, Queensland, Australia. Personal commun., 1993.

3). However, for lutjanids it appears that a Pb/Ba mass ratio <0.2 probably indicates that the assumption of a low initial activity ratio (R) is valid, whereas the three samples where the Pb/Ba mass ratio is 0.3–0.6 indicate that the assumption of low R may be invalid. The Pb/Ba ratios are, therefore, a useful test of the validity of the low R assumption.

Finally, this appears to be the first instance where radiometric methods are more consistent with whole-otolith ages rather than sectioned-otolith ages. All previous radiometric studies of fish from temperate and subtemperate waters have verified section counts (Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1990, 1991; Smith et al., 1991). The metabolic effects of the annual cycle of inorganic and organic deposition in otoliths may be more pronounced in these environments resulting in clear annuli in otoliths of fish from more temperate regions.

Conclusions

This study has shown that radiometry using ^{210}Pb/^{226}Ra activity ratios in both whole and cored otoliths can accurately estimate the ages of fish as young as 3 years. Stable lead:barium mass ratios were used to identify samples that may invalidate the assumption of constant uptake of allogenic lead (R=0). For the lutjanids examined, ring counts in sectioned otoliths were shown to overestimate fish ages. Methods such as marginal increment analysis do not verify that the ageing method used is accurate unless the pattern is demonstrated to be consistent for all age classes. This indicates that tropical fish should be aged by two independent methods where possible to help minimize possible ageing errors.

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