Abstract.—Dorsal spines, otoliths, scales, and vertebrae collected from yellowtail kingfish (*Seriola lalandi*) in NSW, Australia, were assessed for usefulness in estimating age. Legibility of growth zones, the time scale at which zones form, and precision of age estimates were evaluated for fish sizes from 323 to 1090 mm FL. All calcified structures contained growth zones, but dorsal spines were unsuitable for age determination because it was likely that early growth zones were lost. From marginal increment analysis, it appeared that one zone was laid down per year for otoliths and possibly scales, but a clear pattern was not found for vertebrae. Although exact agreement between repeated age readings was relatively low (50–66%), agreement within one zone was higher (92–96%) and scales provided the most precise readings. Precision decreased with increasing age of fish. Growth curves derived from otoliths and scales were similar for all ages except fish from the first age class; those derived from otoliths and vertebrae were similar for all fish with less than eight growth zones. Although statistical differences were found between the growth curves of scales and vertebrae for some age classes, with the exception of the first age class these differences were not biologically important. Growth rates estimated from length-frequency (age-based) and mark-recapture (length-based) data compared favorably with those estimated from calcified aging structures. Otoliths, scales, and vertebrae all showed promise as structures for aging kingfish, but further work is needed to determine the position of the first zone and to validate estimates for all age classes. Until such work is completed, we recommend that scales and either otoliths or vertebrae be used for aging kingfish.

Aging methods for yellowtail kingfish, *Seriola lalandi,* and results from age- and size-based growth models

Bronwyn M. Gillanders
NSW Fisheries Research Institute
PO Box 21, Cronulla, NSW 2230, Australia
Present address: School of Biological Sciences A08
                University of Sydney
                New South Wales 2006, Australia
E-mail address: bronwyn@bio.usyd.edu.au

Douglas J. Ferrell
Neil L. Andrew
NSW Fisheries Research Institute
PO Box 21
Cronulla, New South Wales 2230, Australia

Yellowtail kingfish, *Seriola lalandi*, is a popular recreational species and supports significant commercial fisheries throughout temperate regions of the world. In Australia, the major commercial fishery for yellowtail kingfish is in New South Wales where 400–600 tonnes are caught per year. Despite the existence of a commercial fishery and persistent controversy about exploitation of the species, very little is known about its biology. For future management of the fishery and for stock assessment purposes, information on age and growth is needed.

Estimates of age of *Seriola* spp. have been derived from a variety of methods and structures, reflecting the difficulty of aging *Seriola* and other pelagic species. The Japanese species (*Seriola quinqueradiata*) is the most studied species in the genus because of its importance in aquaculture. Studies in the 1950s used scales, vertebrae, and opercular bones for aging (e.g. Mitani, 1955, 1958; Mitani and Sato, 1959). More recent studies have focused on the use of vertebrae (e.g. Munekiyo et al., 1982; Murayama, 1992). Scales have also been used to age *S. lalandi* (formerly *S. dorsalis,*

Baxter, 1960), as have otoliths (Penney[1]). Recently, sectioned otoliths were used to determine ages of *Seriola dumerili*, although it was acknowledged that age and growth determinations were difficult (Manooch and Potts, 1997). Despite the use of a variety of structures for aging *Seriola* spp., there has been no comparative analysis to determine which structure provides the most reliable estimates. In addition, most studies have assumed that growth zones are annual and there have been few validations of age estimates (but see Mitani and Sato, 1959; Baxter, 1960).

The specific objectives of this study were 1) to assess the usefulness of several structures (scales, otoliths, dorsal spines, and vertebrae) for determining the age of kingfish, 2) to compare multiple age estimates for different structures in order to determine the most precise method for determining age and growth parameters, 3) to provide information on size-at-age and 4) to compare growth rates obtained

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[1] Penney, A. J. 1992. Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa. Personal commun.

from age-length data (from counts of zones in calcified structures) to those obtained from length-frequency and mark-recapture (tagging) data. We acknowledge that the data from these three approaches for estimating growth are not directly comparable (Francis, 1988a), but follow the recommendations of Francis (1995) in interpreting differences.

Materials and methods

Fish collection and treatment

Yellowtail kingfish, *Seriola lalandi*, specimens were collected from New South Wales, Australia, between August 1995 and July 1996 by commercial or recreational fishermen. Fish caught by commercial fishermen were obtained after being processed by filleting. Fish were measured (total length, fork length) and sagittal otoliths, dorsal spines, scales, and vertebrae removed. Dorsal spines were examined but considered unsuitable for aging because the center (core) region was either occupied by vascular bony tissue or was hollow. The hollow core in large fish was found to have a larger diameter than the whole spine of small fish. For this reason, it was likely that early growth zones were lost in older fish and therefore spines were considered unsuitable for aging.

Sagittae

Whole sagittae were burned for 7 min at 500°C. They were viewed under a low-power dissecting microscope (6× magnification) with reflected light against a black background. Assignments of age were based on counts of opaque (light) zones or ridges (or both) that were usually most visible at the base of the rostrum on the ventral surface (Fig. 1A). Sagittae were also embedded in clear resin, sectioned in a transverse plane with a low speed saw, the sections (≈350 mm thickness) mounted on glass slides, and viewed under a compound microscope (40× magnification) with reflected light against a black background.

Scales

Scales were removed from a position anterior and ventral to the pectoral fin. It was necessary to remove scales from such a position because most fish had been processed prior to the removal of scales. Scales from each fish were soaked in a solution of sodium hydroxide for 3 h, then rinsed and soaked in water for a further 3–12 h. Clean, nonreplacement (i.e. original scales showing typical ctenoid shape) scales were dry-mounted between two glass micro-scope slides. Scales were read under a compound microscope (20× magnification) with reflected light against a black background. Presumed annuli were identified by cutting over (*sensu* Bagenal and Tesch, 1978) in the lateral fields or by clear zones, where circuli were more widely spaced, in the anterior field.
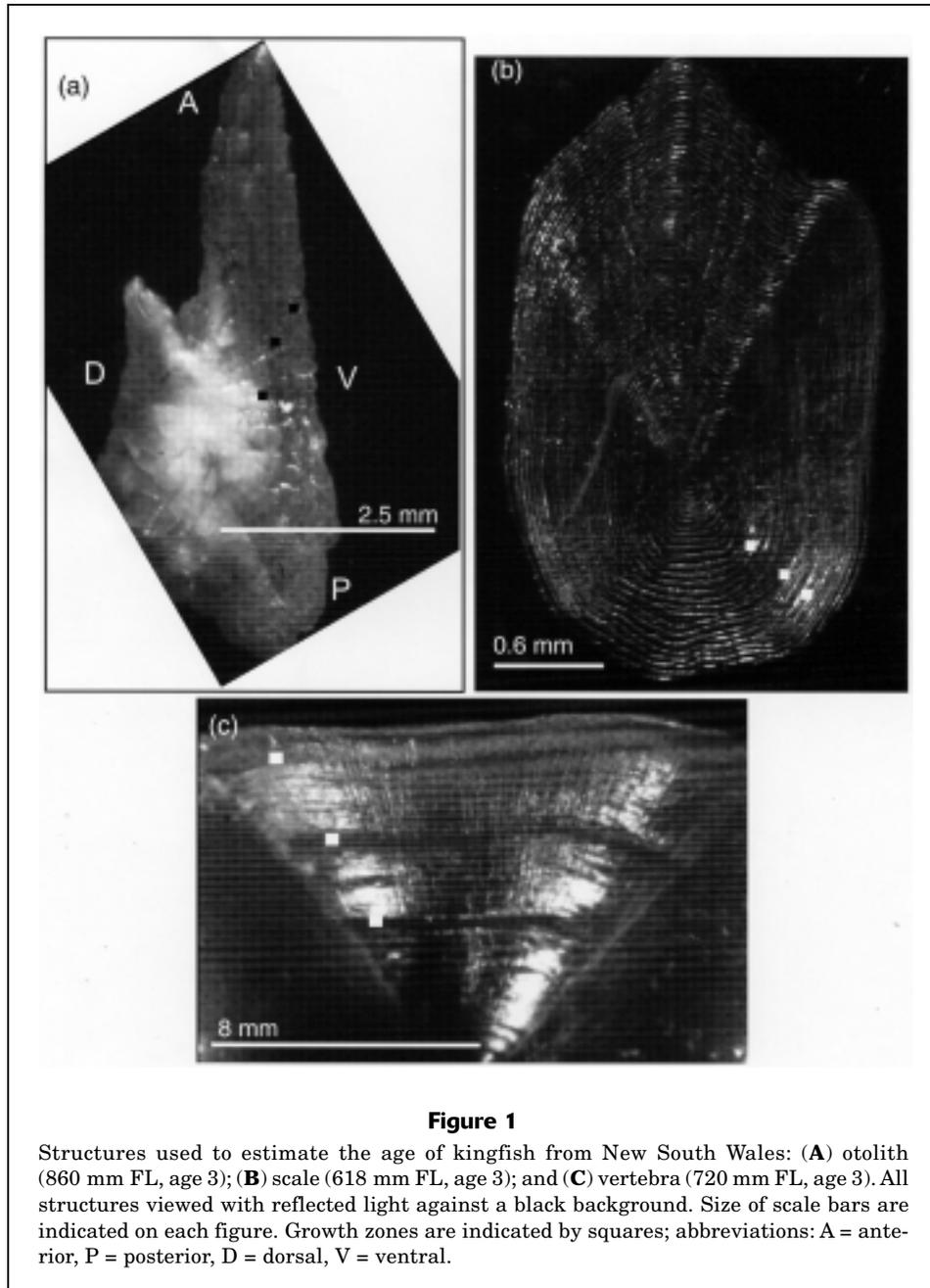
Vertebrae

The second vertebra of 24 vertebrae present in kingfish was chosen because it was most easily obtained from processed fish. Vertebrae were either stored frozen with flesh intact, or the flesh was removed, and the vertebrae were separated from each other and stored dry. The spines were removed and each vertebra cut in half along the longitudinal–horizontal plane and stained in a solution of alizarin red S (following Berry et al., 1977) for 8 h, rinsed in tap water for at least 1 min, and dried at room temperature. Vertebrae were read under a dissecting microscope (6–12× magnification) with reflected light from a blue-filtered, high-intensity bulb against a black background. Age was estimated from counts of ridges on the inner surface of the vertebra from the core to the outer edge of the centrum (Fig. 1C).

Assessment of aging techniques

To determine whether the zones would be reliably interpreted, two replicate counts of zones were made for each structure by the same person. Counts were usually separated by one month. All readings were done in a random order, with no knowledge of date of collection, size of fish, or knowledge of previous counts. Preliminary investigations of transverse sections of otoliths from 50 fish (ranging from 323 to 1090 mm FL) found that growth zones were not interpretable for any fish (Fig. 2).

Multiple counts of zones (two counts for each aging structure) were used to estimate the probability of assigning an age a to a fish with estimated "true" age b following maximum-likelihood estimation procedures outlined in Richards et al. (1992). This procedure requires the estimation of a classification matrix where there are columns for each "true" age and rows for each assigned age, and the entries refer to probabilities of assigning age a to a fish, given its true age b. "True" age is best described as the most probable age, and it does not refer to the accuracy of the age estimate nor does it substitute for age validation procedures. It is assumed that fish will be assigned to the true (or most probable) age class with the highest probability (Richards et al., 1992).
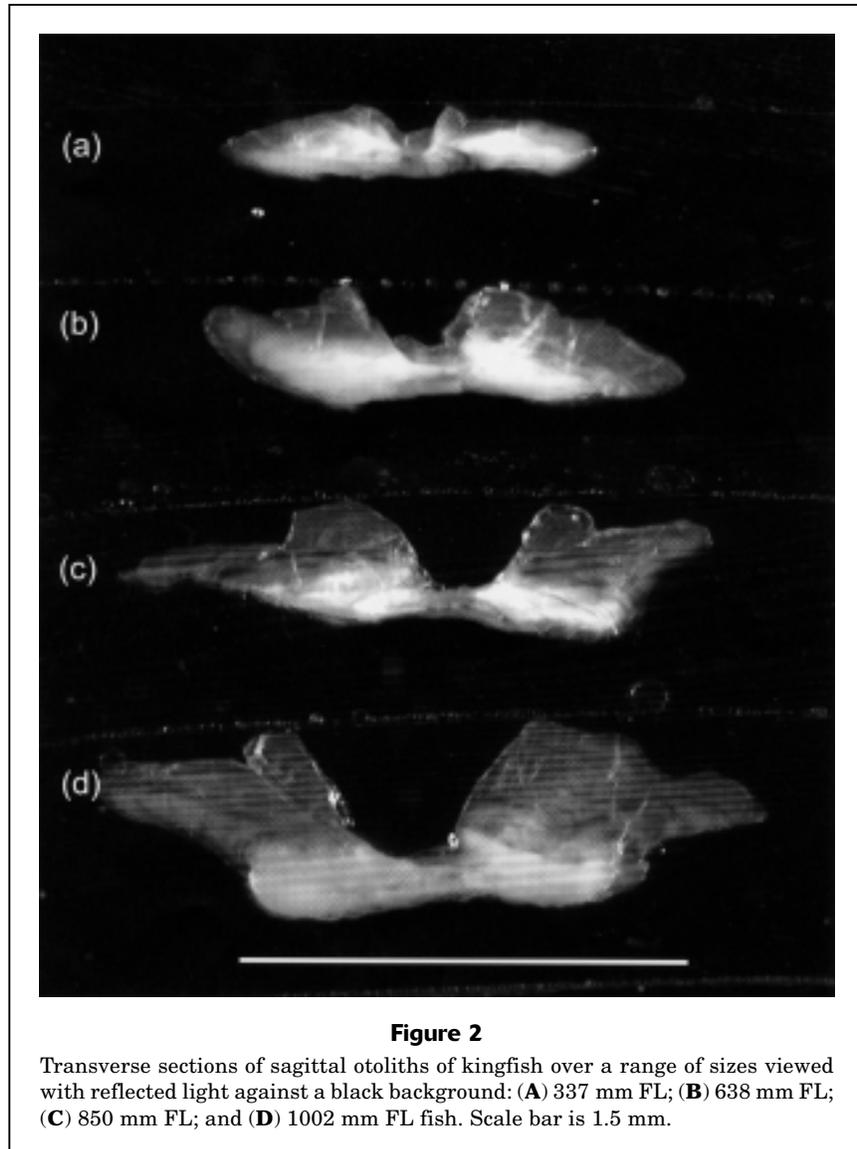
The classification matrix is defined by up to four parameters, where the first two parameters, σ_1 and

Figure 1

Structures used to estimate the age of kingfish from New South Wales: (**A**) otolith (860 mm FL, age 3); (**B**) scale (618 mm FL, age 3); and (**C**) vertebra (720 mm FL, age 3). All structures viewed with reflected light against a black background. Size of scale bars are indicated on each figure. Growth zones are indicated by squares; abbreviations: A = anterior, P = posterior, D = dorsal, V = ventral.

$\sigma_{A,}$ are estimates of the standard deviation for the observation a at age 1 and A respectively. The third parameter, α, determines nonlinearity of $\sigma(b)$, the standard deviation of the observation a. The fourth parameter, β, controls the extent that the classification matrix may be dominated by its diagonal entries (Richards et al., 1992). Two possible representations of the classification matrix were used, namely a normal and an exponential representation (*sensu* Richards et al., 1992, p. 1803) and the α parameter was constrained to 0 during one fit of each of the normal and exponential representations, allowing four different cases of the model to be fitted for each aging structure. The appropriate model structure, or best fit model, for the classification matrix was then selected by using the Akaike information criterion (AIC) where a model with a low AIC value in relation to other models was considered to provide a good fit (Richards et al., 1992).

Initially, data from each aging structure (otoliths, scales, and vertebrae) were analyzed separately and an age assigned to each fish from each structure. The

Figure 2

Transverse sections of sagittal otoliths of kingfish over a range of sizes viewed
with reflected light against a black background: (**A**) 337 mm FL; (**B**) 638 mm FL;
(**C**) 850 mm FL; and (**D**) 1002 mm FL fish. Scale bar is 1.5 mm.

classification matrix for the best model (see above)
was used to estimate the most probable age of each
fish by determining the probability that a fish would
be from each true age class given its two assigned
ages. Each fish was assigned to the age class with
the highest probability (Richards et al., 1992). This
estimate of age was used for growth models. Only
the first five age classes (0–4) were used in the clas-
sification matrix because, although older fish oc-
curred, sample sizes were small and some extrapo-
lation for missing age classes would be necessary.
Because data from older fish are important in esti-
mating growth models, fish not used in the classifi-
cation matrix were assigned an age by randomly se-
lecting one of their two age readings.

The data matrix comprising the two age readings
for each of the three aging structures was then ex-
amined to determine possible effects of the different
aging structures and to determine a final age for each
fish. Classification matrices for each aging structure
were determined following a modification of the
methods of Richards et al. (1992; outlined above).
Results from running the models for each structure
separately showed that the model of best fit was ob-
tained by using a normal model with $\alpha = 0$; there-
fore, in its simplest form, the model contained the
parameters σ_1, σ_A, and terms for the relative bias of
each method (r_1 and r_2; $r_3 = 0 - r_1 - r_2$). Parameters de-
termining the change in bias with age (γ) and non-
linearity of bias with age (η) were also added alone
and indexed by aging structure. Different combina-
tions of the model parameters were therefore tested
to determine which model provided the best fit to
the data and to determine relative biases by method.

Table 1

Summary of the different cases of Schnute's (1981) size-at-age growth model that was fitted to age estimates from different calcified structures and Francis's (1995) mark-recapture analogue of Schnute's growth model that was fitted to the tagging data.

	Schnute's (1981) size at age model	Francis's (1995) mark-recapture analogue of Schnute's (1981) growth model
Case 1: a≠0, b≠0	$Y(t) = \left[y_1^b + (y_2^b - y_1^b) \dfrac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{\frac{1}{b}}$	$\Delta Y = -Y_t + \left[Y_t^b e^{-a\Delta t} + c(1 - e^{-a\Delta t}) \right]^{\frac{1}{b}} \; \frac{1}{b}$
Case 2: a≠0, b≠0	$Y(t) = y_1 \exp \left[\log(y_2 / y_1) \dfrac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]$	$\Delta Y = -Y_t + Y_t^{\exp(-a\Delta t)} \exp\left[c(1 - e^{-a\Delta t}) \right]$
Case 3: a≠0, b≠0	$Y(t) = \left[y_1^b + (y_2^b - y_1^b) \dfrac{t - \tau_1}{\tau_2 - \tau_1} \right]^{\frac{1}{b}}$	$\Delta Y = -Y_t + \left[Y_t^b + (\lambda_1^b - y_1^b)\Delta t \right]^{\frac{1}{b}} \; \frac{1}{b}$
Case 4: a≠0, b≠0	$Y(t) = y_1 \exp \left[\log(y_2 / y_1) \dfrac{t - \tau_1}{\tau_2 - \tau_1} \right]$	$\Delta Y = -Y_t + Y_t(\lambda_1 / y_1)^{\Delta t}$

Meaning of terms

$Y(t)$ = fish size (FL) at age t, τ_1 and τ_2 = lower and upper ages of fish respectively where $\tau_2 > \tau_1$, y_1 and y_2 = mean sizes at ages τ_1 and τ_2, respectively. a and b describe the shape of the curve.

ΔY = mean growth

Y_t = size at marking

y_1 and y_2 = lower and upper sizes of fish, respectively, where $y_1 < y_2$

g_1 and g_2 = mean annual growth for fishes of sizes y_1 and y_2 respectively,

b = describes curvature in model,

$\lambda_1 = y_1 + g_1$ and $\lambda_2 = y_2 + g_2$,

$a = \ln\left[\dfrac{y_2^b - y_1^b}{\lambda_2^b - \lambda_1^b} \right]$ if $b \neq 0$ or

$a = \ln\left[\dfrac{\ln(y_2 / y_1)}{\ln(\lambda_2 / \lambda_1)} \right]$ if $b = 0$,

$c = \dfrac{y_2^b \lambda_1^b - y_1^b \lambda_2^b}{\lambda_1^b - y_1^b + y_2^b - \lambda_2^b}$ if $b \neq 0$ or

$c = \dfrac{\ln(y)\ln(\lambda_1) - \ln(y_1)\ln(\lambda_2)}{\ln(\lambda_1 y_2) - \ln(\lambda_2 / y_1)}$ if $b = 0, \Delta t = 1$

To determine the timing of zone formation, the edges of the various structures were examined. The growth of the structure, subsequent to the most recent zone, was estimated as a percentage (20, 40, 60, and 80%) of the previously completed zone. It was also noted whether the zone was considered to be on the edge of the structure. Only fish with 2–4 growth zones were used. Fish were examined individually by structure in a random order with no knowledge of date of collection.

Estimation of growth models from calcified structures

Growth models using age estimates from different calcified structures were derived by using procedures outlined in Schnute (1981). Schnute's model relates size (FL) to age by several parameters, including two that describe the shape of the curve (a and b; Table 1). These latter parameters combine to describe a range of common growth curves, including the von Bertalanffy ($a>0$, $b=1$), Richards ($a>0$, $b<0$), logistic ($a>0$, $b=-1$) and Gompertz ($a>0$, $b=0$) (Table 1; Schnute, 1981). The other parameters in Schnute's growth model were y_1 and y_2, the mean sizes at ages τ_1 and τ_2 respectively, where the value of τ_1 and τ_2 are specified, but usually chosen to be near the lower and upper ends of the range of ages in the data. In this study, τ_1 and τ_2 were set at 1 and 5 respectively. All growth models were calculated by minimizing sums of squares and using additive errors because variation in size-at-age was similar for all ages of fish (see "Results" section).

Initially, a two-parameter model (y_1 and y_2) was fitted to the data (case 4 in Table 1). Two types of a three-parameter model [parameters were a, y_1, and y_2 (case 2), and b, y_1, and y_2 (case 3)] and a four-

parameter model (a, b, y_1, and y_2, case 1) were then fitted to the data (Table 1). To determine whether the addition of extra parameters resulted in a significantly better fit, significance tests based on the F-distribution were used (Schnute, 1981). Where the same number of parameters were present in the models (e.g. comparison of the two models with three parameters), the model with the lowest residual sums of squares was selected as the best fit.

Estimation of rates of growth from tagging data

Seriola lalandi tagged as part of the NSW Fisheries Gamefish Tagging program (Pepperell, 1985, 1990) were used to estimate growth. A major limitation of these data were that measurement methods were not standard and some measurements appeared spurious. Although most anglers measured total length, some measured fork length only. Where this occurred (17% of fish), fork length (mm) was converted to total length with the equation TL (mm)$=1.122 \times FL + 9$. This equation was calculated from fish obtained for aging in which both fork and total lengths were measured ($n=570$). All fish for which tagging data were available ($n=816$) were initially included in analyses even if the data were highly improbable, as with measurements indicating shrinkage between 100 and 350 mm (Fig. 3A).

Growth estimates were obtained from the tagging data by using the maximum-likelihood method and the computer program GROTAG (Francis, 1988b). The growth model fitted was Francis's (1995) mark-recapture analog of Schnute's (1981) size-at-age model (Table 1). This model provides estimates of g_1 and g_2, the mean annual growth of fish of lengths y_1 and y_2 respectively, where y_1 and y_2 are chosen to span the range of lengths at tagging. A simple three-parameter model was initially fitted and then additional parameters (growth variability, seasonal growth variation, measurement error, and curvature in the model) were added in a stepwise manner by selecting the parameter that gave the greatest increase in log likelihood. At each step, likelihood ratio tests were used to determine whether addition of parameters resulted in significantly better fits (Francis, 1988b). Better estimates of the growth parameters can be obtained if measurement error is known (Francis, 1995). There was no way of estimating measurement error without using the current data set; therefore, measurement error was not fixed and this may have compromised estimates of growth. After fitting of the growth model, plots of residuals against length at tagging, time at liberty and expected growth increment were examined for any possible lack of fit of the model.
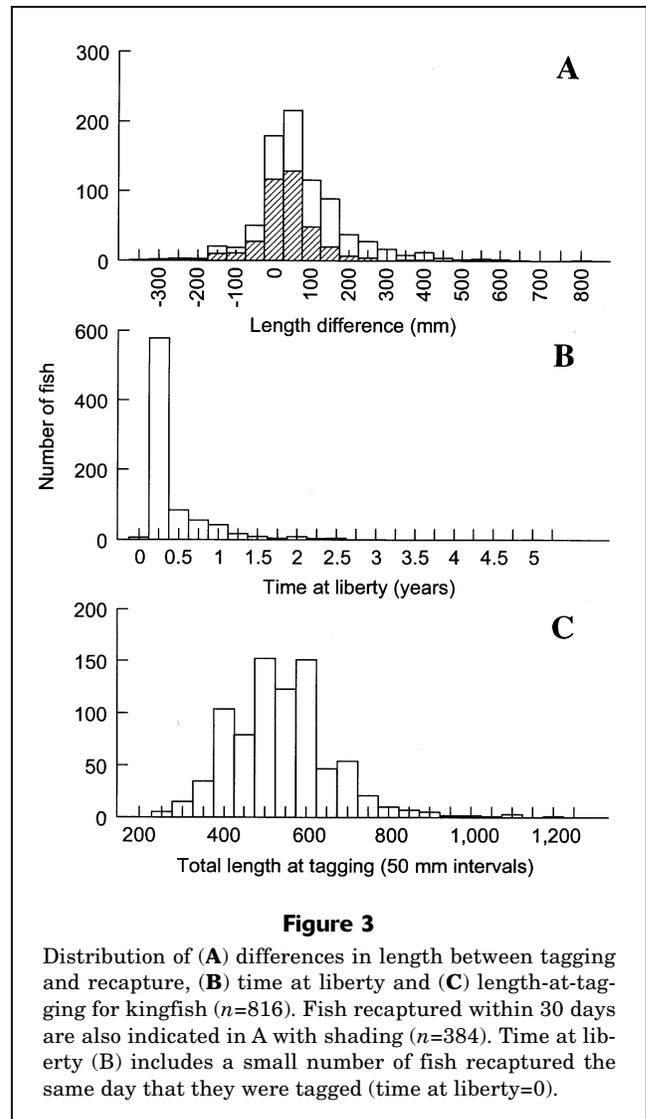

Figure 3
Distribution of (**A**) differences in length between tagging and recapture, (**B**) time at liberty and (**C**) length-at-tagging for kingfish ($n=816$). Fish recaptured within 30 days are also indicated in A with shading ($n=384$). Time at liberty (B) includes a small number of fish recaptured the same day that they were tagged (time at liberty=0).

Estimation of rates of growth from length-frequency data

Length-frequency data were obtained from fish sold at the Sydney Fish Markets between November 1985 and December 1989, prior to the introduction of a size limit of 600 mm TL in February 1990. Data were collected haphazardly amongst months and at locations ranging from 30°S to 37°S. Fork length of fish was measured to the nearest 10 mm and the sampling date and fishing area were recorded. Measurements of approximately 16,000 fish were made, enabling stratification of samples by month but not by year or area.

The von Bertalanffy (VB) model was fitted to the time series of 12 monthly length-frequency distributions by using MULTIFAN software (Fournier et al., 1990, 1991). Likelihood-based methods were used to simultaneously analyze the length-frequency distri-

butions sampled at different times to estimate the number of cohorts in the population, the growth parameters (asymptotic length [L_∞] and growth coefficient [K] of the von Bertalanffy growth equation), the age of the first cohort (assuming that the VB curve passes through the origin) and the proportions at age. The simplest model assumes that mean lengths-at-age lie on the VB growth curve and that the standard deviations of length-at-age are identical for all cohorts. More complex models were also tested that allowed 1) sampling bias for the first cohort, 2) age-dependent standard deviation in length-at-age, and 3) seasonally oscillating growth to be added as additional parameters in the model. The more complex models incorporated all possible combinations of these parameters and used likelihood ratio tests to identify the model of best fit. The significance of improvement of fit within models by adding year classes was tested for significance at the 0.10 level (see Fournier et al., 1990), and significance of improvement of fit between models by adding extra parameters was tested at the 0.05 level.

The seasonal form of the von Bertalanffy equation for the length-frequency data is

$$\mu_{ja} = m_1 + (m_N - m_1)\frac{1-\rho^{[(j-1)+(t_a/12)+f(t_a)]}}{1-\rho^{(N-1)}},$$

where $\quad f(t_a) = \dfrac{\phi_1}{2\pi}\sin\left[2\pi\left(\dfrac{t_a+1}{12}-\phi_2\right)\right],$

μ_{ja} = the mean length of fish of the jth age class in the ath length-frequency data set;

m_1 = the mean length of the first age class;

m_N = the mean length of the last age class;

ρ = the Brody growth coefficient;

t_α = the number of months after the presumed birth month of the fish in the ath length-frequency data set;

N = the number of age classes present; and

ϕ_1 and ϕ_2 describe the amplitude and phase of the seasonal component, respectively (Fournier et al., 1990, 1991; Francis and Francis, 1992).

Comparisons of rates of growth from calcified structures and from tagging and length-frequency data

Rates of growth were estimated from aging structures and from length-frequency (both age-based) and mark-recapture (length-based) data with methods outlined in Francis (1995). The aging error model of Richards et al. (1992) that showed the best fit to the data matrix comprising two age readings from each of the three aging structures was used to determine a single age for each fish. Schnute's growth curve (case 2) was then fitted to the age-size data and this mean age-size relationship was used as a basis with which to compare the estimates of growth from the different data sets. The annual growth for the age-size data and length-frequency data was calculated as the mean size at age x minus the mean size-at-age $(x+1;$ Francis, 1995). Annual growth at corresponding points on the size-based line was then estimated at the size the fish was at age x, as determined from the fit to the mark-recapture data obtained by using GROTAG.

Results

Structures for aging *Seriola lalandi* were collected from a total of 572 fish ranging in size from 323 to 1090 mm FL, although not all structures were collected from all fish. Although *S. lalandi* is reported to reach a total length of almost 2000 mm (1700 mm FL) and a weight of 60 kg, fish of this size are rare. In New South Wales, few fish over 20 kg (about 1200 mm FL) are caught by commercial fishermen and the largest fish recorded in surveys of amateur fishermen has been 1140 mm FL (Steffe et al.[2]). We were unable to obtain fish larger than 1100 mm FL.

All structures showed zones that could be interpreted as annuli (Fig. 1); however, zones were not interpretable in all fish. Growth zones in whole otoliths were more easily interpretable than those in sectioned otoliths (Fig. 2); the latter showed numerous striations that could rarely be interpreted. Zones in sectioned otoliths were, however, clearer in some larger fish (Fig. 2). A large number of scales had to be collected because preliminary results showed that two-thirds of fish had at least some regenerated scales. Vertebrae did not always stain well and showed pronounced ridges which reduced readability in many fish.

Validation of aging methods

Analysis of marginal increments showed different patterns among structures (Table 2). Otoliths and scales revealed that one zone was laid down per year, in August–September (otoliths) and between Decem-

Table 2

Results of analyses of marginal increments for kingfish aged by otoliths, scales, and vertebrae. Each category is the growth of the structure, subsequent to the most recent zone, as a percentage of the previously completed zone. The percentage of fish in each category for each two-month period is shown; sample sizes are also indicated (in parentheses beside month). Only fish aged 2–4 were used for analyses. For each row, the highest percentage of fish is shown in bold.

Month	Category Edge	20	40	60	80
Otoliths					
Aug–Sep (34)	**44**	35	15	0	6
Oct–Nov (149)	16	**36**	24	10	13
Dec–Jan (87)	9	7	18	24	**41**
Feb–Mar (68)	1	13	**31**	24	**31**
Scales					
Aug–Sep (0)					
Oct–Nov (181)	15	12	21	24	**29**
Dec–Jan (94)	22	**34**	21	7	15
Feb–Mar (101)	1	19	28	**34**	19
Vertebrae					
Aug–Sep (51)	8	16	16	10	**51**
Oct–Nov (173)	16	20	**24**	16	23
Dec–Jan (50)	14	12	**28**	20	26
Feb–Mar (70)	14	13	**37**	11	24

Figure 4

Differences between repeated counts of zones for three structures used to age kingfish. Each comparison represents independent counts from a single reader.

ber and January (scales; Table 2). No data were, however, obtained for scales in August–September and sample sizes were small between April and July (n=1–7 fish per month) for all structures. No clear pattern of marginal zones was observed in vertebrae (Table 2).

Precision within and among structures

Comparisons of two independent counts of zones in a structure resulted in a relatively low level of agreement (50–66%). Depending on the structure, between 92% and 96% of readings agreed within one zone (Fig. 4). Differences in counts of zones varied by up to four zones (Fig. 4). Mean coefficients of variation among counts ranged from 7.6% (scales) to 12% (otoliths).

Comparison of readings between structures showed a large amount of variation, with differences between structures varying by up to six growth zones (Fig. 5). Agreement between any two methods decreased with age, but otoliths and vertebrae had the greatest concordance in fish aged 4 and over. Fish were never assigned an age of 0 when aged with scales; fish assigned 0 or 1 with other structures were assigned an age of 1 with scales. Readings between structures agreed within one zone between 88% (be-
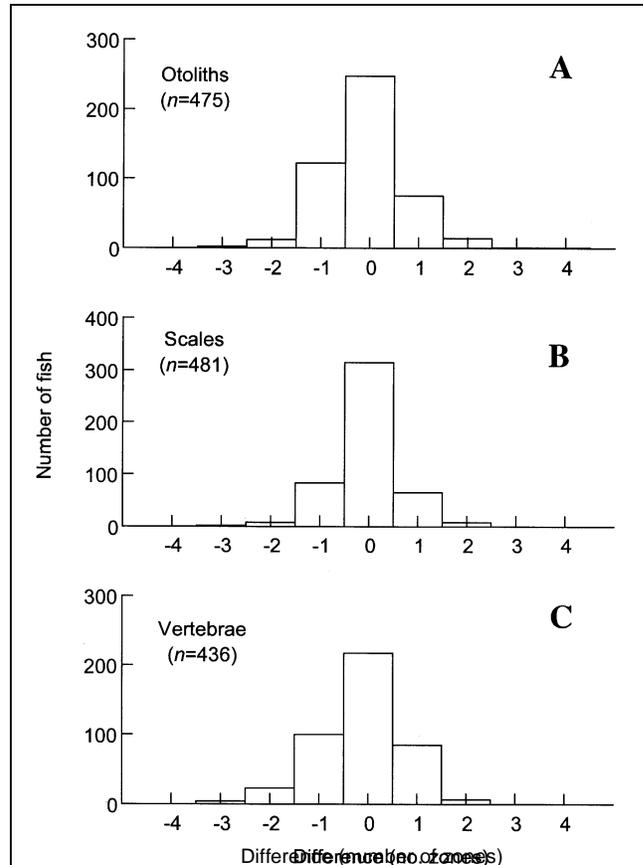
tween vertebrae and otoliths) and 91% (between scales and otoliths) of the time.

Estimates of aging error

Analysis of aging precision with the methods of Richards et al. (1992) showed that the estimates of assigned age were more precise for young fish (Fig. 6A). For example, with otoliths, 98% of fish with an estimated most probable age of 0 were likely to be aged as 0, whereas only 74% of fish with a most probable age of 4 were likely to be aged as 4. This precision can be compared with those obtained from other structures (e.g. scales and vertebrae; Fig. 6A). Fish aged with scales had a higher probability of being consistently assigned ages 1 and 2. Fish aged with vertebrae or otoliths, however, had a higher probability of being consistently assigned age 4, whereas there was little difference between the three structures in assigning fish to age 3 (Fig. 6A).

A more complex aging error model, with parameters that accounted for effects due to aging structures showed that fish in their first year (i.e. 0 growth zones) were likely to be overestimated with scales and vertebrae than with otoliths. Otoliths underestimated the age of fish in their first year, although this is due to the relative nature of the model because vertebrae and scales overestimated the age of these fish (Fig. 6B). Scales showed less bias in relation to the other structures for fish aged 1–4 (Fig. 6B).
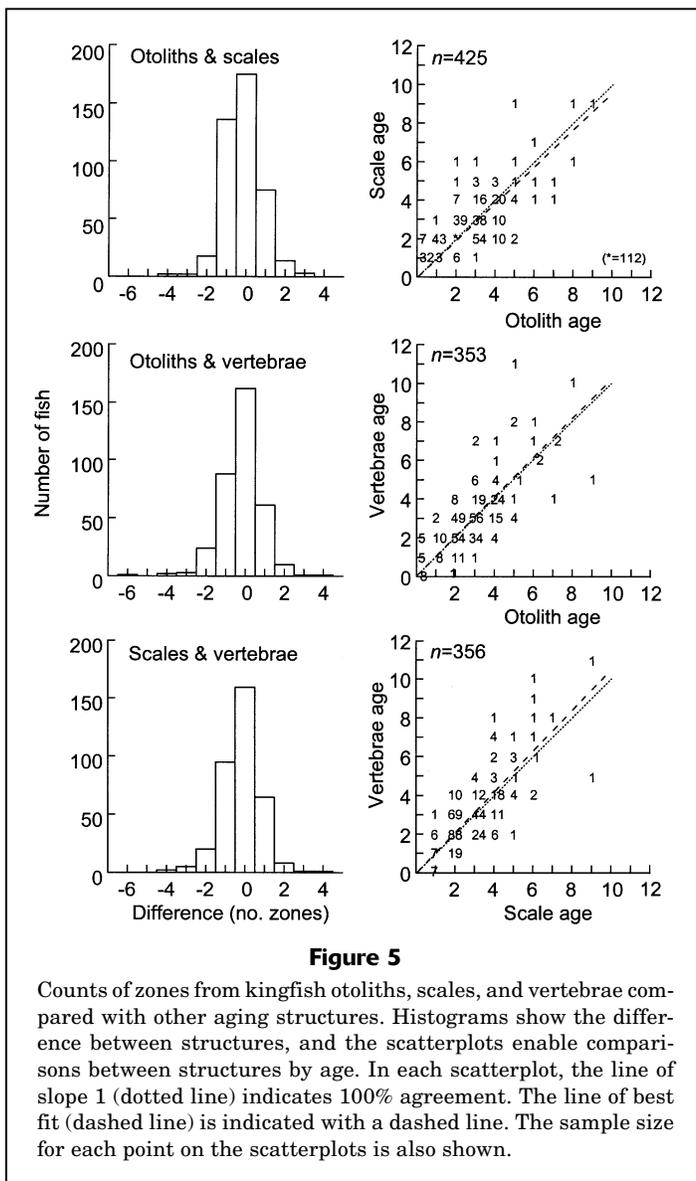
Estimates of rates of growth

Patterns in growth of kingfish from NSW were obtained from Schnute's (1981) growth model fitted to the estimated most probable ages of fish calculated

Figure 5

Counts of zones from kingfish otoliths, scales, and vertebrae compared with other aging structures. Histograms show the difference between structures, and the scatterplots enable comparisons between structures by age. In each scatterplot, the line of slope 1 (dotted line) indicates 100% agreement. The line of best fit (dashed line) is indicated with a dashed line. The sample size for each point on the scatterplots is also shown.

from the different aging structures (Fig. 7). Size-age data were best fitted by three-parameter models for otoliths, vertebrae (both case 2, see Table 1) and scales (case 3). Using the best fitting model for each structure, we estimated that the average lengths (± standard error) of fish with one growth zone were 499 (±5), 418 (±9), and 485 (±7) mm FL for otoliths, scales, and vertebrae respectively. At age 5, fish were 807 (±8), 823 (±8), and 788 (±6) mm FL for otoliths, scales, and vertebrae respectively. The maximum age of fish was 9 yr for otoliths and scales, compared to 11 yr for vertebrae (Fig. 7). Vertebrae tended to produce higher age estimates than did otoliths and scales, with 5% of fish showing greater than five growth zones in vertebrae compared with only 2% for scales and otoliths. Using a single age for each fish, we estimated an age-length key for fish sampled during the current study (Table 3). Fish in all length classes were found in more than one age class (Table 3).

The different aging structures showed significant differences in mean size-at-age for some age classes. Scales showed significantly different mean size-at-age to otoliths and vertebrae for fish with one growth zone (t-tests, $P<0.05$). Otoliths and vertebrae gave similar estimates of mean size-at-age for fish with less than eight growth zones (t-tests, $P<0.05$). With the exception of fish with one growth zone, scales gave similar estimates of mean size-at-age to otoliths for all other age classes (t-tests, $P<0.05$). Although differences between scales and vertebrae were statistically significant for some age classes (fish with 4–6 growth zones), these differences were not likely to be biologically important.

Kingfish that were measured at both tagging and recapture were at large for between 0 days (i.e. recaptured the same day that they were tagged) and 5 years (Fig. 3B). Growth of recaptured fish ranged from a decrease of 350 mm to an increase of 800 mm (Fig. 3A). The frequency distribution of fish at large <30 days showed that fishermen were just as likely to underestimate the length of fish as they were to overestimate the length of fish (Fig. 3A). The mean difference in size of fish between tagging and recapture for fish recaptured within 30 days was 11.6 mm (±0.4, SE), suggesting that there was little bias in measurements between tagging and recapture. Size of fish at tagging ranged from 220 to 1200 mm, although the majority of fish were between 400 and 600 mm TL (Fig. 3C).

The best fit to the complete tag-recapture data set (model 1 in Table 4) showed a high proportion of outliers (P=0.04). Twenty-two fish (or 2.7%) that had absolute standardized residu-

als greater than 3 in the model 1 fit were removed from the data set. Initially, a simple three-parameter model was fitted (model 2 in Table 4), which indicated growth rates of 255 mm and 176 mm for 400-mm and 600-mm fish, respectively. The first additional parameter selected was that describing the shape of the growth curve (model 3 in Table 4). Model 3 showed annual growth rates of 270 and 140 mm. There was a significant improvement in fit when a term describing growth variability was added (model 4 in Table 4). Additional parameters (e.g. seasonal growth terms) did not result in significant improvements of fit. The best fitting model was therefore case-1 model in Table 1. Plots of standardized residuals against length at tagging, time at liberty, and expected growth increment showed no pattern (correlations were 0.022, 0.003, and 0.005, respectively) suggesting that the model was appropriate.

The best fitting model for the kingfish length-frequency data set identified five cohorts aged from 1.73 to 5.73 years (Table 5; Fig. 8). The standard deviation of the predicted length estimates for each age class increased with age. Parameters for first length bias and seasonal growth were also included in the best fitting model (Table 5; Fig. 9). Estimates of the mean length-at-age (and standard deviation) for the length-frequency data set are given in Table 5. The mean lengths and proportions of the modes predicted by MULTIFAN generally fitted the observed data (Fig. 8). There were large numbers of small fish (e.g. 1 yr) in the catch during the summer months (e.g. November and December), whereas 2-yr fish dominated the catch at other times. Small numbers of large fish (e.g. greater than 5 yr) were found throughout the year (Fig. 8). The seasonal form of the von Bertalanffy growth equation showed that the projected value of L_∞ was 1252 mm FL and the rate of change in growth increment (K) was 0.189 (Fig. 9).

Comparison of annual growth between age-based (age-length and length-frequency) and length-based (mark-recapture) data, although not strictly comparable, showed a decrease in growth with age and size of fish (Fig. 10). Estimates of annual growth were similar among the three methods for 2–4 year fish ($\approx$550–750 mm SL) but varied by $\approx$50 mm for 1-yr-old fish.

Discussion

All structures showed patterns of growth that were, to varying degrees, quantifiable. Delineation of each zone was, however, sometimes difficult, as has been
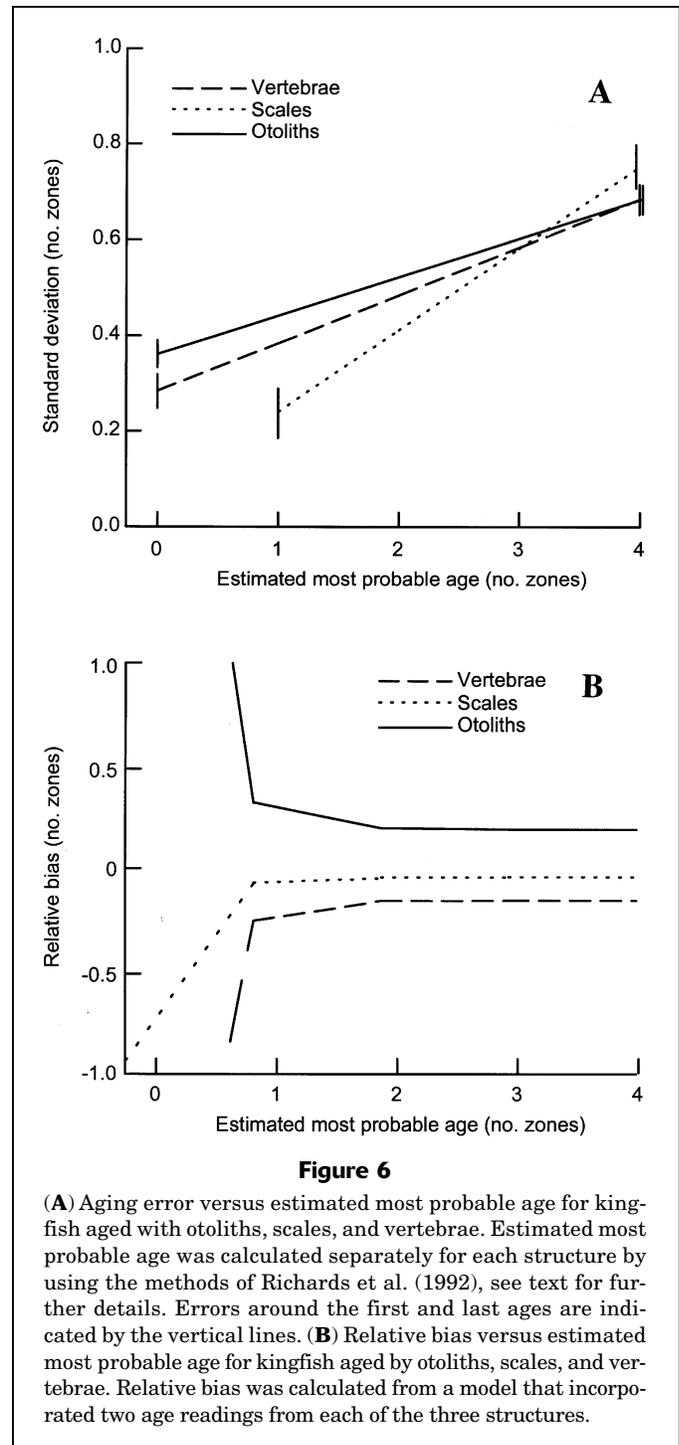

Figure 6
(**A**) Aging error versus estimated most probable age for kingfish aged with otoliths, scales, and vertebrae. Estimated most probable age was calculated separately for each structure by using the methods of Richards et al. (1992), see text for further details. Errors around the first and last ages are indicated by the vertical lines. (**B**) Relative bias versus estimated most probable age for kingfish aged by otoliths, scales, and vertebrae. Relative bias was calculated from a model that incorporated two age readings from each of the three structures.

found in other studies (e.g. Brennan and Cailliet, 1989; Manooch and Potts, 1997), and the clarity of zones varied among individuals for all structures. Because pelagic fishes including *Seriola* spp. are known to be difficult to age, these results were not surprising.

To accurately reflect the age of a fish, the zones must be formed on a regular and determinable time scale.

Small sample sizes during the winter months (from April to July), due in part to small numbers of fish being taken in the fishery, made analysis of marginal increments problematic, especially for scales because samples were also not obtained in August–September. With the exceptions of otoliths and possibly scales, our data were not sufficient to confirm that only one zone

was formed per year. No single category of marginal growth ever had more than 50% of fish for any structure. A previous study (Mitani and Sato, 1959) also found that fish (*Seriola quinqueradiata*) collected in any one time period showed a wide range of marginal growth conditions. Growth zones on the edge of the otoliths of *S. dumerili* were also found over five months of the year (Manooch and Potts, 1997). The wide range of marginal growth patterns in our study may in part be due to grouping of samples into two-month intervals or because fish from three age classes (2–4 growth zones) were used in analyses. Fish from different age classes have previously been shown to lay down zones at slightly different times of year (e.g. Francis et al., 1992).

Analysis of marginal increments often provides only partial validation of age estimates because older fish with slower growth often do not show seasonality in formation of zones. A method should not be considered accurate until all reported ages are validated (Beamish and McFarlane, 1983). Validation of age estimates in older fish will require a mark-recapture study, but further work on validation in younger fish may use a variety of approaches (e.g. length-frequency analyses if cohorts are easily recognized, mark-recapture etc). In the present study, few tagged fish were at large more than a year (Fig. 3B), which suggests that many fish would have to be tagged in a mark-recapture study to recover sufficient fish to make this approach feasible.

There have been few validation studies on *Seriola* spp. and all have involved analysis of marginal increments. Mitani and Sato (1959) have suggested that one zone is laid down each winter in opercular bones of *S. quinqueradiata* and Baxter (1960) found that zones are formed between November and January in scales of *S. lalandi* (formerly *dorsalis*). In otoliths of *S. lalandi* opaque zones appear to be laid down in August or September. Timing of zone formation in scales and vertebrae was more variable and may differ between structures because processes involved in deposition vary among bone, scales, and otoliths (Simkiss, 1974).

Figure 7

Relationship between fork length and age for the different structures used to age kingfish (**A–C**) and (**D**) comparison of the three growth curves. The growth curves were calculated by using Schnute's growth model. R^2, overall standard deviation (SD), and the parameters (standard error) describing the growth model are shown. y_1 is size at age 1, y_2 is size at age 5, a and b are parameters that describe the shape of the curve. The formulae for the growth curves are found in Table 1.

Precision of aging estimates

Exact agreement among age estimates for each structure was generally poor; agreement within one zone was reasonable for all structures. The use of percent agreement (i.e. percent of fish aged alike between sets of multiple readings) has been criticized because it fails to take into account the range of year classes of fish and therefore can be used only for age-specific comparisons (Kimura
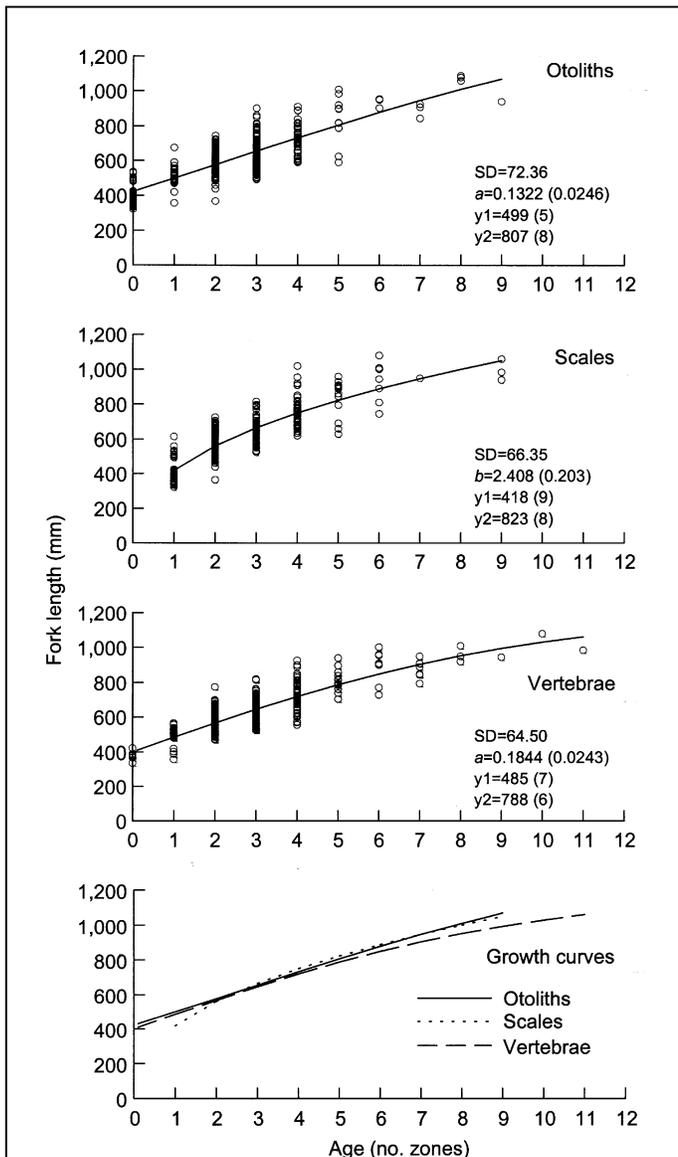
Table 3

Kingfish age-length (FL, mm) distribution for fish collected from New South Wales, Australia, between August 1995 and July 1996. Shown are the number of fish and the percentage of the length class (in parentheses). Ages were estimated from the aging error model that showed the best fit to the data matrix comprising two age readings from each of the three aging structures where fish had less than five growth zones or by randomly selecting one of the six age readings where fish had five or more growth zones.

Length class	Age (yr)										Total
	0	1	2	3	4	5	6	7	8	9	
300–350	4 (66.7)	1 (16.7)	1 (16.7)								6
351–400	11 (47.8)	7 (30.4)	5 (21.7)								23
401–450	4 (40.0)	4 (40.0)	2 (20.0)								10
451–500		11 (34.4)	19 (59.4)	2 (6.3)							32
501–550		11 (10.6)	85 (81.7)	8 (7.7)							104
551–600		1 (1.1)	67 (71.3)	26 (27.7)							94
601–650			54 (50.9)	51 (48.1)	1 (0.9)						106
651–700			14 (19.2)	52 (71.2)	6 (8.2)	1 (1.4)					73
701–750			5 (13.2)	16 (42.1)	14 (36.8)	2 (5.3)	1 (2.6)				38
751–800			1 (3.1)	9 (28.1)	16 (50.0)	4 (12.5)	1 (3.1)	1 (3.1)			32
801–850				3 (21.4)	4 (28.6)	4 (28.6)	3 (21.4)				14
851–900					2 (62.5)	5 (62.5)	1 (12.5)				8
901–950					1 (18.2)	2 (18.2)	4 (36.4)	3 (27.3)		1 (9.1)	11
951–1000							1 (33.3)		1 (33.3)	1 (33.3)	3
1001–1050						1 (33.3)	1 (33.3)		1 (33.3)		3
1051–1100									1 (33.3)	2 (66.7)	3
N	19	35	253	167	44	19	12	4	3	4	560

Table 4

Log likelihood function values, growth parameter estimates, and standard errors (model 4 only) for kingfish (*Seriola lalandi*) tagging data. * indicates that parameters were held fixed. Standard errors of parameter estimates were estimated from simulated data ($n=100$ simulations). Growth rates are shown for 400 mm (g_{400}) and 600 mm (g_{600}) TL fish. The best model fit (model 4) is the case-1 model from Table 1.

Parameter		Model 1	Model 2	Model 3	Model 4	SE
Log-likelihood		2890.67	2797.80	2735.35	2706.21	
Mean growth rate	g_{400} (mm)	263.8	255.3	269.6	260.3	8.1
	g_{600} (mm)	132.1	176.4	140.1	131.1	7.3
Seasonal variation	u (year)	0.164	0*	0*	0*	
	w (year)	0.706	0*	0*	0*	
Growth variability	v	0.397	0*	0*	0.40	0.045
SD measurement error	s (mm)	66.9	82.1	75.8	66.4	1.70
Outlier contamination	P	0.037	0*	0*	0.000	
Curvature in model	b	5.47	0*	5.21	5.66	0.568
Sample size	n	816	794	794	794	

and Lyons, 1991). More recently, the belief that percentage agreement is inappropriate has been questioned. Although it is acknowledged that percent agreement is not interpretable as a property of the species or stock, it is thought to be more intuitive than other methods (Hoenig et al., 1995). Coefficient

of variation (CV) is thought to adjust for the absolute age of the fish and therefore is frequently used to make comparisons among species of varying ages. Kingfish had values of CV within those of previous studies, but at the higher end (present study 7.6–12% versus other species 3.2-12.9% [Kimura and

Lyons, 1991]) suggesting that *S. lalandi* was a more difficult species to age. For kingfish, scales (7.6%) had lower values of CV than did otoliths (12%) and vertebrae (11%). The lowest CV values were for structures where no fish were in their first year (e.g. scales), and the highest values were for structures where fish were aged as in their first year (e.g. otoliths and vertebrae). Similarly, Kimura and Lyons (1991) found that the CV was highest for species in which 1-year age classes were present and lowest where the youngest age classes were 2 or 3 years. Coefficient of variation therefore depends on the minimum age of fish and we suggest that its use be limited to comparisons where fish have the same range of ages. Such indices, if averaged over all fish, are also thought to simplify the data because any trends that might occur with age are ignored (see Hoenig et al., 1995). Precision of aging decreased with age of fish for all structures, suggesting that estimates of precision should not be averaged over all age classes. We believe that the methods of Richards et al. (1992) give a better indication of aging error, and therefore precision, than did methods that summarized over all age classes.

Length at age

Estimates of mean size-at-age calculated from growth models suggested that the resulting growth curves from otoliths, scales, and vertebrae were similar for all but the youngest age class. Although other aging studies on *Seriola* spp. have calculated average length-at-age (e.g. Mitani, 1955; Mitani and Sato, 1959), few have fitted models to the data (but see Baxter, 1960; Manooch and Potts, 1997). Growth models from all aging structures were within the range of growth of *Seriola* spp. described elsewhere (e.g. Mitani, 1955, 1958; Mitani and Sato, 1959; Baxter, 1960; Murayama, 1992).

Further research needs to focus on the position of the first zone in all structures because this may contribute to differences in the shape of the growth curves between structures. No fish were found to be in their first year (i.e. 0) when aged with scales, but fish were found to be in their first year when aged with otoliths and vertebrae. There are also differences in estimated mean size between scales and both otoliths and vertebrae for fish with one growth zone, which is also likely to be due to the detectability of the first zone. Either scales lay down a false first zone or the first zone is not detected in otoliths and vertebrae, possibly because it is close to the edge of the structure. Collections of fish from recruitment over a 12-month period and sampling of all structures may help elucidate the position of the first zone.
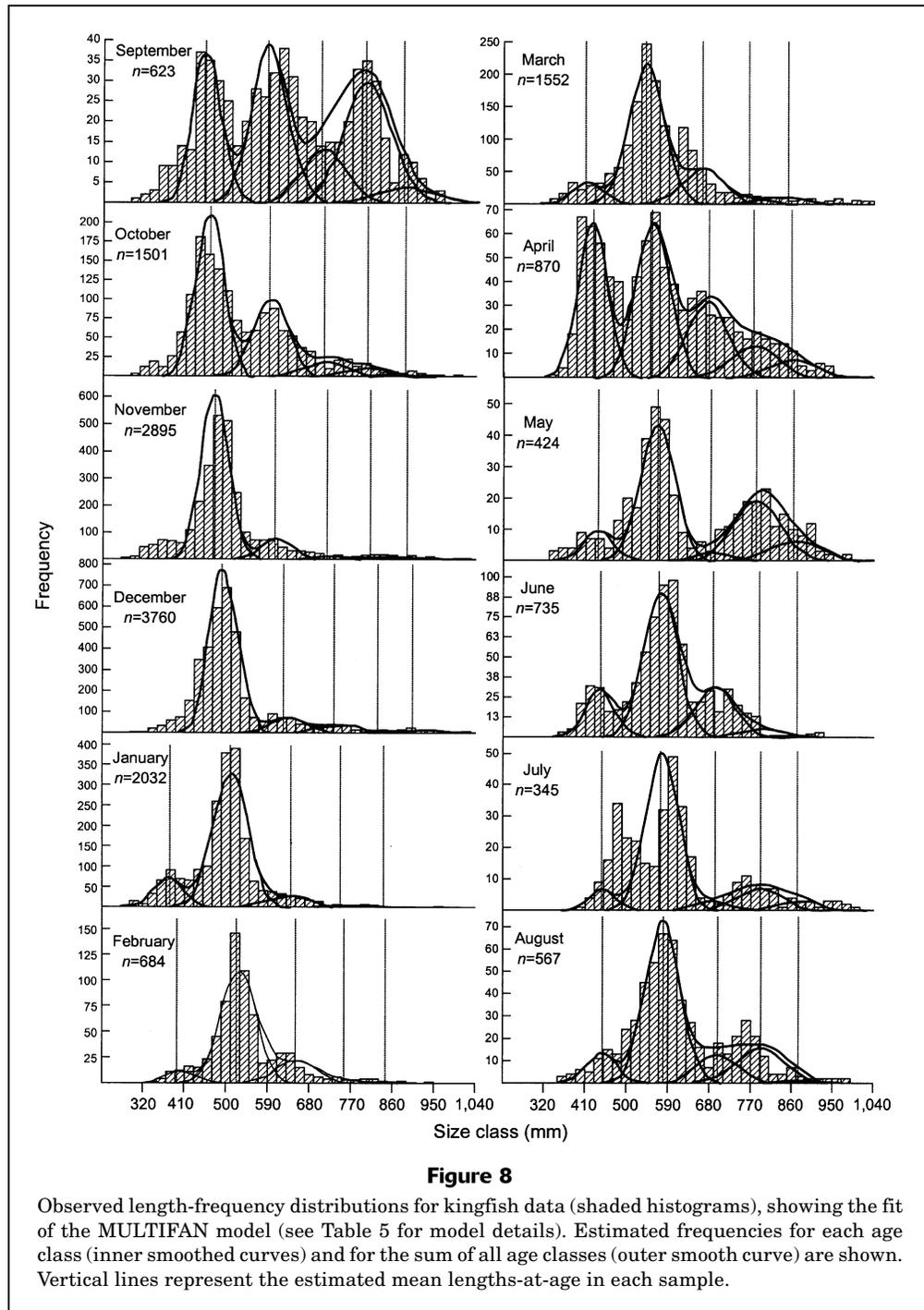
Table 5

Estimated parameters from the MULTIFAN analysis of the length-frequency data, with predicted fork lengths (FL) and standard deviations (SD) of lengths at age.

Parameter	Estimated value
Number of cohorts (N)	5
von Bertalanffy K	0.189/year
von Bertalanffy L_∞	1,252 mm
Brody's rho (ρ)	0.828
First length (m_1)	349.5 mm
Last length (m_N)	828.4 mm
Age of first year class	1.73 years
Mean length sampling bias	26.13 mm
Seasonal growth amplitude (ϕ_1)	0.611
Seasonal growth phase (ϕ_2)	0.087 years
Mean SD	44.4 mm
Ratio of first to last SD	1.897

Age	Predicted FL (mm)	Length-at-age SD
1	349.5	32.2
2	505.0	39.7
3	633.7	47.1
4	740.2	54.3
5	828.4	61.1

Although, it is well known that age estimates from scales are inaccurate once growth becomes asymptotic (Beamish and McFarlane, 1987), scales did not appear to underestimate ages of kingfish in relation to otoliths in the present study but may have underestimated ages of older fish in relation to vertebrae (e.g. Fig. 5). In a previous study on *S. lalandi,* spaces between circuli became increasingly narrow after the seventh year, so that it was impossible to differentiate between one year's growth and the next (Baxter, 1960). Few fish, however, had greater than seven growth zones in the current study.

Many studies have found that sectioned otoliths are preferable to whole otoliths for aging because examination of whole otoliths does not take into account the asymmetric deposition of material (Campana, 1984). After a certain age, deposition may thicken the otolith and growth along the anteroposterior axis may decline; therefore only transverse sections would reveal recently formed growth zones (Beamish, 1979). Growth zones on whole otoliths were interpretable for aging kingfish, but zones could rarely be interpreted on sectioned otoliths. This is unusual because in many studies, sectioned otoliths have been found to give more precise and accurate estimates of age than whole otoliths (e.g. Beamish,

Figure 8

Observed length-frequency distributions for kingfish data (shaded histograms), showing the fit of the MULTIFAN model (see Table 5 for model details). Estimated frequencies for each age class (inner smoothed curves) and for the sum of all age classes (outer smooth curve) are shown. Vertical lines represent the estimated mean lengths-at-age in each sample.

1979; Campana, 1984). Manooch and Potts (1997) have used sectioned otoliths to age *S. dumerili* but commented that age and growth determinations were very difficult. Measurements could only be made on 48% of samples and zones could only be counted on 71% of samples and thus may have biased estimates of growth in their study. Whole otoliths were examined in their study solely to determine the plane of sectioning (Manooch and Potts, 1997). Because whole oto-

liths may underestimate age of large fish (e.g. Beamish, 1979; Campana, 1984), it may also be useful to look at transverse sections of otoliths of kingfish for extremely large fish (>20 kg).

Comparison of age- and length-based data

Although not strictly comparable (see Francis, 1988a, 1995), estimates of growth from length-frequency,

age-length (both age-based data), and tagging data (length-based) showed agreement for fish aged 2–4 years but varied for fish with one growth zone. Differences in rates of growth were greater for younger fish than for older fish and may have been caused by inaccuracies in aging, influence of tagging on growth (e.g. McFarlane and Beamish, 1990), within- or between-year differences, and variations in year-class strength. Although estimates of growth from tagging data provide some indication that age-length data
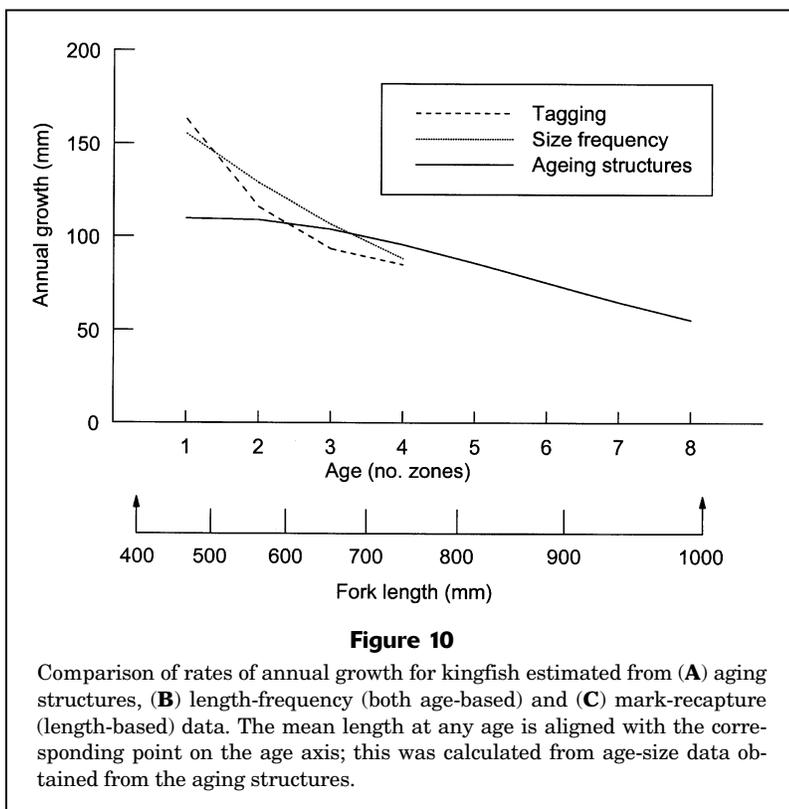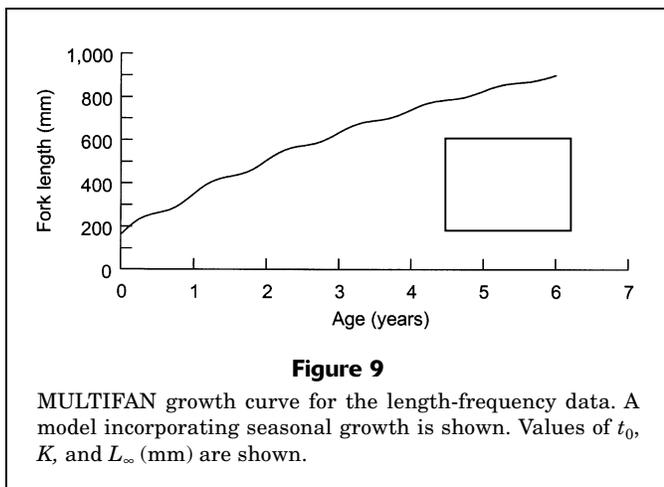
may be reasonable, they should not be used as a means of validation (see Francis, 1988a).

Tagging data also suggest that *S. lalandi* in New South Wales has greater annual growth than the same species in New Zealand and the United States (Baxter, 1960; Holdsworth[3]). For *S. lalandi* in New South Wales, annual growth rates of 144 mm were found for 500-mm-FL fish, compared with 93 mm (New Zealand) and a range of 34–109 mm (US) for similar size fish. In New Zealand, annual growth of 44 mm was found for 1000-mm-FL fish, which is within the range found in the United States (19–70 mm). Few large fish were tagged in New South Wales, preventing estimates of annual growth at this larger size.

Practicalities of aging kingfish

With the exception of dorsal spines, which did not appear useful for aging kingfish, only scales can be easily collected without altering the market value of the fish because *Seriola lalandi* are preferentially sold whole in NSW. Scales showed similar estimates of mean size-at-age to otoliths for all age classes except fish with one growth zone, but their use in aging kingfish can only be recommended with caution until the position of the first growth zone is better understood. The usefulness of otoliths and vertebrae may be limited by the cost of fish, but, if possible, collections of at least one of these structures should be made. The similarity of age estimates among structures suggests that, if validations are possible, kingfish may be aged reliably.

Figure 9

MULTIFAN growth curve for the length-frequency data. A model incorporating seasonal growth is shown. Values of t_0, K, and L_∞ (mm) are shown.

Acknowledgments

Figure 10

Comparison of rates of annual growth for kingfish estimated from (**A**) aging structures, (**B**) length-frequency (both age-based) and (**C**) mark-recapture (length-based) data. The mean length at any age is aligned with the corresponding point on the age axis; this was calculated from age-size data obtained from the aging structures.

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[3] Holdsworth, J. C. 1997. Ministry of Fisheries, 17 Keyte Street, Kensington, private Bag 9013, Whangarei, New Zealand. Unpubl. data.

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Literature cited

Bagenal, T. B., and F. W. Tesch.
  1978.   Age and growth.   Chap. 5 *in* T. B. Bagenal (ed.), Methods for assessment of fish production in fresh waters, p. 101–136.   Blackwell Scientific Publications, Oxford, 365 p.
Baxter, J. L.
  1960.   A study of the yellowtail *Seriola dorsalis* (Gill).   State of California Department of Fish and Game, Fish Bull. 110:96.
Beamish, R. J.
  1979.   Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths.   J. Fish. Res. Board Can. 36:141–151.
Beamish, R. J., and G. A. McFarlane.
  1983.   The forgotten requirement for age validation in fisheries biology.   Trans. Am. Fish. Soc. 112:735–743.
  1987.   Current trends in age determination methodology.   *In* R. C. Summerfelt and G. E. Hall (ed.), Age and growth of fish, p. 15–42.   Iowa State Univ. Press, Ames, IA, 544 p.
Berry, F. H., D. W. Lee, and A. R. Bertolino.
  1977.   Age estimates in Atlantic bluefin tuna—an objective examination and an intuitive analysis of rhythmic markings on vertebrae and in otoliths.   Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap., Madrid 6:305–317.
Brennan, J. S., and G. M. Cailliet.
  1989.   Comparative age-determination techniques for white sturgeon in California.   Trans. Am. Fish. Soc. 118:296–310.
Campana, S. E.
  1984.   Comparison of age determination methods for starry flounder.   Trans. Am. Fish. Soc. 113:365–369.
Fournier, D. A., J. R. Sibert, J. Majkowski, and J. Hampton.
  1990.   MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*).   Can. J. Fish. Aquat. Sci. 47:301–317.
Fournier, D. A., J. R. Sibert, and M. Terceiro.
  1991.   Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method.   Can. J. Fish. Aquat. Sci. 48:591–598.
Francis, M. P., and R. I. C. C. Francis.
  1992.   Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*).   Aust. J. Mar. Freshwater Res. 43:1157–1176.
Francis, R. I. C. C.
  1988a.   Are growth parameters estimated from tagging and age-length data comparable?   Can. J. Fish. Aquat. Sci. 45:936–942.
  1988b.   Maximum likelihood estimation of growth and growth variability from tagging data.   N.Z. J. Mar. Freshwater Res. 22:42–51.
  1995.   An alternative mark-recapture analogue of Schnute's growth model.   Fish. Res. 23:95–111.
Francis, R. I. C. C., L. J. Paul, and K. P. Mulligan.
  1992.   Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection.   Aust. J. Mar. Freshwater Res. 43:1069–1089.
Hoenig, J. M., M. J. Morgan, and C. A. Brown.
  1995.   Analysing differences between two age determination methods by tests of symmetry.   Can. J. Fish. Aquat. Sci. 52:364–368.
Kimura, D. K., and J. J. Lyons.
  1991.   Between-reader bias and variability in the age-determination process.   Fish. Bull. 89:53–60.
Manooch, C. S. III, and J. C. Potts.
  1997.   Age, growth and mortality of greater amberjack from the southeastern United States.   Fish. Res. 30:229–240.
McFarlane, G. A., and R. J. Beamish.
  1990.   Effect of an external tag on growth of sablefish (*Anoplopoma fimbria*), and consequences to mortality and age at maturity.   Can. J. Fish. Aquat. Sci. 47:1551–1557.
Mitani, F.
  1955.   Studies on the fishing conditions of some useful fishes in the western region of Wakasa Bay—11. Relation between the scale of the yellowtail, *Seriola quinqueradiata* T. & S., and fork length and age.   Bull. Jpn. Soc. Scient. Fish. 21:463–466.
  1958.   Studies on the growth and age of the yellow-tail, *Seriola quinqueradiata* T. & S., found in Japan and the adjacent region—1. A fundamental consideration on age estimation by vertebrae.   Bull. Jpn. Soc. Scient. Fish. 24:626–631.
Mitani, F., and T. Sato.
  1959.   Studies on the growth and age of the yellowtail, *Seriola quinqueradiata* T. & S., found in Japan and the adjacent region—11. Estimation of age and growth from the opercular bone.   Bull. Jpn. Soc. Scient. Fish. 24:803–808.
Munekiyo, M., M. Sinoda, and O. Sugimura.
  1982.   A possibility of fish age estimation by means of a replica of the vertebral centrum.   Bull. Jpn. Soc. Scient. Fish. 48:1371–1374.
Murayama, T.
  1992.   Growth of the yellowtail *Seriola quinqueradiata* in the Japan Sea and coast in recent years.   Nippon Suisan Gakkaishi 58:601–609.
Pepperell, J. G.
  1985.   Cooperative game fish tagging in the Indo-Pacific region.   *In* R. H. Stroud (ed.), World angling resources and challenges, p. 241–252.   International Game Fish Association, Fort Lauderdale, Florida.
  1990.   Australian cooperative game-fish tagging program, 1973–1987: status and evaluation of tags.   Am. Fish. Soc. Symp. 7:765–774.
Richards, L. J., J. T. Schnute, A. R. Kronlund, and R. J. Beamish.
  1992.   Statistical models for the analysis of ageing error.   Can. J. Fish. Aquat. Sci. 49:1801–1815.
Schnute, J.
  1981.   A versatile growth model with statistically stable parameters.   Can. J. Fish. Aquat. Sci. 38:1128–1140.
Simkiss, K.
  1974.   Calcium metabolism of fish in relation to ageing.   *In* T. B. Bagenal (ed.), The ageing of fish, p. 1–12.   Unwin Brothers Ltd, London, 234 p.