

Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae)

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Slow-growing fish tend to have heavier, larger otoliths than fast-growing fish of the same length, because otoliths continue to grow even when somatic growth has slowed or stopped (e.g., Templeman & Squires 1956, Mosegaard et al. 1988, Reznick et al. 1989, Secor & Dean 1989, Secor et al. 1989, Campana 1990, Pawson 1990). This uncoupling has important implications for the back-calculation of fish lengths from check marks in the otoliths. If the relationship between an otolith dimension and fish length varies with growth rate, the back-calculated lengths may be biased (Campana 1990). This bias may be largely overcome by specifying a "biological intercept" (such as otolith and somatic size-at-hatching) and incorporating time-varying growth (as measured by daily increment widths) into the back-calculation equation (Campana 1990).

Pagrus auratus (Bloch & Schneider 1801) is a commercially-important sparid fish that ranges through most of the temperate to subtropical Western Pacific Ocean (Paulin 1990). It has been reported previously under a variety of synonyms, especially *P. major* (Japan), *Chrysophrys auratus* (Australia and New Zealand), and *C. unicolor* (Australia) (Paulin 1990). The common name for *P. auratus* in New Zealand

and Australia is "snapper," though it is not a true snapper (Lutjanidae).

Uncoupling of otolith and somatic growth has been demonstrated in reared larval and presettlement juvenile *P. auratus* from Japan (Secor et al. 1989). In this study, we report uncoupling of otolith and somatic growth in wild, post-settlement, juvenile New Zealand snapper. We also discuss the implications this has for back-calculation of juvenile snapper lengths using otolith daily increments.

Methods

Snapper were caught using a small otter trawl net equipped with a 20 mm stretched-mesh codend. Samples were collected near Kawau Island, Hauraki Gulf, New Zealand (36°25'S, 174°46'E), January 1987 to March 1989. Fish were chilled on capture, and frozen within 24 h. After thawing, snapper were measured to the nearest mm fork length (FL). Trial measurements before and after freezing and thawing showed that shrinkage was minimal (mean shrinkage=2.03%, SD=1.09%, n=42), thus no length corrections were made.

In New Zealand, snapper have a prolonged summer spawning season from October to February (Scott & Pankhurst 1992), and we follow

Paul (1976) in taking the theoretical birthday as 1 January. Each year-class was numbered after its first full year; e.g., snapper spawned during the 1986–87 austral summer were assigned to the 1987 year-class. Age-0+ fish were identified from length-frequency modes; they grow to about 80–140 mmFL at the end of their first year (Paul 1976; M.P. Francis, unpubl. data).

Sagittae were removed, and one of each pair was weighed and measured for maximum length (anterio-posterior axis) and height (dorso-ventral axis). For snapper <200 mmFL, transverse sections¹ were prepared from a subsample of sagittae, and sulcal width was measured as the distance between the sulcal side of the metamorphic mark (Francis et al. In press) and the sagitta margin at the ventral edge of the sulcus. This measurement was used in preference to total sagitta width because the antisulcal face of sagittae varied considerably in shape, making it a poor reference surface, and because most of the increase in sagitta width occurred on the sulcal surface. The collective term "size variables" is used here when referring to sagitta weight, length, height, and sulcal width.

A series of analyses of covariance (ANCOVA) were used to investigate the effects of year-class (1987 and 1988) and seven sampling periods (Table 1) on the relationship between the four size-variables and FL in 0+ snapper.

Data from snapper samples collected in Periods 2 and 3 (Table 1) were used to determine whether sagitta size at any given FL depends

¹Terminology used to describe otolith planes and ageing follows Wilson et al. (1987).

Table 1

Sampling periods for age-0+ snapper *Pagrus auratus*, 1987 and 1988 year-classes.

Period	1987	1988
1	27 January	4 February
2	2 March	15 March
3	28 April	6 April
4	30 June	30 May–7 June
5	24–27 August	25 July–4 August
6	19 October	31 October
7	14 December	29 Nov–20 Dec

on somatic growth rate. Regressions were fitted to plots of size-variables vs. FL, and the residuals were plotted against somatic growth rate. The latter was estimated by the equation

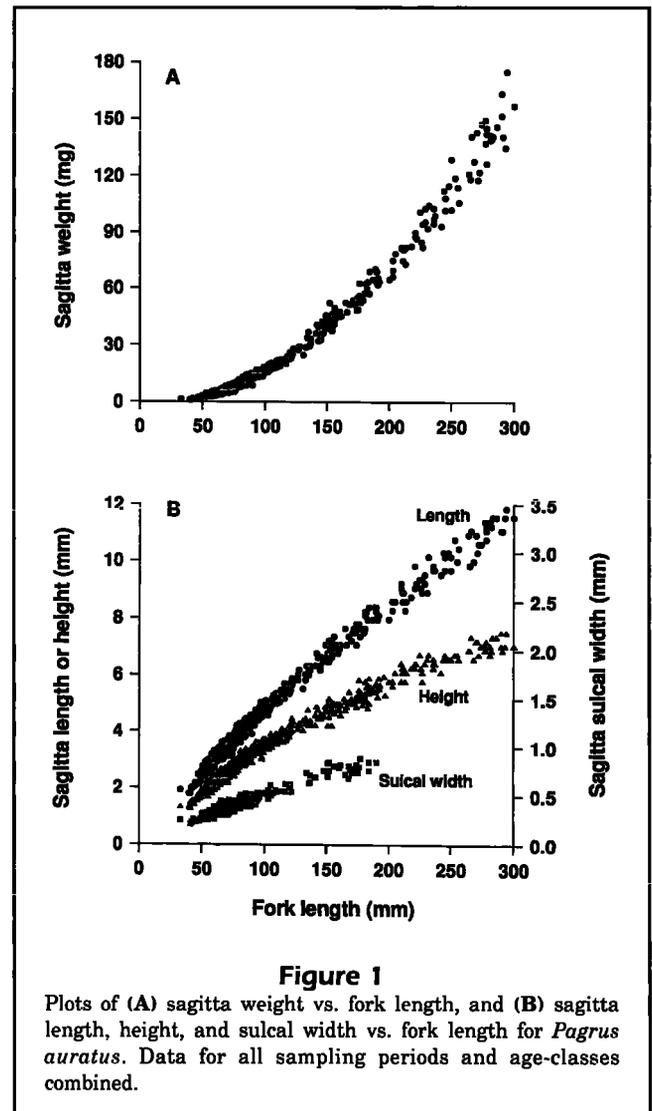
Somatic growth rate = $(FL-8)/(\text{post-metamorphic age})$,

where the constant 8 represents approximate mean length of snapper at metamorphosis (Fukuhara 1985 and 1991, Foscarini 1988, Battaglione & Talbot 1992). Post-metamorphic age-at-capture was estimated from transverse sections by counting daily increments between the metamorphic mark and the section margin (see Francis et al. [In press] for validation of daily increments). Post-metamorphic age was used rather than post-hatch age because only about 10% of our sections contained cores; use of post-hatch age would have severely limited sample sizes. Similar analyses were not performed on data from Period 1 because of small sample size, nor on data from Periods 4–7 because daily increments deposited during winter are not resolvable with a light microscope (Francis et al. In press).

Results

Figure 1 shows plots of sagitta size-variables vs. FL for all sampling periods and age-classes combined. Sagitta weight increased exponentially with FL (Fig. 1A). Plots of sagitta length, height, and sulcal width vs. FL were convex, with slopes decreasing over the range 35–300 mmFL (Fig. 1B).

Data for 0+ snapper of the 1987 and 1988 year-classes collected in Periods 1–7 were extracted for further analysis by ANCOVA. Because only linear relationships can be analyzed by ANCOVA, sagitta weight and FL were \log_{10} transformed before the relationship between them was analyzed. Relationships between the other three size-variables and FL are clearly

**Figure 1**

Plots of (A) sagitta weight vs. fork length, and (B) sagitta length, height, and sulcal width vs. fork length for *Pagrus auratus*. Data for all sampling periods and age-classes combined.

nonlinear (Fig. 1B). However, ANCOVAs fit linear regressions to individual samples (i.e., sagittae of snapper from one year-class caught in one period), which span only short segments of the lower end of the FL range shown in Fig. 1B. All samples were tested for nonlinearity by regressing size-variables against FL, and plotting the residuals against FL. There were no trends in the residuals, so the untransformed data were used in the ANCOVAs.

The first set of four ANCOVAs (one for each size-variable) tested the effects of year-class and sampling period on sagitta size, using FL (or $\log_{10}FL$) as the covariate. There were no significant interaction terms involving year-class, and the year-class factor itself was not significant ($p > 0.05$) in any ANCOVA. Therefore, data for the two year-classes were pooled for subsequent analyses.

A second set of four ANCOVAs tested the effect of the seven sampling periods on sagitta size. In each case, the slopes of the regression lines differed significantly among sampling periods (Table 2). Slope coefficients declined markedly between Periods 4 and 5 (Table 3); consequently, a third set of four ANCOVAs was limited to data for Periods 1–4. Whereas slopes did not differ significantly for sagitta length, height, or sulcal width, the intercepts did (Table 2). The three size-variables increased relative to FL between time-periods, i.e., snapper sampled later in the year had larger sagittae than those sampled earlier (Fig. 2B). The only sample-pairs that did not differ were Periods 1 and 2 for sagitta height and sulcal width measurements

Table 2

Summary of results of ANCOVAs of sagitta size-variable data for snapper *Pagrus auratus*, 1987 and 1988 year-classes combined. Separate analyses were performed with the variables length, height, sulcal width, and \log_{10} (weight). The covariate was fork length for the first three analyses and \log_{10} (fork length) for the last. NS = not significant; * $p < 0.05$, ** $p < 0.01$.

Sagitta size-variable	Periods	Test for slope differences	Test for intercept differences	Periods for which intercepts did not differ ($p > 0.05$) ¹
Length	1–7	**		
	1–4	NS	**	Nil
Height	1–7	**		
	1–4	NS	**	1 & 2
Width	1–7	*		
	1–4	NS	**	1 & 2
Log(weight)	1–7	**		
	1–4	**		

¹Conditional Tukey-Kramer test.

Table 3

Regression slopes for the relationships between sagitta size-variables and fork length for snapper *Pagrus auratus* during seven sampling periods. Sagitta length, height, and sulcal width were regressed against fork length, and sagitta \log_{10} (weight) against \log_{10} (fork length). Data for Periods 1–4 are shown in Fig. 2. N = sample size.

Period	Length		Height		Width		Log(weight)	
	N	Slope	N	Slope	N	Slope	N	Slope
1	17	0.045	22	0.032	14	0.0035	18	2.69
2	83	0.042	92	0.031	44	0.0039	88	2.30
3	38	0.040	58	0.033	53	0.0036	40	2.14
4	84	0.041	86	0.033	42	0.0036	83	2.32
5	61	0.037	65	0.028	22	0.0033	62	2.08
6	71	0.037	72	0.027	20	0.0027	72	2.05
7	45	0.038	47	0.029	16	0.0024	44	2.12

(Table 2). In the ANCOVA of sagitta weight vs. FL, slopes differed significantly among the four periods; thus the intercepts could not be tested (Table 2). However, sagitta weight followed the same trend as the other size-variables, being greater in snapper sampled later in the year than in those sampled earlier (Fig. 2A).

Periods 2 and 3 data were used independently to investigate the effect of growth rate on size-variables within sampling periods. The data represent juveniles with estimated post-metamorphic ages of 53.5–136.0 d, and lengths of 43–96 mm FL. Estimated growth rates, averaged over the whole juvenile life, ranged from 0.54 to 0.93 mm/d. Residuals from regressions of Period-2 size-variables vs. FL were negatively correlated with somatic growth rate ($r = -0.87, -0.70, -0.74, \text{ and } -0.54$ for sagitta weight, length, height, and sulcal width, respectively; $p < 0.01$ in all cases). Therefore, sagittae were heavier and larger (in all dimensions) in slow-growing than in fast-growing snapper. Sagitta weight residuals are plotted against growth rate in Fig. 3.

Residuals from regressions of Period-3 size-variables vs. FL were also negatively correlated with somatic growth rate ($r = 0.45, -0.39, -0.13, \text{ and } -0.26$ for sagitta weight, length, height, and sulcal width, respectively). However, only the sagitta weight correlation was significant ($p < 0.05$).

To determine whether differences in somatic growth rate might explain the observed differences in sagitta size variables between sample periods (Fig. 2), an analysis of variance was performed on growth-rate estimates for Period-2 and -3 snapper. Variances for the two periods were homogeneous ($F_{46,60} = 1.15, p > 0.05$). Period-2 snapper had significantly higher growth rates (\bar{x} 0.81 mm/d, range 0.68–0.94 mm/d) than Period-3 snapper (\bar{x} 0.66 mm/d, range 0.55–0.82 mm/d, $F_{1,106} = 128.0, p < 0.001$).

Discussion

Residuals analysis showed that in Period 2 and over the length range 43–90 mmFL, slow-growing snapper had larger sagittae (relative to FL) than fast-growing snapper. In Period 3, a similar but weaker pattern was found. This study, therefore, demonstrates uncoupling of sagitta and somatic growth in wild age-0+ snapper, and extends a previous report of such uncoupling in reared Japanese snapper up to 30 mmSL (Secor et al. 1989).

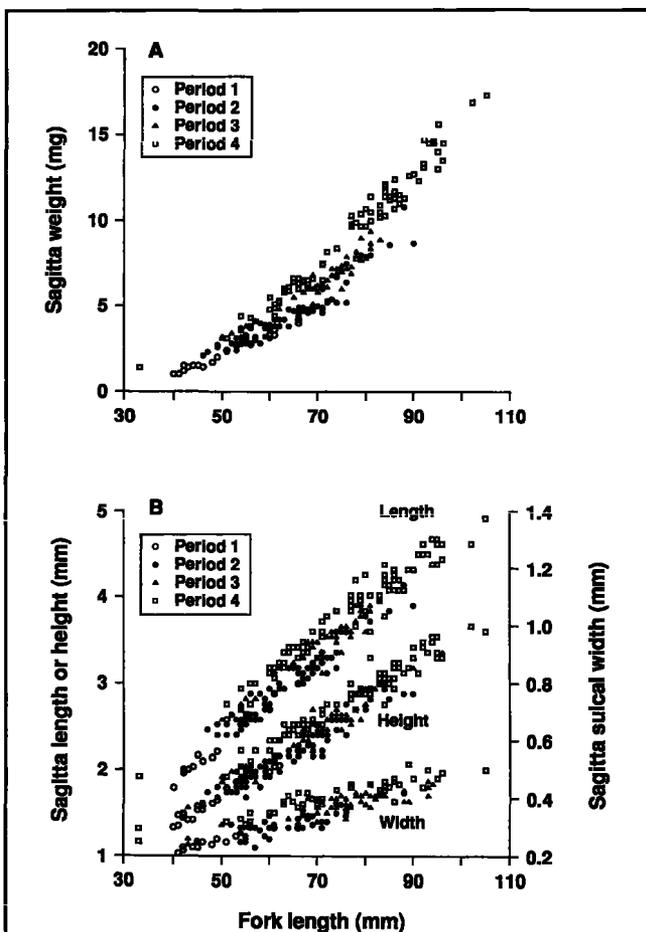


Figure 2

Plots of (A) sagitta weight vs. fork length, and (B) sagitta length, height, and sulcal width vs. fork length for age-0+ *Pagrus auratus*, 1987 and 1988 year-classes, sampled during Periods 1-4 (see Table 1).

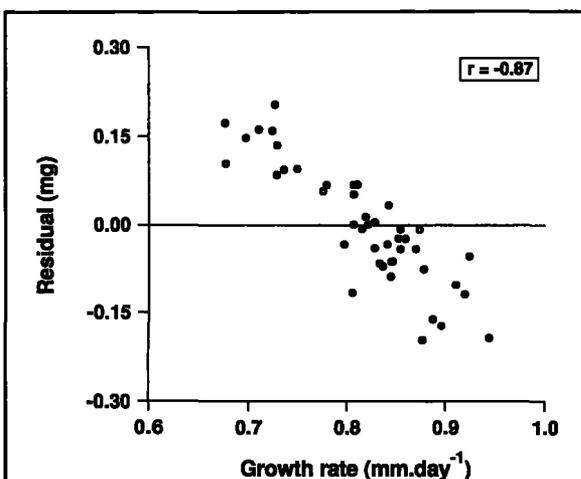


Figure 3

Residuals from a \log_{10} (sagitta weight) vs. \log_{10} (fork length) regression of the Period-2 data from Figure 2A plotted against *Pagrus auratus* post-metamorphic growth rate.

Increases in sagitta size-variables **between** Periods 2 and 3 are also consistent with a growth rate effect: snapper with lower growth rates (Period 3) had larger sagittae than those with higher growth rates (Period 2). Snapper growth rate generally declines between summer and winter (Paul 1976), so the pattern of increasing sagitta size over Periods 1-4 (summer-winter) is also consistent with a growth-rate effect.

Between Periods 4 and 5, the slopes of single-sample plots of size-variables vs. FL decreased. A reduction in slope during the winter months suggests that somatic growth slows faster in small than in large snapper, leading to relatively larger sagittae in the former. The reduction in slope is responsible for the curvilinear trends observed when data from all periods are pooled (Fig. 1B). A similar effect of season on sagitta-somatic relationships has been reported in other species (Reay 1972, Thomas 1983).

When sagitta and somatic growth rates are uncoupled, back-calculated lengths may be biased (Campana 1990). To reduce this bias, Campana (1990, eq. 4) connected the growth trajectory end-points (i.e., sagitta and somatic sizes-at-capture) with a "biological intercept" (he suggested sagitta and somatic size-at-hatching). Snapper larvae are about 2 mmSL (equivalent to ~2.5 mmFL) at hatching, and have circular sagittae that are 0.010-0.012 mm in diameter (M.P. Francis, unpubl. data). These values would form an appropriate biological intercept for daily increment back-calculations using measurements in either the antero-posterior (length) or dorso-ventral (height) axes.

Francis (1990) reviewed back-calculation methods, but was not aware of Campana's (1990) study. Francis identified two back-calculation hypotheses: scale (=sagitta) proportional, and body (=somatic) proportional. He pointed out that the commonly used Fraser-Lee equation follows neither hypothesis, and recommended that it be replaced with an equation that does. Campana's equation 4 is a modification of the Fraser-Lee equation, and also does not follow scale- or body-proportional hypotheses. This is easily shown by considering the point at which growth trajectories converge. For scale-proportional methods, this point is on the body-size axis; for body-proportional methods, the point is on the scale-size axis; for Campana's method, the point is at the biological intercept which will usually have some small, positive value on both axes (Campana 1990, Francis 1990). Campana's method, therefore, represents a third back-calculation hypothesis, which is based on the idea that the proportional relationship between scale and body size is initiated at some growth stage, such as hatching. (The Fraser-Lee equation was also based on this idea, but, in practice, most authors using that equation calculated the intercept from a regression line rather than from biological data [Francis 1990]).

The key factor that must be considered when deciding which back-calculation method to use is the accuracy with which it estimates back-calculated lengths. Comparison of mean back-calculated lengths with mean observed lengths can detect only gross errors (Francis 1990), and is not a good test for accuracy. Campana (1990) used simulations to show that his method removed much of the bias associated with a sagitta-somatic growth-rate effect. The existence of a strong growth-rate effect in juvenile snapper suggests that Campana's method should be used to overcome the expected bias.

Campana's (1990) equation 4 corrects for growth-rate variability among fish, while assuming linear sagitta-somatic trajectories for individual fish. The need for the latter assumption can be overcome by incorporating time-varying growth into the model (Campana 1990, eq. 7). However, there are two obstacles to use of the time-varying model for snapper: First, the model takes no account of sagitta and somatic size-at-capture, which limits its use to back-calculation of mean lengths; second, the model requires width measurements from all daily increments between the biological intercept and capture, plus a proportional relationship between increment width and somatic growth. For snapper, the relationship between increment width and somatic growth is unknown. Furthermore, recent work on other species has shown that changes in increment width may lag or be unrelated to changes in somatic growth (Molony & Choat 1990, Wright 1991). For these reasons, we recommend that back-calculation of snapper lengths from daily increments be done using Campana's equation 4.

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