

A STATISTICAL PROCEDURE FOR VALIDATING AGE ESTIMATES FROM OTOLITH BANDS USING MARK-RECAPTURE DATA, WITH AN ILLUSTRATION FOR *POMATOMUS SALTATRIX*

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A study of age and growth in *Pomatomus saltatrix* from KwaZulu-Natal was undertaken on the basis of otolith readings. Validation of periodicity of otolith banding was attempted by developing a model that estimated growth parameters from age-length data. The model assumed arbitrarily chosen band-deposition periodicities, and then simultaneously predicted growth increments of tagged individuals based on these growth parameters. The assumption of annual banding led to the best prediction of growth increments of tagged individuals, with small coefficients of variations in the parameter estimates. However, because only a few tagged animals were used in the analysis, more research is needed to verify the reliability of this technique.

The description of fish growth is fundamental to age-structured stock assessment models. Historically, age estimates for fish have been obtained from hard structures, such as scales or otoliths, by enumerating seasonally deposited opaque or translucent bands in the calcified tissue (Beamish and McFarlane 1987). Such ageing methods are based on the assumption that the periodicity of band deposition is known or can be validated. To date, the only direct method of validation has been the use of chemical dyes such as tetracycline, which mark the hard structure. This fluorescent mark then serves as a reference point from which the periodicity of the seasonal bands can be deduced once sufficient somatic growth has accrued. Other indirect techniques for the validation of hard-structure banding include marginal increment analysis, back-calculation methods, and the analysis of modal progression of length frequency data in conjunction with age data (Hecht and Smale 1986).

In this study, a growth model is developed that utilizes mark-recapture data to validate the periodicity of opaque band deposition in the otoliths of *Pomatomus saltatrix* captured off KwaZulu-Natal, South Africa. The method is based on the assumption that, if a growth curve (derived from size-at-age data and assuming an arbitrary periodicity of the banding in the hard structure) can reasonably predict the observed growth increment of tagged individuals between the times of marking and recapture, then the growth parameters and the periodicity assumed for the seasonal bands must be valid.

MATERIAL AND METHODS

Age estimates for *P. saltatrix* were obtained from reading whole otoliths ($n = 340$). Otoliths were collected on an irregular basis during the period 1992–1994 from various angling sites along the KwaZulu-Natal coast. Most samples were obtained from fish caught illegally that were confiscated by the former Natal Parks Board (now the KwaZulu-Natal Nature Conservation Service) and were representative of the size range of *P. saltatrix* in the region. Small specimens that were generally smaller than the permitted minimum size (30 cm total length) were sampled from seine-net catches. Otoliths were immersed in ethanol and were examined against a black background using a low-power dissecting microscope; specimens were illuminated by reflected light. The number of opaque bands was counted from the nucleus to the outer margin of the otolith. Each otolith was read twice and there was a minimum of one month between readings. The second reading was performed without references to the first. If both readings of the same otolith were coincident, this was taken as the age estimate. However, if the readings differed by one or more bands, the otoliths were rejected. This rejection criterion was used in order to improve the reliability of age readings.

Mark-recapture data for *P. saltatrix* were obtained from the Sedgwick's/ORI/WWF tagging programme. The history and methodology details of this programme are discussed fully in Van der Elst (1990). Since the

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programme's inception in 1984, some 3 676 *P. saltatrix* have been tagged and 152 recaptures reported (a return rate of 4.13%). Tagging and recapture of *P. saltatrix* took place along the south-eastern seaboard of South Africa, mainly by shore-based anglers. Unfortunately, most anglers either did not measure the fish they tagged or recaptured, whereas others merely guessed the size. Those anglers who measured their catch sometimes failed to indicate/remember if their measurements were of total lengths. As a result, length data from only 18 marked and recaptured *P. saltatrix* could be verified. In three cases, although length measurements were accurate, negative growth was recorded. These individuals were not excluded from the present analysis, although the model developed only describes positive growth.

Growth model incorporating mark-recapture data to validate age estimates

The model allows age estimates that have been derived from scales or otoliths to be validated using corresponding mark-recapture data for a given fish species. The model is based on the assumption that, if a growth equation derived from size-at-age data reasonably predicts the growth increment during the time-at-liberty of tagged individuals, then the estimated growth parameters and the assumed time period for deposition of the seasonal bands are appropriate. The model consists of two components. The first estimates growth parameters from size-at-age data based on different deposition periods of hard structure bands. The second then predicts the growth increment during the time-at-liberty of recaptured tagged individuals, using the growth parameters derived from the first model component. If the growth increments are reasonably predicted, then the assumption of periodicity in hard structure deposition is assumed to be valid.

FIRST MODEL COMPONENT

For this study, it was assumed that the Von Bertalanffy growth function adequately describes the growth of *P. saltatrix*. This assumption could have been relaxed, but it was made to keep the number of model parameters to a minimum. Other studies have assumed Von Bertalanffy growth in *P. saltatrix* (Van der Elst 1976, Bade 1977, Krug and Haimovici 1989, Barger 1990, Chiarella and Conover 1990). The traditional parameterization of the Von Bertalanffy function was discarded in favour of that of Schnute (1981). Some studies (e.g. Schnute 1981, Ratkowsky 1986) have shown that this parameterization results in statistically

more stable parameter estimates. Schnute's parameterization of the Von Bertalanffy growth function, which is also a three-parameter model, is given as:

$$Y(t) = Y(1) + [(Y(2) - Y(1)) \frac{[1 - \exp(-a(t - T(1)))]}{[1 - \exp(-a(T(2) - T(1)))]}] \quad (1)$$

where $Y(t)$ is the size of a t -aged fish, $Y(1)$ is the mean size of $T(1)$ -aged fish, $Y(2)$ is the mean size of $T(2)$ -aged fish, and a is a constant, where $a \neq 0$, $Y(2) > Y(1)$ and $T(2) > T(1)$.

In Equation 1, the variable t is redefined as:

$$t_i = \frac{B_i}{P} \quad ,$$

where t_i is the age of fish i , B_i is the number of otolith (or hard structure) bands counted for fish i , and P is the periodicity of the otolith band assumed (P is an integer > 0). If $P = 1$, then one hard structure band is deposited annually, whereas if $P = 2$, then the periodicity is biannual.

The traditional Von Bertalanffy parameters (L_∞ , k and t_0) can be obtained from the parameters of Equation 1 (Schnute 1981):

$$L_\infty = \frac{\exp[aT(2)]Y(2) - \exp[aT(1)]Y(1)}{\exp[aT(2)] - \exp[aT(1)]}$$

$$k = a \quad ,$$

$$t_0 = T(1) + T(2) - \frac{1}{a} \ln \left[\frac{\exp[aT(2)]Y(2) - \exp[aT(1)]Y(1)}{Y(2) - Y(1)} \right].$$

Given a matched data set of otolith band readings and fish size measurements for a particular species, and assuming a time period for otolith band deposition (e.g. $P = 1$ or 2), parameter values of Equation 1, i.e. $Y(1)$, $Y(2)$ and a , can be obtained by specifying the ages $T(1)$ and $T(2)$ and then minimizing an appropriate objective function.

The additive error structure was considered for the model:

$$Y(t)_{i,obs} = Y(t)_{i,pred} + \epsilon_i \quad ,$$

where $Y(t)_{i,obs}$ and $Y(t)_{i,pred}$ are the observed and predicted sizes of fish i aged t respectively, and ϵ_i are the "model errors". The error terms ϵ_i are assumed to be independent, random variables that follow a normal distribution with mean = 0 and a variance (σ^2). Given size-at-age data based on an assumed value for P , estimates of $Y(1)$, $Y(2)$ and a can be obtained by specifying the ages $T(1)$ and $T(2)$ prior to using a

non-linear minimization routine that will find optimum parameter estimates which satisfy the criteria:

$$SS = \sum_{i=1}^n (Y(t)_{i,obs} - Y(t)_{i,pred})^2 \quad ,$$

where n is the number of fish aged.

SECOND MODEL COMPONENT

In the following section, Equation 1 is transformed to predict the growth increments, given the times-at-liberty and size-at-marking of tagged individuals, and the parameter estimates obtained from the size-at-age data. To derive the mark-recapture model corresponding to Equation 1, t is first made the subject of Equation 1:

$$t = T(1) - (1/a) \ln [1 - [1 - \exp(-a(T(2) - T(1)))] \frac{Y(t) - Y(1)}{Y(2) - Y(1)}] \quad (2)$$

If fish grow from size $Y(m)$, when marked at age $t(m)$, to size $Y(r)$, when recaptured at age $t(r)$, then from Equation 2:

$$t(m) = T(1) - (1/a) \ln [1 - \exp(-a(T(2) - T(1)))] \frac{Y(m) - Y(1)}{Y(2) - Y(1)} \quad (3)$$

and

$$t(r) = T(1) - (1/a) \ln [1 - [1 - \exp(-a(T(2) - T(1)))] \frac{Y(r) - Y(1)}{Y(2) - Y(1)}] \quad (4)$$

Subtracting Equation 4 from 3 and rearranging to solve for $Y(r)$ yields:

$$Y(r) = Y(m) \exp[-a(t(r) - t(m))] + [Y(2) - Y(1) \exp[-a(T(2) - T(1))]] \times \frac{1 - \exp[-a(t(r) - t(m))]}{1 - \exp[-a(T(2) - T(1))]} \quad (5)$$

Equation 5 can be rewritten as:

$$Y(r) = [Y(m) \exp(-a\Delta t) + v(1 - \exp(-a\Delta t))] \quad , \quad (6)$$

where v can be found by comparing Equations 6 and 5, and $\Delta t = t(r) - t(m)$, i.e. the time-at-liberty. Noting that $Y(r) = Y(m) + \Delta l$ where Δl is the growth increment (either positive or negative) during the time-at-liberty, substitution into Equation (6) results in:

$$\Delta l = (Y(m) [\exp(-a\Delta t) - 1] + v[1 - \exp(-a\Delta t)]) \quad . \quad (7)$$

Using the parameter estimates $Y(1)$, $Y(2)$ and a from

Equation 1 (derived from otolith banding-size data and a range of assumed P values), the best estimates of P , $Y(1)$, $Y(2)$ and a are deemed those that minimize the criteria

$$SS_{tag} = \sum_{i=1}^M (\Delta l - \Delta g)^2 \quad , \quad (8)$$

where Δg is the observed growth increment during the time-at-liberty for fish i , and M is the number of tagged fish for which mark-recapture data are obtained. Note that Equation 8 is not minimized during the estimation process; rather it is evaluated after estimates are obtained once the SS function is minimized.

Comparing the fits between the different models of P

The size-at-age model was tested for randomness of the residuals using a runs test (Draper and Smith 1966) and a visual assessment of the residual plot: $(Y(t)_{i,pred} - Y(t)_{i,obs})$ v. $(Y(t)_{i,pred})$, to detect any systematic trend (Butterworth *et al.* 1989).

The choice between different models of P was achieved by a simple plot of the residuals, i.e. the difference between observed and predicted growth increments $(\Delta l_i - \Delta g_i)$ was plotted against Δl_i . The residual plot that showed no systematic trend was then the chosen model.

Estimating standard errors using the "parametric" bootstrap technique

The "parametric" bootstrap technique (Efron 1981, Punt and Butterworth 1993) was used to calculate standard errors for the parameters $Y(1)$, $Y(2)$ and a of the Schnute growth curve, as well as the derived quantities L_∞ , k and t_0 . The "parametric" bootstrap technique was employed because, besides estimating standard errors for the parameters of a model, it also provides estimates of standard errors for quantities derived from those parameters (Punt 1992). The standard error for a parameter K is estimated from a series of artificially generated datasets. As the method is computationally intensive, only 100 pseudo-datasets were generated. Each pseudo-dataset (which has sample size n equal to that in the original dataset) is generated from the formula

$$Y(t)_{i,art} = Y(t)_{i,pred} + \epsilon_i \quad ,$$

where $Y(t)_{i,art}$ and $Y(t)_{i,pred}$ are the artificially generated and original model predicted size-at-age respectively,

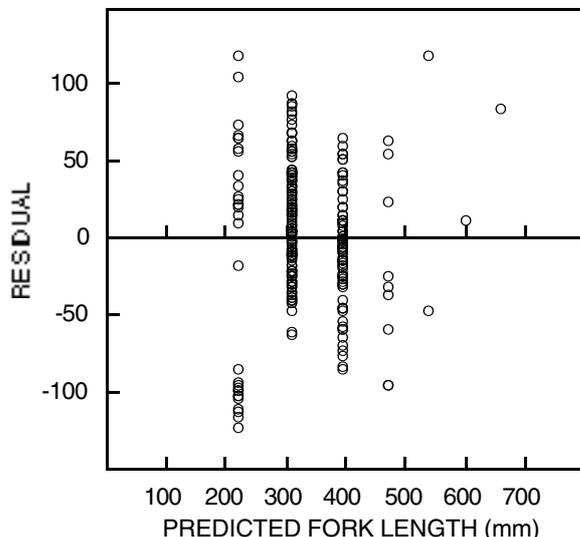


Fig. 1: Residual plot of the Schnute (1981) growth model fitted to observed size-at-age data for *P. saltatrix*

whereas ϵ_i is an artificially generated residual selected at random for each $Y(t)_{i,pred}$. The residuals are generated from a normal distribution, given the original mean and standard deviation of the residuals. To each pseudo-dataset or bootstrap, a new set of parameter estimates is obtained by fitting the model to these bootstraps. The standard error of a parameter K is then obtained from

$$SE(K) = \sqrt{\sum_{s=1}^{100} \frac{(K^s - K_{mean})^2}{100-1}}$$

where K^s is the value of the K parameter from the s th artificially generated dataset, and K_{mean} is the average of the K^s values.

RESULTS

In Table I the lengths at marking and recapture and the observed times-at-liberty and growth increments of tagged *P. saltatrix* are given. Some lengths that were reported by anglers as total lengths were converted to fork lengths using the equation $FL(\text{mm}) = 0.885 TL(\text{mm}) + 1.19$ ($r^2 = 0.99$, $n = 55$). At the time of marking, the fish ranged in size from 270 to 573 mm, with times-at-liberty ranging from 49 to 605 days (Table I).

Of the 340 otoliths that were read, 256 (75%) age estimates were coincident for both readings. The

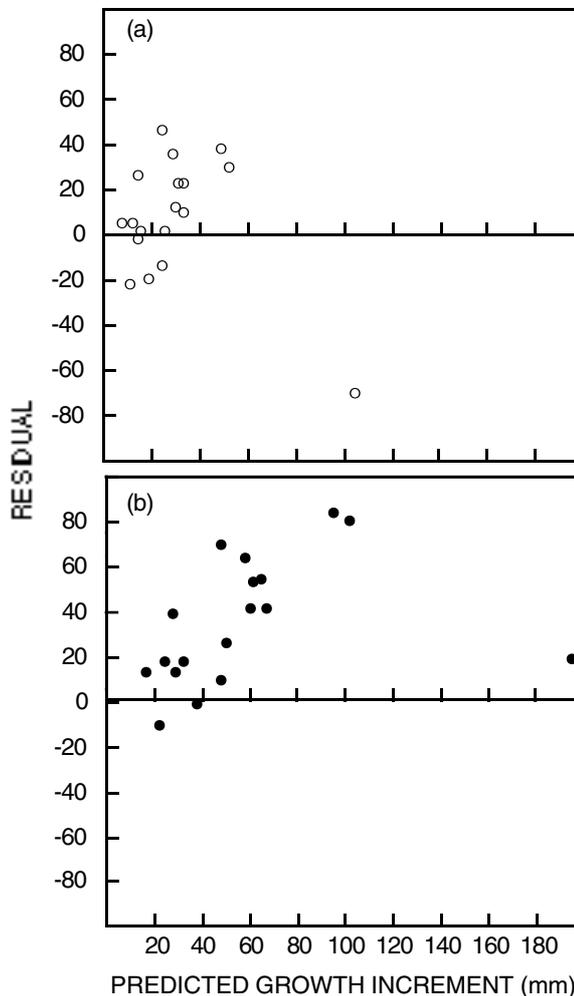


Fig. 2: Residual plot of the growth increment model (Equation 7) fitted to observed growth increments of tagged *P. saltatrix*, based on the assumption of (a) annual deposition ($P=1$) and (b) biannual deposition ($P=2$) of the otolith bands

Schnute and corresponding Von Bertalanffy growth parameter estimates, their coefficients of variation and estimates of SS_{tag} (Equation 8) for the various P models fitted are given in Table II.

The Schnute size-at-age model passed the runs test for randomness of residuals, and there was no systematic visual trend in the residuals (Fig. 1). Therefore, the Schnute model, assuming an additive error model, is considered to describe adequately the observed size-

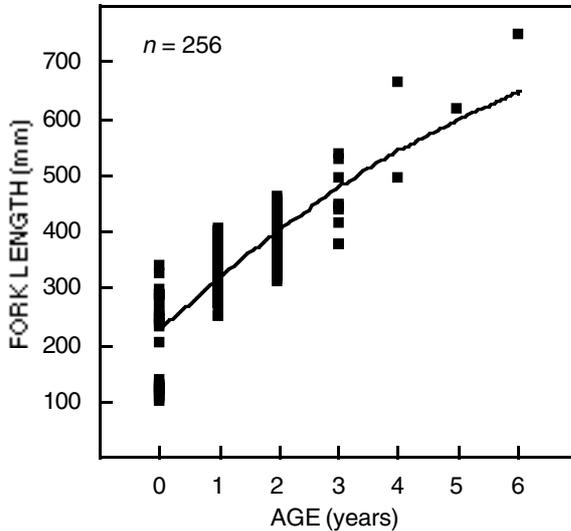


Fig.3: Observed age-length data for *P. saltatrix*, showing the model fit for an additive error structure and assuming annual periodicity of the otolith bands

at-age data (Butterworth *et al.* 1989).

The assumption that otolith bands are deposited annually resulted in a smaller residual sum of squares between the observed and predicted growth increments (SS_{tag}) for the tagged *P. saltatrix*, than that obtained under an assumption of biannual deposition (Table II). Not only does the annual model show less of a trend in the residual plot of the growth increments than the biannual model (Fig. 2), but the biannual model overestimates the growth increments of the tagged fish more than the annual model (Fig. 2). This overestimation of the biannual model increases as predicted growth increment increases, which results in a systematic trend in the residuals (Fig. 2b). This effect was much more marked as the P value was increased to 3 and 4. Both models indicate that fish with long times-at-liberty were growing slower than expected on the basis of otolith readings. A possible reason may be that tagging retards growth, but the evidence is not conclusive.

Generally, the annual model resulted in parameter estimates having smaller CVs than the biannual model (Table II). The fairly large CVs for the L_{∞} and a , k parameters (for both models) are because the age-length data for *P. saltatrix* are only slightly curvilinear (Fig. 3), and hence the asymptotic length and the a , k parameters (which describe the “bend” in the curve) are poorly defined.

Table I: Fork lengths at marking and recapture, the observed times-at-liberty and growth increments of the 18 tagged *P. saltatrix* obtained from the Sedgwick's/ORI/WWF tagging programme

Fish number	Fork length (FL, mm) at marking (mm)	Fork length (FL, mm) at recapture (mm)	Time-at-liberty (days)	Growth increment
1	355	389	49	34
2	270	286	66	16
3	370	394	243	24
4	515	692	605	177
5	390	410	142	20
6	370	388	67	18
7	310	315	36	5
8	420	430	151	10
9	431*	444*	243	13
10	573*	585*	198	12
11	320	328	52	8
12	410	390	116	-20
13	380	375	135	-5
14	420	410	68	-10
15	380	420	88	40
16	280	320	101	40
17	364*	390	116	26
18	320*	346*	146	26

* Converted from total length

The additive model that assumes an annual otolith banding pattern produced the smallest SS_{tag} value, with low CV estimates of the parameters. For this, and other reasons (see discussion), this model was selected as that which best describes the age-length data of *P. saltatrix*. The observed and predicted growth increments for both periodicity models are given in Figure 4.

Table II: Schnute and corresponding Von Bertalanffy growth parameter estimates (%CVs in parenthesis) derived from age-length data of tagged *P. saltatrix*. The sums of squares of the observed and predicted growth increments (SS_{tag}) are also shown. Note that the Schnute parameter a is equivalent to the parameter k in the Von Bertalanffy growth function. All Schnute models passed the runs test for randomness of residuals. For the model assuming annual periodicity, $T(1) = 0$ years and $T(2) = 6$ years, whereas for the biannual model, $T(1) = 0$ years and $T(2) = 3$ years

Error model	Periodicity	Parameter					
		a, k	$Y(1)$	$Y(2)$	L_{∞}	t_0	SS_{tag}
Additive	Annual ($P = 1$)	0.094 (25)	222 (2.9)	663 (4.3)	1 247 (86)	-2.09 (8.7)	13 393
Additive	Biannual ($P = 2$)	0.19 (42)	222 (3)	1 247 (3.8)	663 (98)	-1.05 (13)	33 936

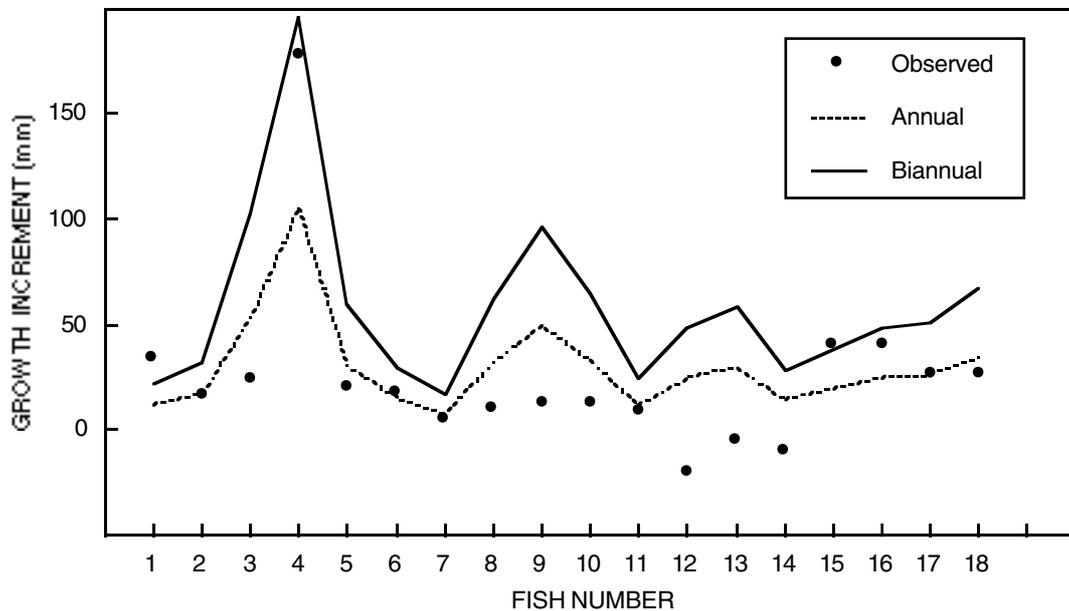


Fig. 4: Observed and predicted growth increments for *P. saltatrix* based on the annual and biannual models

DISCUSSION

The assumption that otolith bands are laid down annually, and not biannually, resulted in estimates of growth parameters that better fit the age-length data, and at the same time reasonably predict the growth increments of tagged individuals. The assumption of annual deposition of otolith bands in *P. saltatrix* is in keeping with other studies. Van der Elst (1976) validated the periodicity of the bands on scales as annual, by means of marginal zonal analysis. The present author showed that the opaque zone on the scales was primarily deposited from July to September, prior to their peak spawning period. Similar conclusions were also reached in a captive study (J. B. Mann-Lang, Oceanographic Research Institute, unpublished data) using a limited number of tetracycline-marked *P. saltatrix*. However, the opaque zone was laid down from October to January, which coincides with the time of spawning. It was also noted from that study that the position of the fluorescent band varied between individuals, which implies differences in the timing at which the opaque zone is formed. This can be attributed to individual differences in growth, and to the fact that *P. saltatrix* has a prolonged asynchronous spawning season (Van der Elst 1976, Beckley and Connell

1996). Given that *P. saltatrix* shows high individual variability in growth, it is encouraging that the model developed here indicates an annual rather than a bi-annual pattern of otolith bands. This is so because the model implicitly assumes that the timing of zone formation is the same in all fish and that variability in individual growth is negligible.

The Von Bertalanffy parameters estimated in this study differ from those reported by Van der Elst (1976, Fig. 5). It should be noted, however, that the growth values reported by Van der Elst (1976) are incorrect. The correct values (using Van der Elst's data and a Walford plot) are $L_{\infty} = 67$ cm (fork length), $k = 0.18 \cdot \text{year}^{-1}$ and $t_0 = -1.23$ years, which indicates that growth is faster than was initially reported. Moreover, Van der Elst's data can also yield even faster growth, if a nonlinear technique is used to estimate the parameters (Hughes 1986). Hughes (1986) did not report the actual values, but using the technique described by that author, they were calculated to be $L_{\infty} = 64$ cm (fork length), $k = 0.21 \cdot \text{year}^{-1}$ and $t_0 = -1.1$ years. Therefore, the difference in *P. saltatrix* growth parameters as assessed by Van der Elst (1976) and as presented in this study is a result of differences in the parameter-estimation technique. Van der Elst (1976) used a Walford plot to estimate the Von Bertalanffy parameters from mean length-at-age data, whereas a nonlinear parameter

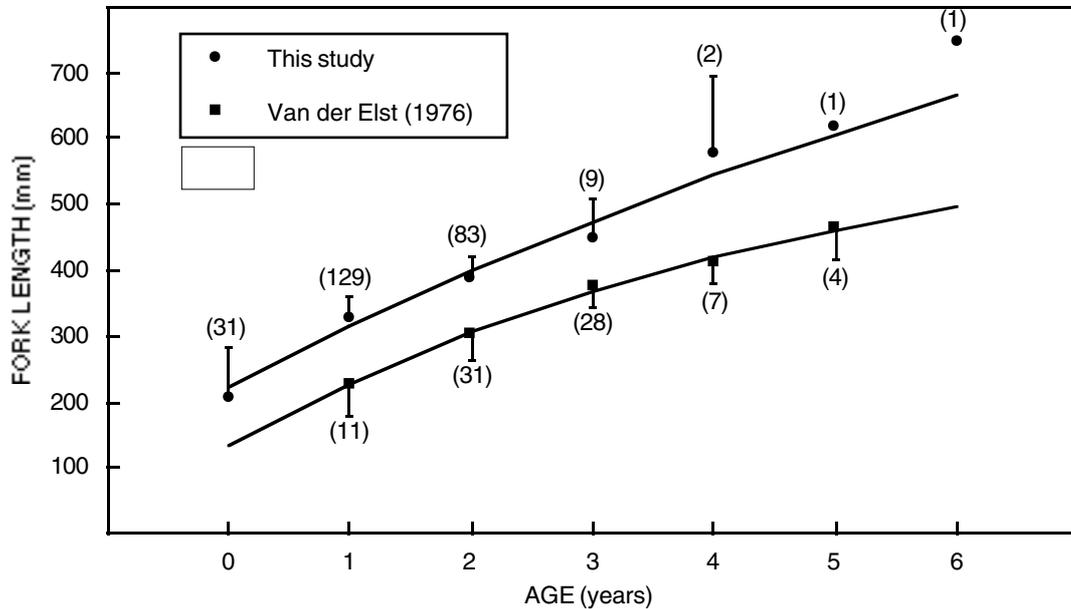


Fig. 5: Mean length-at-age and fitted Von Bertalanffy growth curves for *P. saltatrix*. The growth parameter estimates from Van der Elst (1976) are based on the estimation method of Hughes (1986), i.e. $L_{\infty} = 64$ cm (fork length), $k = 0.2 \cdot \text{year}^{-1}$ and $t_0 = -1.1$ years. Bars represent one standard deviation and the number of samples is shown in parenthesis

estimation technique utilizing all individually observed length-at-age data, as well as a statistically superior reparameterization of the Von Bertalanffy growth function, have been used here.

There are also differences in the mean length-at-age reported by Van der Elst (1976) and those recorded in this study (Fig. 5). Van der Elst (1976) reported smaller mean lengths-at-age, which indicates a slower growth rate. However, in both that study and the present investigation there is a large variability in mean length-at-age (large standard deviations). As a result, there is overlap between the mean lengths-at-age reported here and in Van der Elst (1976), and hence some similarity in growth.

Recent research has indicated that faster growth in *P. saltatrix* increases survival rate. Hare and Cowen (1995) found that, within a *P. saltatrix* larval cohort, individuals growing faster had a higher probability of survival. This suggests that cohorts with faster growth rates have higher recruitment probabilities. Furthermore, juvenile *P. saltatrix* display an early shift in diet from planktivory to piscivory, which could account for the rapid growth of young-of-year *P. saltatrix* (Juanes and Conover 1994). All these factors would contribute

to rapid growth early in the life history of *P. saltatrix*, and result in fast adult growth, as observed here.

The combination of mark-recapture and age-length data to validate the periodicity of hard structure banding is a useful technique. The method is useful in cases when ageing material cannot be obtained throughout the year, e.g. when catches are seasonal or when the fishing season is restricted to a portion of the year. Indirect validation methods, such as marginal increment analysis, ideally require monthly samples of otoliths or scales. It may not be possible to obtain these if the fishery is a seasonal one or if fishing is restricted to an open season, as in the case of *P. saltatrix* (Hecht and Smale 1986). The model developed here can, with slight modification, accommodate other growth curves, such as the logistic or Gompertz curves.

In conclusion, the model described here can be used in conjunction with traditional validation methods to validate periodicity in hard-structure banding. It is useful in cases when age material cannot be obtained throughout the year, a requirement for most indirect validation techniques. With modification, the model can incorporate growth curves other than the Von Bertalanffy growth function.

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